

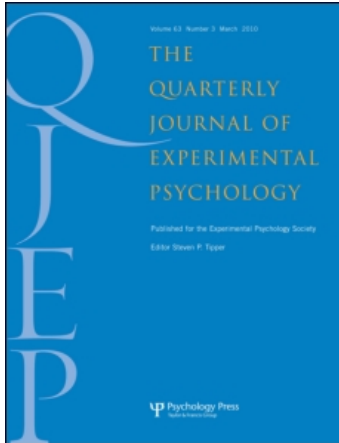
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Publisher Psychology Press

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The Quarterly Journal of Experimental Psychology

Publication details, including instructions for authors and subscription information:

<http://www.informaworld.com/smpp/title~content=t716100704>

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First published on: 30 January 2008

To cite this Article Fischer, Martin H. and Zwaan, Rolf A.(2008) 'Embodied language: A review of the role of the motor system in language comprehension', *The Quarterly Journal of Experimental Psychology*, 61: 6, 825 – 850, First published on: 30 January 2008 (iFirst)

To link to this Article: DOI: 10.1080/17470210701623605

URL: <http://dx.doi.org/10.1080/17470210701623605>

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Embodied language: A review of the role of the motor system in language comprehension

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A growing body of research suggests that comprehending verbal descriptions of actions relies on an internal simulation of the described action. To assess this motor resonance account of language comprehension, we first review recent developments in the literature on perception and action, with a view towards language processing. We then examine studies of language processing from an action simulation perspective. We conclude by discussing several criteria that might be helpful with regard to assessing the role of motor resonance during language comprehension.

Keywords: Embodied cognition; Language processing; Mirror neurons; Motor resonance; Perception and action.

Taking the right actions is the result of efficient cognition. Yet, for much of the time spent studying human cognition, actions have been considered as trivial appendages to the seemingly more sophisticated mental operations subserving “higher level” cognition, such as object identification, language comprehension, or decision making. Traditionally, movement-related processes have been reduced to simple button presses in order to isolate, as much as possible, the central cognitive processes that were of interest (see Abrams & Balota, 1991, for an early critique

of this approach). As a result of this “neglect of motor control in the science of mental life and behavior” (Rosenbaum, 2005), several recent reports of effects of movement-related processes on higher level cognition have had the advantage of surprise and have gained much attention in a community interested in a more general understanding of human cognition. Examples of such findings include action effect blindness (Müsseler & Hommel, 1997), where the preparation of a lateralized response temporarily hinders perception of stimulus attributes with the same lateralized

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MHF is a member of the Marie Curie Research and Training Network: Language and Brain (RTN: LAB), which is funded by the European Commission (MRTN-CT-2004–512141) as part of its Sixth Framework Program (for details see <http://www.hull.ac.uk/RTN-LAB/>). RAZ was supported by Grants MH-63972 from the National Institutes of Health and BCS-0446637 from the National Science Foundation. The authors thank Art Glenberg, Marc Jeannerod, and two anonymous reviewers for their helpful comments.

features, or the action sentence compatibility effect (ACE; Glenberg & Kaschak, 2002), where the verbal description of spatially directional actions facilitates movements in the same direction. The latter finding, and others to be reviewed below, illustrates the intriguing possibility that language comprehension may incorporate, and possibly even require as an essential component, some activity of the motor system that could be characterized as “motor resonance” (Zwaan & Taylor, 2006). Interactions between language processing and motor processing, and the idea of “motor resonance” in particular, are the focus of the present review.

Inspired by findings of unexpected facilitation and inhibition, and motivated by a need to incorporate such effects into a valid understanding of human cognition, the increasingly prevalent view today is that perceptual and action-related processes are tightly linked to each other, as well as to more abstract cognition (e.g., Barsalou, 1999, 2007). In turn, a proper account of cognition is predicated on an understanding of its links with perception and action. This notion, that cognition is *grounded* in perception and action, is encapsulated in the term “embodiment”: A principled understanding of cognition ought to relate cognition to the mechanisms that govern the perceptual processes feeding into cognition, as well as the actions selected by and guided through cognition. The physical instantiation of the cognitive apparatus as a brain inside a body provides such principles, be it physical laws or biomechanical constraints (e.g., Shepard, 1984, 1994).

The purpose of this article is to provide a systematic overview of how motor processes, and in particular the metaphorical motor resonance, may subserve visual cognition, action understanding, and especially language comprehension. The Section 1 of this article describes some current views of the relationship between perception and action, including the two-visual-pathways theory, the theory of event coding, the mirror system hypothesis, and the recently proposed view of motor cognition. We then discuss in Section 2 possible mechanisms for motor resonance in two domains of visual cognition—namely, affordance

computation during object recognition and motor resonance during action observation, with a view towards the suitability of the resonance metaphor for language processing. In Section 3 we review the current evidence of motor resonance in language processing, organized in increasing levels of language complexity. The article concludes with an outlook on future research.

1. Current views of the relationship between perception and action

In order to better understand the current debate about possible links between action-related and language-related processes, a brief review of recent theoretical developments is in order. This will also help us to introduce some of the key facts that constrain this discussion, some of which will be revisited towards the end of this review.

1.1. *The two-visual-pathways theory*

Visual information processing has traditionally been understood as the input stage to higher level cognition, with action being the mere reflection and implementation of the outcomes of this central process. However, in recent years this notion of a single and serial information processing chain has been replaced by a more differentiated conceptualization in which the same visual information is processed differently for perceptual and action-related tasks. Based on pioneering animal studies by Schneider (1969) and by Ungerleider and Mishkin (1982), and further inspired by performance dissociations in a patient with visual agnosia (Goodale & Milner, 2004; Milner & Goodale, 1995/2006), this view distinguishes two visual pathways in the brain, one for conscious perception of objects and the other subserving the visual control of ongoing actions. In this model, vision for action relies on egocentrically coded information about the location and other spatial attributes of targets, whereas object identification uses allocentrically coded or scene-based information. These two processes are considered to be largely segregated into distinct parts of each hemisphere in the primate brain,

with object identification in the temporal lobes or ventral stream and action control in the parietal lobes or dorsal stream.

Research with normal participants has provided some surprising support for the two-visual-pathways hypothesis. For example, visual context can induce distorted perceptual impressions about the size of objects while at the same time leaving action control largely unaffected (for recent review and discussion, see Glover, 2004). As documented in Bridgeman's short review (Bridgeman & Hoover, 2008 this issue), such dissociations between perceptual reports and visually guided motor action can be found in normal observers, both in the laboratory and in the real world. We discuss some examples of this work below (see Section 3.2). For now, we note that this view of the relationship between perception, cognition, and action as originating from a common input stage but subsequently being anatomically and functionally segregated seems to further isolate cognition from perception and action by taking higher level planning processes "out of the loop", rather than embedding cognition and providing its experiential grounding. Nevertheless, the two-visual-pathways view places important constraints on the idea that we simulate internally the actions described by language. For example, it assumes that action control relies on rapid visuo-motor updating that creates short-lived but veridical representations of the environment to ensure successful motor performance. The exact time course of this updating mechanism is a matter of contention, but it seems clear that spatial visual changes can modify ongoing actions within 150 ms and that such rapid modifications can occur without conscious control (cf. Desmurget, Pelisson, Rossetti, & Prablanc, 1998; Pisella et al., 2000). As we see later, this estimate is in harmony with findings from brain imaging studies on the time course of motor activation from verbal processing (see Section 2.3). What is at issue is whether these results can be taken as converging evidence for the notion that action simulation is part of language comprehension.

1.2. *The theory of event coding*

A competing view of the relationship between perception and action has recently been offered

by the theory of event coding (TEC; e.g., Hommel, 2004; Hommel, Müsseler, Aschersleben, & Prinz, 2001; Knoblich & Prinz, 2005). This theoretical development is based on the notion that actions are cognitively represented in terms of their perceived effects. To overcome the conceptual schism between separate representational domains for perception and action, TEC proposes a common representational medium for perceptual and action features (a "common code"). To illustrate the idea of common coding, consider "action effect blindness", where the preparation of a spatially selective action (e.g., a left key press) temporarily reduces perceptual sensitivity selectively for visual features with the same spatial attribute (e.g., a left pointing arrow; Müsseler & Hommel, 1997). To understand such surprising effects of action planning on perception, the proponents of TEC abandon strictly serial models of sequentially ordered and discrete information processing stages. Instead, they assume that motor planning operates on feature-based representations in the same way as perception and also requires some binding mechanism to generate goal-directed actions. When features such as the "left" code of a response become bound into an action plan, they are temporarily unavailable to code corresponding visual information about the location or direction of a stimulus, thus leading to the inability to properly represent and perceive particular visual stimuli.

TEC is inspired by the idea that actions are the result of the anticipation of sensory consequences, a proposal that originates with ideomotor theories of cognition (for a short historical review, see Stock & Stock, 2004). According to this view, an agent already knows what to expect from a forthcoming action, and this anticipated goal state helps to select and guide the action. Such predictive knowledge might well be the result of an internal action simulation process (Wolpert, Doya, & Kawato, 2003). One important advantage of using the ideomotor principle to conceptualize action planning and action simulation is the resulting emphasis on learning and development. Clearly, any knowledge of sensory consequences to be expected from one's own

action must be due to having previously experienced the same contingencies between one's own actions and their consequences. The agent's learning history can explain the bidirectionality of the associations between sensory and motor representations, which is necessary for the concept of action simulation to work. Moreover, this association learning principle can be extended to language-based action simulations as well (see Glenberg et al., 2008 this issue) and can thus account for intriguing associations that have recently been documented between lexical and motor processing (see Section 3.2).

However, in a recent elaboration on their original finding of action effect blindness, Hommel and Müsseler (2006) showed that preparing a verbal utterance such as "left" or "right" had a detrimental effect only on the visual perception of words but not on the visual perception of arrows. Thus, a domain-specific overlap between stimulus features and response features is necessary for this "blinding from binding" to occur, whereas the more abstract semantic overlap of features (which would be a characteristic of language processing) appears to be ineffective.

Depending on one's interpretation, the common coding view, as represented in TEC, either offers an even more reductive role for cognition (because all goal-directed planning eventually dissolves into the common feature representations for perception and action), or else successfully abandons the conundrum of how traditionally separated representational domains can communicate (because it abolishes the distinction between perception, cognition, and action). In any event, the use of TEC for a better understanding of language-induced motor resonance seems limited in the light of its rejection of semantic mediation of feature overlap (Hommel & Müsseler, 2006, p. 520). However, Kaschak and Borregine (2008 this issue) provide an example of how it may still be possible to account for the time course of motor resonance from language processing by using this framework.

1.3. *Mirror neurons*

The idea of a common code for perception and action as proposed by TEC has received strong

support from an important neurophysiological discovery. Using single-cell recordings, Rizzolatti and his colleagues discovered so-called "mirror neurons" in the ventral premotor area F5 of the macaque monkey (e.g., Di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Rizzolatti, Fogassi, & Gallese, 2001). In addition, area PF/PFG in the inferior parietal cortex has also been identified as containing such neurons. These neurons are sensitive to movement as well as to vision. Specifically, they increase their firing rates when the monkey performs object-directed actions, as well as when it observes an experimenter or conspecific performing a similar action. In this sense, the mirror neurons are perspective independent. The degree to which the observed and executed actions must be similar to each other to be coded by a single mirror neuron is a matter of debate. This debate has led to further subdivisions of mirror neurons into "broadly congruent" and "strictly congruent" types, depending on whether only the overall goal (e.g., picking up an object) or also the means of achieving it (e.g., with a power grip or a precision grip) is coded by the neuron (for review, see Rizzolatti & Craighero, 2004). Mirror neurons do not respond to the observation of an object alone (neurons with this type of selectivity are called "canonical neurons"), nor to the mere sight of a hand mimicking an action in the absence of an object. Thus, all three components of a transitive action (agent, patient, and action) are necessary to activate a mirror neuron in the monkey's brain. This feature of mirror neurons may be relevant in the light of the effectiveness of different syntactic constructions in inducing motor resonance (see Section 3.3). However, Ferrari, Gallese, Rizzolatti, and Fogassi (2003) showed that some mirror neurons discharge in response to intransitive actions such as lip smacking or tongue protrusion, actions that are not object directed (although one possibility is that, during the observation of an intransitive action, the monkey reconstructs internally a goal-directed action).

Interestingly, some degree of abstraction from the visually given information can be tolerated by mirror neurons; they are activated by the sight of actions towards hidden objects as long as the monkey knows they are present (Umiltà et al., 2001). Other such abstraction properties of mirror neurons include the fact that action sounds, such as the sound of tearing paper or crushing peanuts, are sufficient to drive mirror neuron activation (Keyzers et al., 2003; Kohler et al., 2002) and their ability to discriminate the meaning of a given action on the basis of the context within which it is performed (Fogassi et al., 2005). Today it is widely believed that several areas in the monkey brain encompass a “mirror system” for action observation and understanding. This system encompasses parietal and frontal areas of the brain, in particular area F5 (the premotor cortex) and also relies on additional activation from the superior temporal sulcus (which contains neurons tuned to body parts but not movement).

Recent PET (positron emission tomography) and fMRI (functional magnetic resonance imaging) studies suggest that humans also possess a mirror system (e.g., Lamm, Fischer, & Decety, 2007; Koski et al., 2002) and that this system might be somatotopically organized (e.g., Aziz-Zadeh, Wilson, Rizzolatti, & Iacoboni, 2006; Buccino et al., 2001; Gazzola, Aziz-Zadeh, & Keyzers, 2006). These studies show that mere observation of actions activates the Broca area, an inferior frontal brain area considered to be homologous to area F5 in the macaque monkey. In contrast to monkey neurons, human mirror neurons seem to be more broadly tuned, and this ability to abstract from specific, visually available situations is of key importance for the notion of motor resonance to language input. One main observation implying a broad and abstract tuning of the human mirror system is that it codes intransitive (gestural) as well as transitive (object-directed) actions, as documented in an influential TMS (transcranial magnetic stimulation) study by Fadiga, Fogassi, Pavesi, and Rizzolatti (1995). The authors first determined the minimal amount of left motor

cortical stimulation required to detect its presence in muscle evoked potentials (MEPs) over the right arm. Then they investigated whether passive observation of various video sequences (of objects, arm actions, object-directed actions, and luminance changes) would selectively modulate the transduction characteristics of the nervous system. It was found that observing both transitive and intransitive arm actions increased the excitability of the observer’s motor cortex and thus improved the gating of cortical stimulation into the periphery (see Fadiga, Craighero, & Olivier, 2005, for recent review).

Another important difference between the human and monkey mirror system appears to be that static images that only imply an action seem to be sufficient to trigger the human mirror system. This was first illustrated by Nishitani and Hari (2002) whose participants watched photographs of a person adopting various lip postures while their brain activity was measured with high temporal and spatial resolution through MEG (magneto-encephalography). Both speech-related and nonverbal lip postures triggered a series of activations in successive processing stages of the brains of the viewers, and both their amount and their timing were very similar under passive viewing and active imitation conditions. This result indicates that considerable motor resonance resulted from viewing static facial postures of others (see also Urgesi, Moro, Candidi, & Aglioti, 2006, described in Section 2.3).

Overall, these results obtained in humans indicate that their mirror neurons are even less dependent on specific, visually accessible action information than are the monkey’s mirror neurons. Their ability to abstract from the visually given makes mirror neurons interesting to those trying to understand language-induced action simulations. But there may be a cost associated with the abstractness of language-based compared to vision-based input to the mirror system. Buccino et al. (2005) made this point when comparing the processing of sentences with the processing of pictures by means of brain activation in the mirror system. They suggested that, in the latter case, there is less ambiguity about details of the

action to be imagined, so that there can be facilitation from vision. In the case of verbal descriptions, however, there is always a comparative lack of precision, thus either activating too many competing actions, or not activating any action simulation strongly enough. We describe Buccino et al.'s (2005) study in more detail below (see Section 3.3).

Illustrating yet another possible difference between human and animal mirror systems, Buccino et al. (2005) suggested that motor resonance for oral communication in humans may be limited to conspecifics. In this brain imaging study, they showed their participants mouth-related action videos of other humans (lip-reading), of monkeys (lip smacking), and of dogs (barking). There was a systematic reduction of brain activity in the frontal operculum, with most activation for observing the actions of conspecifics, less activation for observing monkeys, and no activation for dogs. The fact that barking did not induce any frontal lobe activation over and above baseline suggests that motor resonance in the human mirror system could be the result of matching the observed actions against the observer's action repertoire, with the degree of match reflected in the corresponding increase of mirror system activity. However, Buccino et al. (2005) used static images as a baseline and subtracted their associated activation from activation in the experimental conditions. In the light of findings by Nishitani and Hari (2002, see also Fischer, Prinz, & Lotz, 2008 this issue; Urgesi et al., 2006), this leaves open a possibility that even actions outside one's action repertoire can induce motor resonance.

A more compelling examination of the relationship between motor repertoire and motor resonance was recently reported by Calvo-Merino, Glaser, Grèzes, Passingham, and Haggard (2005) who compared the brain activity of dancers who had expertise in either capoeira (a martial arts dance style) or classical ballet. All participants watched dancers performing movements that either were or were not part of the observer's specialized dance repertoire. The authors found more activation in motor areas of

the brain, including parietal and prefrontal areas of the mirror system, when the visual input and motor expertise overlapped. A follow-up study ruled out the possibility that this resonance effect merely reflected visual familiarity and not truly motor familiarity. These two are usually confounded, either because one dances in front of a mirror or because one's fellow dancers are practising the same style. Calvo-Merino, Grèzes, Glaser, Passingham, and Haggard (2006) utilized the fact that there are gender-specific movements that are performed by either male or female ballet dancers. This implies that male dancers who mostly perform with female dancers have a motor repertoire that is distinct from their visual repertoire for ballet movements. When such dance movements were presented to participants in a brain scanner, stronger premotor, parietal, and also cerebellar activity was again found when the visual stimuli matched the observers' action repertoires. Most recently, Cross, Hamilton, and Grafton (2007) trained their participants to perform novel dance moves and subsequently found a positive correlation between their perceived motor expertise and activation in brain areas typically involved in both action observation and action simulation.

The existence of mirror neurons provides direct evidence for common coding at the neurophysiological level. The characteristics of the human mirror system include perspective independence as well as sensitivity to implied motion and to communicative gestures regardless of whether they are transitive or not. Importantly, the human mirror system also includes Broca's area, the left-lateralized centre for speech production (Gallese & Goldman, 1998). These features make it a plausible candidate for language-based action simulation and have led to new predictions for behavioural testing of the embodiment of cognition (e.g., Gentilucci & Dalla Volta, 2008 this issue; Glenberg et al., 2008 this issue; Masson, Bub, & Newton-Taylor, 2008 this issue). Given that language acquisition precedes reading acquisition, the neural implementation of part of the human mirror system in a speech area might also

provide a mechanism mediating motor resonance in reading (see Kaschak & Borreggine, 2008 this issue; Nazir et al., 2008 this issue; Taylor & Zwaan, 2008 this issue).

1.4. *Motor cognition*

A final and very recent theoretical development with implications for our understanding of the link between language processing and motor control is the emerging field of “motor cognition” (Haggard, 2005; Jeannerod, 2001, 2006; Sommerville & Decety, 2006). Defined by Jeannerod (2006, p. v), motor cognition studies “the way actions are thought, planned, intended, organized, perceived, understood, learned, imitated, attributed, or in a word, the way they are represented”. This new perspective on human cognition from a motor perspective has historical roots in pragmatist psychology and the philosophy of language, as well as in cybernetics. It also ties in closely with mental chronometry and with recent developments in cognitive neuroscience and neural modelling.

At the heart of motor cognition is the idea that we simulate our own as well as other people’s behaviour as part of understanding it. The same evidence that we have reviewed so far is taken by proponents of motor cognition to underline the experiential grounding of all representations, regardless of whether they remain unconscious and subserve efficient action control, or whether they become conscious and influence the attribution of agency. Motor cognition differs from the two-visual-pathways theory in that it distinguishes semantic from pragmatic representations within both perception and action, instead of strictly separating perception from action. From this perspective all language behaviour has both semantic and pragmatic aspects, and while speech and also sign language are overt motor behaviours, inner speech and thought are examples of covert movements or action simulations. A key role in language processing is assigned to Broca’s area as a production–comprehension interface, with a ventral-to-dorsal gradient of semantic, syntactic, and phonological processing, respectively (Jeannerod, 2006, p. 156). Clearly, the motor cognition perspective attributes

the various motor resonance phenomena discussed above to action simulation as a necessary component in language comprehension.

2. Mechanisms of action simulation

In this section of our review we briefly describe two candidate mechanisms involved in action simulation—namely, the computation of affordances during object recognition and motor resonance during action observation. Both of these mechanisms may be involved in language comprehension, so we highlight evidence of interactions between these mechanisms and language processing. We also look at evidence regarding the time course of such simulations, in order to provide further constraints for the hypothesized link between action simulation and language comprehension.

2.1. *Affordance computation during object recognition*

Effects of covert action simulation are abundant in the literature on object perception, where the speed and accuracy of lateralized responses are influenced by the distance between an object’s typical contact point (e.g., a handle) and the observer’s hands. For example, when pressing buttons to classify pictures of objects as right side up or upside down, the responses of the hands are facilitated when they are placed next to the protruding handles (e.g., Phillips & Ward, 2002). This robust finding suggests that the motor system spontaneously uses object information to compute possible actions in the light of one’s current posture and to select favourable responses. Whether these so-called affordances are computed does not depend on the object being response relevant. For example, Fischer and Dahl (2007) recently obtained powerful affordance effects when participants pressed left or right buttons in response to colour changes of a fixation point while a cup with a protruding handle continuously rotated in the background. Reaction times were gradually modulated by the irrelevant handle position, leading to two phase-shifted sine-wave-shaped reaction time functions, one for the left

and the other for the right hand. An important and novel control condition, with object translation equivalent to the size and opposite to the side of the handle, ruled out the possibility that this response bias merely reflected the visual asymmetry of the object.

In addition to lateralized (left vs. right side) response biases, affordance effects can also influence different responses within one hand. Tucker and Ellis (2001) recorded the speed of precision and power grasp responses of participants who classified objects as natural or man-made. The two responses were made either by pressing a switch between thumb and index finger, or by squeezing a stick with the remaining fingers of the right hand. There was a congruency effect because response selection was biased by the size of the object. Electrophysiological and brain imaging work shows that also attentional processes are biased toward objects that can be manipulated (Grezes, Armony, Rowe, & Passingham, 2003; Grezes & Decety, 2002; Handy et al., 2005; Handy, Grafton, Shroff, Ketay, & Gazzaniga, 2003).

How are visual affordances related to language processing? Interestingly, affordance effects also emerge when participants are only briefly exposed to a perceptually degraded object or when they only see (Tucker & Ellis, 2004) or hear (Richardson, Spivey, & Cheung, 2001) a word denoting the object. Thus, continuous visual availability is not necessary to create a bias in the motor system, and concept activation seems to be sufficient to do so. These recent findings require a revision of the original idea that affordance computations bypass higher cognitive levels of representation. We provide a more in-depth discussion of this topic in Section 3.2.

A study by Creem and Proffitt (2001) provides further information about the possible interactions between affordance computation and language processing. The authors imposed either a semantic or a spatial secondary task on their normal participants as they picked up household tools that were randomly placed in front of them. When they performed a spatial imagery task they spontaneously picked up all tools by their handles and

thus exhibited an affordance effect. In contrast, when they produced semantic associations the affordance effect was clearly reduced. Both secondary tasks were comparable in difficulty and verbal output modality, so the authors concluded that there is an obligatory connection between semantic processing and action control.

These findings of concept-modulated action effects challenge the two-visual-pathways idea that vision is isolated from cognition and rapidly updates the representation of our environment to provide veridical information for on-line action control. A possible solution to this challenge might be to distinguish between an early planning component and a late control component of goal-directed motor responses. Biases in response selection (such as the affordance effects) would be attributed to early motor planning while the subsequent control phase would reflect veridical and unbiased vision (Glover, 2004). Again, this idea is elaborated in Section 3.2.

The affordance studies mentioned so far describe systematic influences of object perception on motor planning. Consider now the opposite relationship of motor activity biasing object perception. This is an important issue, given the idea that action simulation might rely on the anticipation of outcomes and thus on learned, bidirectional links between actions and goals (see Section 1.2). A number of studies show that the intention to make goal-directed movements leads to systematic biases in visual perception. In addition to the already-mentioned action effect blindness (see Section 1.2), there is also evidence for facilitation. For example, planning to make a goal-directed eye or hand movement leads to improved perception at the target location of the movement (e.g., Deubel, Schneider, & Paprotta, 1998; Fischer, 1997, 1999). This is also true for sequences of eye movements (Gersch, Kowler, & Doshier, 2004; Gersch, Schnitzer, Sanghvi, Doshier, & Kowler, 2006) and sequences of hand movements (Baldauf, Wolf, & Deubel, 2006). Recent evidence for a dependence of such motor-visual priming on the motor repertoire of the observers comes from work by Casile and Giese (2006). In their study, the visual recognition

of gait patterns from point-light stimuli was assessed before and after their participants had learned a novel movement that matched one of the visual test patterns. Despite the absence of vision during training, visual recognition of the learned movement was selectively improved after training and correlated with the acquired motor skill level. These results show that motor learning modulates visual recognition of the learned movement and further suggests that the mirror system with its resonance mechanism might be involved in the effect. We list this particular study here for its methodological demonstration of an effect of action repertoire on action perception. The idea of experience-dependent action processing (“what I can do determines what I can understand”) places important constraints on motor resonance from language processing. For example, it might predict that the processing of negative and counterfactual statements should not lead to motor resonance. In potential conflict with this prediction, however, Kaup and Zwaan (2003; see also Kaup, Yaxley, Madden, Zwaan, & Lüdtkke, 2007) recently demonstrated that negative statements seem to induce a simulation of the positive version of their contents, which may then support motor resonance phenomena.

2.2. *Motor resonance during action observation*

Given the hypothesis of a mirror system in humans that matches observed actions against one's own action repertoire to discover goals or intentions, it appears that the domain of signed language communication and gesturing would be an ideal field to study motor resonance in the context of language processing. Unlike speech perception or reading, sign language processing requires the direct mapping of body movements onto abstract meaning representations. However, a recent review of the relationship between sign language and the human mirror system (Corina & Knapp, 2006) concludes that this link is not as tight as expected. For example, after damage to Broca's area patients can exhibit a dissociation of impaired sign production with intact sign language comprehension, while the opposite dissociation can follow damage to left parietal areas extending into

supramarginal gyrus (e.g., Poizner, Klima, & Bellugi, 1987). While these lesion sites are encompassed by the human mirror system, the double dissociation pattern argues against the notion of a mirror matching mechanism for language comprehension. Furthermore, sign language production seems to rely predominantly on left frontal brain areas while sign language comprehension also involves right frontal areas (Corina & Knapp, 2006, p. 534). This bilateral pattern probably reflects the life-long association between language concepts and space for native signers (Emmorey et al., 2005), but there is also a pervasive association of language production and manual gesturing in all language users, even when listeners cannot observe the gestures, as in phone conversations or conversations between blind speakers (Iverson & Goldin-Meadow, 1998). Gentilucci and Dalla Volta (2008 this issue) discuss further interactions between gesturing and language production in the context of the mirror neuron theory. We now take a broader look at evidence for biases in the motor system as a result of action observation.

Clear evidence for motor resonance during action observations comes from the work of Flanagan and Johansson (2003). These authors set out to test the direct matching hypothesis of action understanding, according to which we understand another person's intentions on the basis of the similarity of their actions with our own repertoire of previously performed actions. Specifically, they focused on the tight link that exists between our hand movements and the eye movements that we make to guide our hands. Their participants either actively stacked blocks with their right hand to replicate a model, or passively observed an actor completing the same task while sitting across the table from them. Hand and eye movements were recorded in both tasks. The key finding was that, in the passive condition, the observer's eyes looked ahead of the actor's hand to the goal of each reaching movement, much as they did in the active condition as a result of normal eye-hand coordination. Flanagan and Johansson (2003) inferred that the action repertoire of the observer was engaged to predict

what the actor intended to do, rather than to merely passively observe (see Rotman, Troje, Johansson, & Flanagan, 2006, for a replication with uncertainty about forthcoming actions). Interestingly, such motor resonance effects can already be observed in the eye movement patterns of 12-month-old children (but not in 6-month-olds; Falck-Ytter, Gredeback, & von Hofsten, 2006).

Eye movements in response to language processing have been thoroughly studied in the “visual world” paradigm, where participants view arrays of objects while listening to auditory statements about the depicted objects. A consistent finding is that they spontaneously fixate on the object that is named next, as soon as the auditory evidence becomes unambiguous (for a recent review, see Altmann & Kamide, 2004). This important observation has led to a flurry of eye movement studies in attempts to understand the nature of language processing and suggests that the simulation mechanism driving the eyes might be very fast. It is also memory driven in the sense that eye fixations are made to blank locations on the screen where the mentioned object had been depicted earlier (Altmann, 2004; see also Kennedy, 1983). A similar finding was reported by Spivey and Geng (2001) who monitored eye movements as participants looked at a blank wall and listened to verbal reports of objects and events. Interestingly, when they heard a description of a tall building, their eye movements were predominantly vertical. These observations are in harmony with the earlier finding that mirror neurons can be driven by the memory of an object (Umiltà et al., 2001). As expected on the basis of the evidence for abstraction in the mirror system (see Section 1.3), the eye movement system can engage in action simulation even in the absence of visible actions—for example, when listening to descriptions.

2.3. *The time course of motor simulation*

As described above (see Section 1.3), Fadiga and colleagues (2005; Fadiga et al., 1995) had shown that a TMS pulse would pass through the nervous systems of their observers much better when they

watched grasping actions instead of other perceptual events at the time of stimulation. Building on this method, Gangitano, Mottaghy, and Pascual-Leone (2004) titrated the time course of motor resonance through mirror neurons. They asked how much of the TMS probe would be gated to their observers’ arms at various times during action observation, or when the observed action would be perturbed to various degrees and at different times during the movement. Delaying the finger aperture in the action video by only 600 ms abolished motor resonance from the earliest time of probing (1,200 ms) and throughout the observation period. This result indicates that observers were sensitive to the absence of small aperture changes between index finger and thumb even at movement onset. It also suggests that there is an all-or-none criterion for activating motor resonance.

Further expanding on this simulation–stimulation approach to embodied cognition, Urgesi et al. (2006) recently presented to their participants static pictures of a resting hand, a grasping hand in (implied) motion, or a hand adopting a final precision grip posture (but always without objects). The authors found TMS gating effects exclusively for the implied motion picture, not for the start or end postures. They conclude that pictures of a hand in action “conveyed dynamic information about forward and backward action paths, whereas the final posture hand provided information only about backward action paths. This would suggest that the motor system was maximally activated by the extrapolation of the future trajectory of body actions” (p. 7948). We note that, in contrast to Gangitano et al.’s participants, who decided during each movie whether a tone occurred while the moving hand was to the left or right of their fixation cross, participants in Urgesi et al.’s study had no motor task and hence were unlikely to be engaged in any kind of response preparation. Also, the fact that their results obtained without objects being present in any of the hand pictures underlines the fact that action goals can be supplied through top-down cognitive inferences (i.e., action simulations), just as they were in the Umiltà et al.’s (2001) study of

single-cell activity with actions towards hidden objects and in Kohler et al.'s (2002; see also Keyers et al., 2003) single-cell study with action sounds.

The conclusions drawn by Urgesi et al. (2006) nicely converge with findings from a recent study of the time course of joint attention from hand postures (Fischer & Szymkowiak, 2004). Observers saw pictures of a static hand, either pointing at or grasping one of three horizontally arranged tangerines. After the hand had returned to a neutral resting position, and following a random delay of 300–700 ms, a visual probe appeared unpredictably over the left or right tangerine, thus creating three trial categories: valid trials, where the probe appeared over the “manipulated” tangerine, neutral trials, where the hand had previously interacted with the central tangerine, and invalid trials, where the probe appeared on the tangerine opposite to the primed tangerine. The observers simply pressed a button to indicate they had detected the probes. Importantly, in the pointing condition they were faster when the probe appeared in the valid than in the neutral and invalid trials, whereas in the grasping condition, they detected the probes faster in the invalid than in neutral and valid trials. The authors suggested that these differences between observing a pointing and a grasping action were due to rapid anticipation (or simulation) of likely future states. Specifically, a pointing hand prompts the observer's attention because it indicates the likely target of a future action, whereas a grasping hand cannot prompt the observer's attention because it depicts an already completed action (but see Fischer et al., 2008 this issue).

In a follow-up study Nuku et al. (2007) showed that low-level perceptual factors contributed to the observed inhibitory pattern for grasping in Fischer and Szymkowiak's (2004) study: Spatial separations between hand postures and objects were smaller in the grasping than in the pointing conditions, thus leading to inhibition of return of attention (e.g., Pratt, Kingstone, & Khoe, 1997). When distances were equally short for pointing and grasping, inhibition in valid trials was present for both pointing and grasping. Thus,

visually similar conditions are important to ensure that any differences can safely be attributed to an internal motor simulation. Interestingly, however, when Nuku et al. (2007) changed the to-be-detected event from an arbitrary onset to a displacement of one of the objects, higher level action simulation in valid trials overruled the low-level inhibition. Thus, it appears that action simulation benefits when observers can establish a causal relation between an observed action and an observed effect.

These findings support the idea of a rapid, obligatory and visually driven action simulation from observing others' grasping postures. As a result of this action simulation, observers allocate their attention to the most plausible target object of the forthcoming action, just as they do when they are about to perform the same action themselves (Baldauf et al., 2006; Deubel et al., 1998). The discrepancy between the positive findings with static end postures in Fischer and Nuku's studies and the negative findings for similar end postures in Urgesi et al.'s (2006) recent TMS study suggests that the visual presence of objects may be advantageous for action simulation after all. Whether such a need to explicitly mention the objects of actions also exists for language-induced motor simulations remains to be investigated. Together, these behavioural results reveal a complex pattern of activation and inhibition during action simulation from implied actions, making it hard to derive clear prediction for language-induced action simulation.

The use of static pictures instead of dynamic sequences in Nishitani and Hari's (2002) study, as well as their use of MEG as a brain imaging technique with high spatial and temporal resolution, allowed these authors to pinpoint the time course and neural implementation of motor resonance in great detail. They found rapid cortical resonance to static lip postures, regardless of the observer's intention to observe or imitate, starting at occipital visual areas (around 110 ms after stimulus onset) and progressing successively through superior temporal sulcus (180 ms), inferior parietal areas (200 ms), and inferior frontal areas (Broca's area, 250 ms) into primary

motor cortex (by 320 ms; see also Nishitani & Hari, 2002). These estimates underline the rapidity of motor resonance phenomena and are in line with recent evidence (also obtained with MEG) on language-induced motor resonance that is reported in Section 3.2.

Further converging evidence that motor resonance also occurs when the result of an action is being viewed comes from the finding that handwritten letters, as compared to printed letters, activate the hand area of the motor cortex (Longcamp, Tanskanen, & Hari, 2006). In other words, viewing the result of an action activates the processes that would bring about that result. This interpretation is consistent with TEC (see Section 1.2), according to which bidirectional links between actions and their anticipated effects must be activated as part of action planning.

3. Motor processes in language comprehension

Although it is tempting to view the comprehension of action sentences as a kind of action observation, it is important not to overlook the differences between the direct observation of an action and the comprehension of a description of that action. Directly observing an action provides analogue online temporal information about the action's unfolding. This is not necessarily true for language comprehension. For example, in hearing a sentence such as *He turned the page*, the speed with which the sentence is processed is predominantly determined by the speaker's rate of speaking, rather than by how quickly the action is performed. However, a recent study shows that speech rate is correlated with the speed of the described event (Shintel, Nusbaum, & Okrent, 2006). Similarly, in reading, the speed with which a described event is processed is codetermined by a number of factors unrelated to the manner of the action (lexical access, syntactic processes, and so on). But again, an author's speech rate influences the reading speed for their text (Kosslyn & Matt, 1977).

Secondly, even if there were a close correspondence between information acquisition via direct

observation and processing times for a corresponding sentence, this would be irrelevant. The action does not unfold in the comprehender's mind as each word is being processed. For example, we don't know what the protagonist is turning until we encounter the noun *page*. For all we know, he or she could be turning a corner, turning his life around, or turning green with envy, among other possibilities. This lack of determinacy means that motor resonance should arise at specific points in the sentence, rather than throughout. It is therefore important to examine how the modulation of motor resonance is modulated by incoming linguistic input. A few recent studies have taken this step (Glenberg et al., 2008 this issue; Taylor & Zwaan, 2008 this issue; Zwaan & Taylor, 2006).

Another difference between action observation and language comprehension is that a great deal of information can be omitted from the latter that is explicit in the former. A sentence does not have to include a description of the actor or the patient, nor of the manner in which the action is being performed. For instance, the example sentence *He turned the page* does not specify who is turning the page other than that it is a male individual. Also, the sentence does not specify of what larger entity the page is a part—a book, magazine, newspaper, calendar? Finally, the sentence does not specify how the action is performed (carefully, quickly, nonchalantly?). This presumably means that language-born motor resonance is more diffuse than motor resonance evoked during action observation or imitation (see also Buccino et al., 2005). More evidence regarding this issue is necessary, however, before firmer conclusions can be reached.

From these preliminary reflections it is already clear that language processing places different constraints on motor resonance than does action observation. With this in mind, it is useful to review the extant findings. The review is organized in terms of level of linguistic units, moving from syllables to discourse.

Before reviewing the literature, it is important to distinguish two types of motor resonance that might occur during language comprehension. *Communicative motor resonance* occurs when the

motor system responds to the communicative act itself, whereas *referential motor resonance* occurs when the motor system responds to the content of the communication. An example may clarify this distinction. If a listener's speech motor system responds to hearing the word "kick", then this would be an example of communicative motor resonance; the motor system is simulating the production of the utterance. However, if the leg area of the premotor cortex responds, this would indicate referential motor resonance; the motor system is simulating the action that is being described by the utterance rather than the production of the utterance itself. The two types of motor resonance presumably occur simultaneously during skilled language comprehension. We speculate that *communicative resonance* helps the comprehender anticipate what the speaker is going to say next, whereas *referential motor resonance* will tell the comprehender what is going to happen next in the situation that is being described. The two types of simulation are presumably mutually constraining (see Pickering & Garrod, 2007, and Zwaan & Kaschak, in press, for further discussion).

3.1. *Phonological processing*

The role of the motor system in speech perception has long been recognized, particularly in the form of the motor theory of speech perception (Liberman, Cooper, Shankweiler, & Studdert-Kennedy, 1967). According to this theory, "the objects of speech perception are the intended phonetic gestures of the speaker, represented in the brain as invariant motor commands" (Liberman & Mattingly, 1985, p. 2; see Galantucci, Fowler, & Turvey, 2006, for a recent review). A great deal of recent evidence supports the notion of motor involvement in speech perception. There is evidence that motor resonance occurs at the level of speech production. For example, Fadiga, Craighero, Buccino, and Rizzolatti (2002) applied a TMS pulse over the motor area controlling tongue muscles while participants listened to Italian words and pseudowords containing a tongue-trilled, double-r sound or a nontrilled, double-f sound. The authors found that MEPs recorded

from tongue muscles were significantly larger when listening to double-r stimuli than double-f stimuli. In other words, listening to linguistic stimuli produced the phoneme-specific activation of speech motor centres (see also Gentilucci & Dalla Volta, 2008 this issue).

These findings suggest that online observation of an action is not necessary for motor resonance, a conclusion supported by finding auditory activation of the mirror system (Keyzers et al., 2003; Kohler et al., 2002; Lewis, Phinney, Brefczynski-Lewis, & DeYoe, 2006). Instead, images of implied actions seem to suffice (see also Lamm et al., 2007; Fischer, 2005). This conclusion is in accordance with the earlier observation that affordance effects can be induced by perceptually degraded object pictures or object words. Apparently, the activation of an action concept is sufficient for motor resonance, as long as the initial input is visual and hence concrete, as opposed to linguistic/abstract.

However, it is surprising to find that a goal depiction leads to the activation of a particular set of muscles, when other muscle activations can lead to the same goal. The link between motor activity and action outcomes is never uniquely specified: Many different actions can lead to the same goal (this is known as equifinality or motor equivalence). Thus, additional assumptions would have to be introduced, such as selection criteria that reduce the degrees of freedom problem by evaluating efficiency criteria (e.g., required effort, end state comfort, or time to reach the goal) or contextual constraints. The contribution of such considerations in motor cognition has been documented by Jeannerod (2006).

In summary, there is strong evidence for motor resonance during speech processing. In addition, there is evidence that the results of linguistic action may produce motor resonance. Importantly, both of these cases are examples of *communicative motor resonance*. The rest of our review is mostly concerned with *referential motor resonance*.

3.2. *Lexical access*

Several behavioural studies have examined whether motor representations are evoked by

single words. Semantic effects have been found on grasp aperture. For example, a word printed on an object of fixed size can affect the movement directed towards that object. Thus, for Italian subjects, the word "GRANDE" ("large") evokes a larger maximum grip aperture than the word "PICCOLO" ("small"; Gentilucci, Benuzzi, Bertolani, Daprati, & Gangitano, 2000, Exp. 4). This finding suggests that concurrent semantic information interferes with action performance, but given that the eventual grasp aperture was accurate, the interference was compensated for during the movement. Glover and colleagues explain this pattern of effects by assuming that semantic activation interfered with the planning of the action rather than with its online control (Glover, Rosenbaum, Graham, & Dixon, 2004). Glover et al. hypothesized that planning and motor control are differentially affected by the words. Specifically, the planning system relies on a visual representation, which is susceptible to interference from cognitive and perceptual variables, leading to large and systematic errors in action planning. On the other hand, the control system relies on the visuospatial properties of the target itself, uncontaminated by other cognitive and contextual variables; this allows it to correct for the influences of these variables in flight.

Glover and colleagues (2004) tested this hypothesis by using nouns denoting concrete objects, associated with a specific hand aperture. This contrasts with Gentilucci and colleagues (2000), who used adjectives that explicitly mentioned size. Glover et al.'s subjects reached for blocks of different sizes after having silently read a word from a computer screen one second earlier. The words referred to either small or large objects (e.g., "GRAPE" or "APPLE"). Subjects were told to pay attention to the words, because they would receive a memory test later. This test was never administered, but subjects were asked instead if they noticed anything special about the experiment. Only one subject noticed the relevance of the size of the objects denoted by the words, but this subject's data fell within one standard deviation of the other subjects' data and were therefore not omitted from

the analyses. As such, it appears that reading an object name interferes with the planning of a grasping movement. Moreover, it appears that this occurs outside the subjects' conscious awareness. These data do not show, however, that motor resonance occurs in the absence of a motor planning task.

Other studies have examined whether qualitatively different types of hand postures (rather than merely hand aperture) afforded by objects are activated by exposure to the associated words. For example, subjects who judged whether objects shown in pictures were natural or man-made by manipulating an input device that required either a power grip or a precision grip exhibited a response compatibility effect (Tucker & Ellis, 2004). Moreover, power grip responses were faster to pictures and words denoting objects that require a power grip than to pictures and words denoting objects requiring a precision grip, whereas the reverse was true for precision grip responses (Tucker & Ellis, 2004, Exp. 3; see also Section 2.1).

Other experiments have shown priming between words denoting similar motor actions (Myung, Blumstein, & Sedivy, 2006; Exp. 1). For example, playing the piano and using a typewriter involve similar manual actions. Accordingly, the corresponding words were found to prime one another in a lexical-decision experiment. Objects affording similar actions tend to be similar in shape, such that priming might be due to visual similarity. To address this problem, Myung et al. had selected words denoting objects that were rated as having high similarity in terms of manipulation, but low visual similarity. Thus, they explained the priming effect by assuming that the words automatically evoked action representations, which mediated the priming from the prime to the target.

This ensemble of behavioural findings supports the conclusion that motor resonance occurs automatically during exposure to action-related words (nouns, verbs, adjectives). Evidence from neuroimaging studies and studies using TMS supports these conclusions. Several of these studies have shown that the naming of

tools, as opposed to the naming of animals, differentially activates the left middle temporal gyrus, which is also activated by action generation tasks, and the left premotor cortex, which is generally activated when participants imagine themselves grasping objects with their dominant hand (e.g., Martin, Wiggs, Ungerleider, & Haxby, 1996). However, stronger evidence for the role of motor resonance in language comprehension would show that exposure to action and tool words evokes motor resonance, which should manifest as activation in motor areas of the brain. Several studies have indeed produced such evidence. Exposure to action verbs and tool words semantically related to actions elicits stronger fronto-central cortical activation than does exposure to object words (Martin et al., 1996; Preissl, Pulvermüller, Lutzenberger, & Birbaumer, 1995; Pulvermüller, Lutzenberger, & Preissl, 1999). More specifically, the action words related to movements of the face, arm, or leg activated fronto-central cortex in a somatotopic fashion (Hauk, Johnsrude, & Pulvermüller, 2004; Shtyrov, Hauk, & Pulvermüller, 2004) consistent with the claim that sensorimotor cortex processes action-related aspects of word meaning (Pulvermüller, 2005).

Further evidence for the automatic activation of motor representations upon exposure to action verbs comes from a study using high-density MEG (Pulvermüller, Shtyrov, & Ilmoniemi, 2005b). Subjects were engaged in a distractor task while listening to words denoting actions involving the leg or face. Different patterns of cortical activation were found for leg and face words in premotor areas. Face-word stimuli activated inferior frontocentral areas more strongly than leg words, whereas the reverse was found at superior central sites. Importantly, these activations occurred within 170 ms after onset of the words, thus making it unlikely that strategic factors contributed to the result. Pulvermüller and colleagues interpret this to reflect the cortical somatotopy of motor actions signified by the words. The results from this study show that meaning access in action word recognition is an early automatic

process reflected by spatiotemporal signatures of word-evoked activity.

If motor resonance is automatically evoked by words, then it might be hypothesized that the process can run in reverse as well. That is, recognition of these words should be facilitated by stimulation of the relevant motor and premotor areas. A recent study provides support for this hypothesis (Pulvermüller, Hauk, Nikulin, & Ilmoniemi, 2005a). Hand and leg areas in the left hemisphere were stimulated 150 ms after word onset using magnetic pulses below motor threshold while healthy right-handed native speakers of English read common arm- and leg-related words intermixed with meaningless pseudowords briefly flashed on a computer screen. Subjects had to respond by a brisk lip movement only when recognizing a meaningful word. Lip movements were chosen for lexical decision responses to minimize interference between semantic and motor preparation processes. In addition to observing somatotopically mapped facilitation, the authors also reported that this effect only emerged after left hemispheric stimulation, in agreement with the typical language dominance of this hemisphere.

These data provide preliminary evidence that word recognition is facilitated by referent-congruent motor activation. However, it should be emphasized that motor activation occurred while the word was already being processed for 150 ms. It is important for future research to examine more closely the temporal relation between the facilitation of lexical access and motor resonance (cf. Nazir et al., 2008 this issue). One caveat about these findings is that they don't necessarily implicate the effector per se. They could implicate the typical goals that one tries to accomplish with a particular effector. For example, we typically act upon objects with our arms and hands (e.g., *grasp, fold, bend*), whereas we use our legs for locomotion (e.g., *walk, trot, run*). Nevertheless, the study by Pulvermüller et al. (2005a) is important, because it demonstrates that accessing action-related words not only evokes motor resonance, but that the process is bidirectional: Lexical access of action words is facilitated by motor

resonance. Such bidirectionality is a key assumption made by TEC (see Section 1.2).

A similar conclusion can be reached based on a recent behavioural study (Lindemann, Stenneken, van Schie, & Bekkering, 2006). In these experiments, participants made lexical decisions to words in a go/no-go task paradigm, after having prepared for a specific action. They had to pick up either a magnifying glass and bring it to the eye or a cup and bring it to the mouth. A letter string was presented after action onset. The target words were *eye* and *mouth*. Preparing for a congruent action (e.g., picking up the magnifying glass for *eye*) facilitated lexical decisions on the associated word. A subsequent experiment ruled out visual associations as a factor. These findings suggest that preparing for an action activates semantic information associated with the goal of the action and thereby primes access to a lexical representation associated with that goal. However, these findings should be interpreted cautiously given that there were just two target words, which were repeated over and over and could thus have given rise to expectancy effects. The results also seem to be in conflict with the previously discussed “action effect blindness” (see Section 1.2) and suggest that the outcome of the interplay between language comprehension and action simulation crucially depends on their relative timing.

A recent study found further evidence that the timing between the planning of a movement and lexical processing is important for the direction of the motor resonance effect. Boulenger et al. (2006) carried out two experiments in which participants had to perform a reaching movement. In the first experiment a letter string appeared right after the onset of their movement. In the second experiment the letter string was presented as the go signal. Participants were instructed to return their hand to the starting position if the string was not a word. The results showed that action verbs affected overt motor performance significantly compared to nouns: Within 200 ms after movement onset, processing action verbs interfered with a concurrent reaching movement. This was evident in a slightly reduced peak wrist acceleration but not in other kinematic

parameters, such as movement time. In the second experiment, the same words assisted the reaching task when processed before movement onset. This priming became evident 550–580 ms after word onset, again only in wrist peak acceleration (see Nazir et al., 2008 this issue, for further evidence).

3.3. Sentence comprehension

Several studies have examined motor resonance evoked during sensibility judgements of sentences. The key manipulation is that the physical response made by the subjects shares some characteristics with the action performed by the subject. In an early study on motor involvement in sentence (or actually, word-pair) processing, subjects judged the sensibility of verb–noun pairs (e.g., *squeeze–tomato*) after having been primed with a hand shape (Klatzky, Pellegrino, McCloskey, & Doherty, 1989). An action-appropriate hand shape was found to prime the comprehension of word pairs describing the manipulation of objects. For example, the sensibility of “Throwing a dart” was judged more quickly when subjects had their hands in the appropriate shape for throwing darts than when not. Crucially, lexical associations were ruled out as a cause of this effect.

A more recent study of embodied sentence comprehension was already mentioned above. In judging the sensibility of sentences such as “*Close the drawer*”, subjects moved their right hand from one button to another one that was either closer to or further away from their body. In this case, the action performed by the subject would be compatible with the sentence if the hand moved away from the body—because our hand usually moves away from our body when we close a drawer—whereas responses toward the subject’s body would be incompatible with the described action. The finding was that action-compatible responses were faster than action-incompatible responses—hence the action–sentence compatibility effect, or ACE (Glenberg & Kaschak, 2002). The ACE has been found not only for imperatives, but also for descriptive sentences of two types: double object (e.g., *Mike handed you the pizza*) and dative

constructions (*Mike handed the pizza to you*). Moreover, the effect was also found for abstract transfer sentences, such as *Liz told you the story*. At first sight, this provides evidence of the generality of motor resonance. On further reflection, however, it poses some problems for the interpretation of the effect as one of mental simulation. Whereas moving the hand away from the body can be plausibly said to be an integral part of closing a drawer, it is not an integral part of telling someone a story. This raises two related questions. First, how did the ACE come about in the latter type of sentence if not as a result of mental simulation, and second, what does it imply about mental simulation?

A potential answer to the first question can be found by distinguishing between lexical items and grammatical constructions. For example, some of the sentences used by Glenberg and Kaschak (2002) had a double-object construction (e.g., *Mike handed you the pizza*). Such structures may have become associated with movement toward or away from the body during early language acquisition, because these structures are associated with verbs of manual transfer, such as *give* or *bring* (Tomasello, 2003). As such, it is possible that the ACE was evoked as a result of the syntactic structure. In part, this is Glenberg and Kaschak's point, but it is important to note that this does then not implicate mental simulation as an explanation of the ACE in these experiments. Rather, the syntactic construction is associated with a certain type of motor resonance independent of the linguistic content. Evidence for a neural dissociation between lexical and constructional representations is emerging (Kemmerer, 2006). If this reasoning is correct, then the motor resonance that is evoked by sentences may be a complex phenomenon. First, there is the action-specific motor resonance invoked by individual words or word combinations (see next paragraph); and second, there is more general motor resonance evoked by the linguistic construction. Presumably, the ACE reported in Glenberg and Kaschak reflects a combination of both of these aspects in the concrete sentences and only the latter aspect in the more abstract

sentences (see also Glenberg et al., 2008 this issue).

In addition to the syntactic issue with the Glenberg and Kaschak (2002) study mentioned earlier, there is another potential limitation to interpreting the ACE as evidence for mental simulation during language comprehension. It cannot be ruled out that motor resonance is a function of making a sensibility judgement rather than comprehending the sentence. To address this issue, recent studies have tried to unpack the ACE by examining the modulation of motor resonance during sentence comprehension. For example, Zwaan and Taylor (2006, Exp. 4) had subjects read sentences like *Because/ the music/ was too loud,/ he/ turned down/ the/ volume*. The sentences were presented in segments, here indicated by slashes. The subjects read the sentences by rotating a knob, with each 5 degrees of rotation resulting in the presentation of the next segment. The reading-rotation direction either matched or mismatched the rotation direction implied by the sentence. Results indicated that motor resonance occurred on the verb (e.g., *turned down*), but had dissipated on the next words. Zwaan and Taylor hypothesized that motor resonance might be subject to linguistic focus, rather than being limited to the verb. They observed that in their experimental sentences, the focus shifted from the action to the patient or the result of the action. They reasoned that maintaining focus on the action should result in continued motor resonance. In order to test this prediction, in a more recent study (Taylor & Zwaan, 2008 this issue), they created sentences such as *The runner/ was very/ thirsty./ A fan/ handed him/ a bottle/ of cold/ water/ which he/ opened/ quickly*. Here, the focus on the action is maintained by the adverb, which modifies the action. In accordance with the linguistic-focus prediction, the match advantage on the verb was now extended to the subsequent word, the adverb.

There is another aspect to these results that is worth noting: They show that motor resonance arises during *comprehension*, rather than merely during lexical access. For example, by itself a word such as *open* does not necessarily imply

(counterclockwise) wrist rotation. One can open one's eyes, open a sunroof, open a bank account, or open a lead in a race, none of which necessarily involves wrist rotation. Moreover, adverbs such as *quickly* and *gradually* do not at all imply wrist rotation without further context. In other words, the findings of Zwaan and Taylor (2006) show that motor resonance occurs when information is integrated. A limitation of these studies is that by themselves they do not implicate motor resonance in comprehension, given the special nature of the reading task, which by necessity involves manual rotation. However, they do show that motor resonance is associated with linguistic content in a very precise manner.

Glenberg et al. (2008 this issue) also examined motor resonance during online sentence comprehension, using TMS. Their results are consistent with those of Zwaan and Taylor (2006) in that they found motor resonance on the verb. In other words, motor resonance occurred during comprehension, rather than as the result of an extraneous task such as making sensibility judgments. Moreover, like the study of Zwaan and Taylor, this study also shows that motor resonance occurs as the result of integration, rather than merely activation.

Kaschak and Borregine (2008 this issue) provided further evidence that timing is important in motor resonance studies. They found a facilitatory effect on a secondary motor task early on, which reversed into a mismatch advantage at later testing intervals (cf. also the results reported by Boulenger et al., 2006). They explain their results by referring to the theory of event coding, TEC (Hommel et al., 2001). According to this explanation, comprehending the sentence "grabs" the feature coding for towards or away, which now cannot be used for planning the motor response, thus resulting in an interference effect.

Evidence that affordances have an immediate influence on sentence comprehension comes from a study employing the visual-world paradigm (Chambers, Tanenhaus, & Magnusson, 2004; see also Section 2.2 above). Subjects listened to sentences describing simple spatial scenes while viewing a display composed of elements relevant

to the sentence and holding or not holding a tool. Chambers and colleagues monitored how the subjects' fixations on the scene were modulated by the linguistic input as a function of holding or not holding the tool. Holding the tool affected syntactic parsing. Specifically, it changed the amount of time spent looking at a (possible) goal location that is likely under one parse or unlikely under the alternative parse.

Of course, this research does not show directly that motor resonance is evoked during "normal" language comprehension. However, it does show that motor resonance occurs very rapidly during comprehension, even before the associated linguistic constituent has been fully processed.

Buccino et al. (2005) used TMS and a behavioural paradigm to assess whether listening to action-related sentences modulates the activity of the motor system. By means of single-pulse TMS, either the hand or the foot/leg motor area in the left hemisphere was stimulated in distinct experimental sessions, while participants were listening to sentences expressing hand and foot actions. Listening to abstract content sentences served as a control. MEPs were recorded from hand and foot muscles. Results showed that MEPs recorded from hand muscles were specifically modulated by listening to hand-action-related sentences, whereas MEPs recorded from foot muscles were modulated by listening to foot-action-related sentences. This modulation consisted of an amplitude decrease of the recorded MEPs. In the behavioural task, participants responded with the hand or the foot while listening to actions expressing hand and foot actions, as compared to abstract sentences. In accordance with the TMS results, hand responses were slower during hand-action-related sentences than during abstract sentences, and foot responses were slower during foot-action-related sentences.

A recent neuroimaging study found that regions that were active during action observation were also active during sentence comprehension, in an effector-dependent manner (Aziz-Zadeh et al., 2006). Thus areas in the premotor area that were active during the observation of hand actions were also active during the comprehension

of sentences describing hand action. Again, the question is to what extent this implies an analogy between action observation and language comprehension. As noted earlier, the two are not similar with respect to the timing and manner involved. Action observation is obviously much closer to the actual action than action description via language.

A recent lesion study yielded conclusions that seem somewhat at variance with those of the behavioural and neuroimaging studies discussed earlier (Saygin, Wilson, Dronkers, & Bates, 2004). A total of 29 aphasic subjects and 18 age-controlled subjects were tested on pictorial and linguistic action comprehension. For example, subjects would see a line drawing of a boy licking an ice cream, without an ice-cream cone being in the picture or a sentence fragment (“He licked the _____”). They were then shown two pictures of four categories: (a) the target object; (b) an affordance-related object (e.g., a bouquet of flowers, which affords the same manual interaction as an ice-cream cone); (c) a semantic distractor (e.g., a cake); and (d) an unrelated distractor (e.g., a rooster). Subjects responded which picture best fitted the scene or sentence fragment by pressing the button underneath the corresponding picture. Response accuracies and latencies were recorded. There was no overall correlation between patients’ deficits in pictorial and language comprehension, suggesting that different brain regions were associated with deficits in action comprehension than with deficits in sentence comprehension. However, there were correlations in specific groups of subjects, suggesting that action understanding and language understanding share neural substrates.

3.4. *Discourse comprehension*

There is a real paucity of research on motor resonance in discourse comprehension. This is unfortunate for a number of reasons, chief among them the fact that outside the psychological laboratory, we rarely understand words or sentences as “textoids” presented in isolation. Rather, we understand words and sentences as parts of connected discourse (Graesser, Millis, & Zwaan, 1997).

A recent study is the first to our knowledge to examine the neural substrates of discourse comprehension (Speer, Zacks, Reynolds, & Hedden, 2005). This study tested predictions from the event-indexing model of language comprehension (Zwaan, 2004; Zwaan, Langston, & Graesser, 1995; Zwaan & Radvansky, 1998; Zwaan & Rapp, 2006). Subjects in the scanner read a narrative about the actions performed by a little boy during a day in his life. According to the event-indexing model, the comprehension system monitors several dimensions of the situation described in the text (e.g., time, location, agents, goals, and causation). A shift on each of these dimensions incurs a processing cost, which is evidenced by increased reading times (e.g., Zwaan, 1996; Zwaan, Magliano, & Graesser, 1995) in behavioural experiments, and, as Speer et al. demonstrate, concomitant changes in activation patterns of relevant neural regions. For example, an area of the anterior cingulate, which is known to monitor conflict resolution, increased in activity with the number of situational changes at clause boundaries. Most pertinent to this review is the finding that somatosensory areas involved in imagining and carrying out hand movements increased in activation when readers processed changes in a character’s interactions with an object. This finding is important, because a narrative comprehension paradigm in which subjects are passively reading (e.g., without having to make lexical decisions or sensibility judgements) is arguably more ecologically valid than some of the studies on smaller language segments.

4. **Conclusions and outlook**

As our review of the literature has shown, there is a great deal of evidence that actions are more than mere appendages to cognitive processes. They have been found to infiltrate a variety of processes previously considered purely cognitive, such as lexical access and discourse comprehension. On the other hand, there exists a risk of overstating the role of motor processes in cognition. In order to more clearly delineate the role of motor processes in language comprehension, we propose

that the following questions be considered in future work.

4.1. *The association question*

Are motor representations associated with the performance of a “cognitive” task? That is, does the activation of the motor system co-occur systematically with the performance of a cognitive task? To further specify this question, it could be asked whether the cognitive task performance precedes the onset of motor activation, or whether the onset of motor activation precedes cognitive task performance. Answers to this question can be obtained in behavioural experiments, as well as in neuroimaging studies, for example by showing that motor representations are activated during passive viewing. An important step in this direction has been taken by Pulvermüller et al. (2005a). If further systematic evidence can be obtained that activation of the motor system precedes the activation of higher level cognitive processes, then this provides a step toward addressing the next question, which is the necessity question.

4.2. *The necessity question*

Is the activation of motor representations *necessary* for language comprehension? Pertinent evidence to answer this question can be obtained in lesion studies with neuropsychological patients, or in artificial lesion studies using repetitive TMS stimulation to temporarily deactivate selected brain areas. If a brain area known to subserve particular actions is damaged or incapacitated by a (temporary) lesion, *and* this lesion eliminates or at least significantly impairs the performance of these actions, then it should also significantly impair the comprehension of words, sentences, and discourse describing that action.

4.3. *The sufficiency question*

Is the activation of motor representations sufficient for the comprehension of action words, sentences, discourse? To answer this question, it would be required to obtain an exhaustive listing of all other representations and neural substrates that could be involved in the task and then to assess

comprehension by selectively incapacitating these mechanisms (e.g., by artificial lesions or in dual-task paradigms). An affirmative answer to the sufficiency questions would be in order if it could be demonstrated that comprehension still occurs despite the fact that all other potentially useful sources of information except the motor system have been successfully disabled. It might be argued that such demonstrations are a logical impossibility, given that it may be impossible to know beforehand all of the sources of information that may potentially be useful to comprehend a particular segment of linguistic input. On the other hand, it is not implausible to anticipate that future theories will at some point converge on a catalogue of information sources that may contribute to an understanding of linguistic segments. At such a juncture in the literature, it may be possible to address the sufficiency question. In more general terms, this goal has already been accomplished by the theory of motor cognition (Jeannerod, 2006; Sommerville & Decety, 2006). From the viewpoint of motor cognition language is abstract goal-directed action, and all language comprehension is through covert reenacting.

By systematically addressing the association, necessity, and sufficiency questions, it should be possible to build a theory of the role of motor processes in cognitive performance generally and language comprehension in particular. There are several issues related to language processing for which competing theories would make distinct predictions. Among them are the narrative perspective (first vs. third person), the mapping between the comprehender’s action repertoire and the content of the discourse, the level of abstractness of the narrative, and the presence of specific object descriptions, or its degree of specialization. With respect to the relationship between eye movements and language processing, reading research has made substantial progress (for review, see Rayner, 1998). In reading, there is good evidence that readers internally simulate the events that are described in a text (Barsalou, 1999; Bower & Morrow, 1990; Zwaan, 2004; Zwaan & Radvansky, 1998). However, we are not aware of attempts to use the spatial

characteristics of eye movements to assess spatial aspects of internal action simulations during reading. The different theoretical views on the relationship between perception and action seem to be differentially suited for this future research on embodied language processing. Although the two-visual-pathways theory seems to impose too strict a separation between perception and cognition, it might be taken to make some predictions for action simulation during language processing. A corollary of the theory is the sharp distinction between egocentric and allocentric coding for action and perception, respectively, a claim that is currently being reassessed (Schenk, 2006). Nonetheless, the theory should predict an advantage for simulating first-person over third-person narratives. To our knowledge this prediction has not yet been tested.

The theory of event coding has been identified as an alternative framework but recent new evidence may lead to a revision of the extent to which language-based cognition can be incorporated. Clearly, the mirror neuron theory has already inspired substantial work on language-based motor processes, and the results, although often more conflicting than converging, provide starting points to constrain language-based action simulation. Finally, the theory of motor cognition appears to be the most promising theoretical framework within which to study the link between movement-related processes and higher level cognition.

In the light of the studies reviewed above, it is fair to say that the bulk of current evidence for the role of motor processes can be taken to provide an affirmative answer to the association question. At the same time, the studies comparing experts and nonexperts or conspecifics and non-conspecifics discussed earlier have demonstrated that motor resonance occurs when the observed actions are part of the observer's own motor repertoire. But does this mean that actions are incomprehensible to us when we do not have them in our own repertoire? This seems implausible. At some level, we do understand the action, presumably relying on perceptual processes only, or perhaps also by in addition relying on some very general motor processes that may not be strong

enough to be detected by current neuroimaging and chronometric methods. For example, even though we may not show motor resonance when we see or hear a dog barking, we still understand what the dog is doing. Likewise, although our motor system may not be active when we observe a ballerina perform a jump, we certainly understand the action as being part of a performance that we have chosen to watch, and our motor system may resonate at some level to the general action of jumping.

We draw two conclusions from this review of the literature on language and the motor system. First, action comprehension may not be an all-or-none phenomenon. Second, motor resonance results in a deeper, higher resolution, comprehension. As noted in Section 3.1, there are two types of motor resonance during language comprehension. There is resonance to the actions being performed by the speaker, communicative motor resonance, and there is motor resonance to the events being described, referential resonance. Behaviourally, these types of resonance manifest themselves in an enhanced ability to predict upcoming words at the linguistic level and events at the referential level (see Pickering & Garrod, 2007; Zwaan & Kaschak, in press) and thus increase the fluency of information processing. Therefore, although the current research may not permit one to unequivocally conclude yet that motor resonance is *necessary* or *sufficient* for action or language comprehension, it does suggest that motor resonance *enhances* such comprehension.

First published online 30 January 2008

REFERENCES

- Abrams, R. A., & Balota, D. A. (1991). Mental chronometry: Beyond reaction time. *Psychological Science*, *2*, 153–157.
- Altmann, G. T. M. (2004). Language-mediated eye movements in the absence of a visual world: The “blank screen paradigm”. *Cognition*, *93*, B79–B87.
- Altmann, G. T. M., & Kamide, Y. (2004). Now you see it, now you don't: Mediating the mapping between

- language and the visual world. In J. M. Henderson & F. Ferreira (Eds.), *The interface of language, vision, and action: Eye movements and the visual world*. New York: Psychology Press.
- 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.
- Baldauf, D., Wolf, M., & Deubel, H. (2006). Deployment of visual attention before sequences of goal-directed hand movements. *Vision Research, 46*, 4355–4374.
- Barsalou, L. W. (1999). Perceptual symbol systems. *Behavioral and Brain Sciences, 22*, 577–660.
- Barsalou, L. W. (2007). Situating concepts. In P. Robbins & M. Aydede (Eds.), *Cambridge handbook of situated cognition* (chap. 17). New York: Cambridge University Press.
- Boulenger, V., Roy, A. C., Paulignan, Y., Deprez, V., Jeannerod, M., & Nazir, T. A. (2006). Cross-talk between language processes and overt motor behavior in the first 200 ms of processing. *Journal of Cognitive Neuroscience, 18*, 1607–1615.
- Bower, G. H., & Morrow, D. G. (1990, January 5). Mental models in narrative comprehension. *Science, 247*, 44–48.
- Bridgeman, B., & Hoover, M. (2008). Processing spatial layout by perception and sensorimotor interaction. *Quarterly Journal of Experimental Psychology, 61*, 851–859.
- Buccino, G., Binkofski, F., Fink, G. R., Fadiga, L., Fogassi, L., Gallese, V., et al. (2001). Action observation activates premotor and parietal areas in a somatotopic manner: An fMRI study. *European Journal of Neuroscience, 13*, 400–404.
- Buccino, G., Riggio, L., Melli, G., Binkofski, F., Gallese, V., & Rizzolatti, G. (2005). Listening to action related sentences modulates the activity of the motor system: A combined TMS and behavioral study. *Cognitive Brain Research, 24*, 355–363.
- 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.
- Calvo-Merino, B., Grèzes, J., Glaser, D. E., Passingham, R. E., & Haggard, P. (2006). Seeing or doing? Influence of visual and motor familiarity in action observation. *Current Biology, 16*, 1905–1910.
- Casile, A., & Giese, M. A. (2006). Nonvisual motor training influences biological motion perception. *Current Biology, 16*, 69–74.
- Chambers, C. G., Tanenhaus, M. K., & Magnusson, J. S. (2004). Actions and affordances in syntactic ambiguity resolution. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 30*, 687–696.
- Corina, D. P., & Knapp, H. (2006). Sign language processing and the mirror neuron system. *Cortex, 42*, 529–539.
- Creem, S. H., & Proffitt, D. R. (2001). Grasping objects by their handles: A necessary interaction between cognition and action. *Journal of Experimental Psychology: Human Perception and Performance, 27*, 218–228.
- Cross, E. S., Hamilton, A. F. de C., & Grafton, S. T. (2007). Building a simulation de novo: Observation of dance by dancers. *NeuroImage, 31*, 1257–1267.
- Desmurget, M., Pelisson, D., Rossetti, Y., & Prablanc, C. (1998). From eye to hand: Planning goal-directed movements. *Neuroscience and Biobehavioral Reviews, 22*, 761–788.
- Deubel, H., Schneider, W. X., & Paprotta, I. (1998). Selective dorsal and ventral processing: Evidence for a common attentional mechanism in reaching and perception. *Visual Cognition, 5*, 81–107.
- Di Pellegrino, G., Fadiga, L., Fogassi, L., Gallese, V., & Rizzolatti, G. (1992). Understanding motor events: A neurophysiological study. *Experimental Brain Research, 91*, 176–180.
- Emmory, K., Grabowsky, T., McCullough, S., Ponto, L. L. B., Hichwa, R. D., & Damasio, H. (2005). The neural correlates of spatial language in English and American Sign Language: A PET study with hearing bilinguals. *NeuroImage, 24*, 832–840.
- Fadiga, L., Craighero, L., Buccino, G., & Rizzolatti, G. (2002). Speech listening specifically modulates the excitability of tongue muscles: A TMS study. *European Journal of Neuroscience, 15*, 399–402.
- Fadiga, L., Craighero, L., & Olivier, E. (2005). Human motor cortex excitability during the perception of others' action. *Current Opinion in Neurobiology, 15*, 213–218.
- Fadiga, L., Fogassi, L., Pavesi, G., & Rizzolatti, G. (1995). Motor facilitation during action observation: A magnetic stimulation study. *Journal of Neurophysiology, 73*, 2608–2611.
- Falck-Ytter, T., Gredeback, G., & von Hofsten, C. (2006). Infants predict other people's action goals. *Nature Neuroscience, 9*, 878–879.

- Ferrari, P. F., Gallese, V., Rizzolatti, G., & Fogassi, L. (2003). Mirror neurons responding to the observation of ingestive and communicative mouth actions in the monkey ventral premotor cortex. *European Journal of Neuroscience*, *17*, 1703–1714.
- Fischer, M. H. (1997). Attention allocation during manual movement preparation and execution. *European Journal of Cognitive Psychology*, *9*, 17–51.
- Fischer, M. H. (1999). An investigation of attention allocation during sequential eye movement tasks. *Quarterly Journal of Experimental Psychology*, *52A*, 649–677.
- Fischer, M. H. (2005). Action simulation is not constrained by one's own postures. *Neuropsychologia*, *43*, 28–34.
- Fischer, M. H., & Dahl, C. (2007). The time course of visuo-motor affordances. *Experimental Brain Research*, *176*, 519–524.
- Fischer, M. H., Prinz, J., & Lotz, K. (2008). Grasp cueing shows obligatory attention to action goals. *Quarterly Journal of Experimental Psychology*, *61*, 860–868.
- Fischer, M. H., & Szymkowiak, A. (2004). Joint attention for pointing but not grasping postures. *Cortex*, *40*, 168–170.
- Flanagan, J. R., & Johansson, R. S. (2003). Action plans used in action observation. *Nature*, *424*, 769–770.
- Fogassi, L., Ferrari, P. F., Gesierich, B., Rozzi, S., Chersi, F., & Rizzolatti, G. (2005). Parietal lobe: From action organization to intention understanding. *Science*, *308*, 662–667.
- Galantucci, B., Fowler, C., & Turvey, M. T. (2006). The motor theory of speech perception reviewed. *Psychonomic Bulletin & Review*, *13*, 361–377.
- 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*, *20*, 493–501.
- Gangitano, M., Mottaghy, F. M., & Pascual-Leone, A. (2004). Modulation of premotor mirror neuron activity during observation of unpredictable grasping movements. *European Journal of Neuroscience*, *20*, 2193–2202.
- Gazzola, V., Aziz-Zadeh, L., & Keysers, C. (2006). Empathy and the somatotopic auditory mirror system in humans. *Current Biology*, *16*, 1824–1829.
- Gentilucci, M., Benuzzi, F., Bertolani, L., Daprati, E., & Gangitano, M. (2000). Language and motor control. *Experimental Brain Research*, *133*, 468–490.
- Gentilucci, M., & Dalla Volta, R. (2008). Spoken language and arm gestures are controlled by the same motor control system. *Quarterly Journal of Experimental Psychology*, *61*, 944–957.
- Gersch, T., Kowler, E., & Doshier, B. (2004). Dynamic allocation of visual attention during the execution of sequences of saccades. *Vision Research*, *44*, 1469–1483.
- Gersch, T. M., Schnitzer, B. S., Sanghvi, P. S., Doshier, B., & Kowler, E. (2006). Attentional enhancement along the path of a sequence of saccades. *Visual Cognition*, *14*, 104–107.
- Glenberg, A. M., & Kaschak, M. P. (2002). Grounding language in action. *Psychonomic Bulletin & 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.
- Glover, S. (2004). Separate visual representations in the planning and control of action. *Behavioral and Brain Sciences*, *27*, 3–78.
- Glover, S., Rosenbaum, D. A., Graham, J., & Dixon, P. (2004). Gasping the meaning of words. *Experimental Brain Research*, *154*, 103–108.
- Goodale, M., & Milner, D. (2004). *Sight unseen*. Oxford, UK: Oxford University Press.
- Graesser, A. C., Millis, K. K., & Zwaan, R. A. (1997). Discourse comprehension. *Annual Review of Psychology*, *48*, 163–189.
- Grèzes, J., Armony, J. L., Rowe, J., & Passingham, R. E. (2003). Activations related to “mirror” and “canonical” neurons in the human brain: An fMRI study. *NeuroImage*, *18*, 928–937.
- Grèzes, J., & Decety, J. (2002). Does visual perception of object afford action? Evidence from a neuroimaging study. *Neuropsychologia*, *40*, 212–222.
- Haggard, P. (2005). Conscious intention and motor cognition. *Trends in Cognitive Science*, *9*, 290–295.
- Handy, T. C., Borg, J. S., Turk, D. J., Tipper, C. M., Grafton, S. T., & Gazzaniga, M. S. (2005). Placing a tool in the spotlight: Spatial attention modulates visuomotor responses in cortex. *NeuroImage*, *26*, 266–276.
- Handy, T. C., Grafton, S. T., Shroff, N. M., Ketay, S., & Gazzaniga, M. S. (2003). Graspable objects grasp attention when the potential for action is recognized. *Nature Neuroscience*, *6*, 421–427.
- Hauk, O., Johnsrude, I., & Pulvermüller, F. (2004). Somatotopic representation of action words in

- human motor and premotor cortex. *Neuron*, *41*, 301–307.
- Hommel, B. (2004). Event files: Feature binding in and across perception and action. *Trends in Cognitive Sciences*, *8*, 494–500.
- Hommel, B., & Müsseler, J. (2006). Action-feature integration blinds to feature-overlapping perceptual events: Evidence from manual and vocal actions. *Quarterly Journal of Experimental Psychology*, *59*, 509–523.
- Hommel, B., Müsseler, J., Aschersleben, G., & Prinz, W. (2001). The theory of event coding (TEC): A framework for perception and action. *Behavioral and Brain Sciences*, *24*, 849–937.
- Iverson, J. M., & Goldin-Meadow, S. (1998). Why people gesture as they speak. *Nature*, *396*, 228.
- Jeannerod, M. (2001). Neural simulation of action: A unifying mechanism for motor cognition. *NeuroImage*, *14*, S103–S109.
- Jeannerod, M. (2006). *Motor cognition: What actions tell the self*. Oxford, UK: University Press.
- Kaschak, M. P., & Borreggine, K. L. (2008). Temporal dynamics of the action–sentence compatibility effect. *Quarterly Journal of Experimental Psychology*, *61*, 883–895.
- Kaup, B., Yaxley, R. H., Madden, C. J., Zwaan, R. A., & Lüdtke, J. (2007). Experiential simulations of negated text information. *Quarterly Journal of Experimental Psychology*, *60*, 976–990.
- Kaup, B., & Zwaan, R. A. (2003). Effects of negation and situational presence on the accessibility of text information. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *29*, 439–446.
- Kemmerer, D. (2006). Action verbs, argument structure constructions, and the mirror neuron system. In M. Arbib (Ed.), *Action to language via the mirror neuron system*. Cambridge, UK: Cambridge University Press.
- Kennedy, A. (1983). On looking into space. In K. Rayner (Ed.), *Eye movements in reading: Perceptual and language processes* (pp. 237–251). London: Academic Press.
- Keysers, C., Kohler, E., Umiltà, M. A., Fogassi, L., Nanetti, L., & Gallese, V. (2003). Audio-visual mirror neurons and action recognition. *Experimental Brain Research*, *153*, 628–636.
- Klatzky, R. L., Pellegrino, J. W., & McCloskey, B. P. (1989). Can you squeeze a tomato? The role of motor representations in semantic sensibility judgments. *Journal of Memory & Language*, *28*, 56–77.
- Knoblich, G., & Prinz, W. (2005). Linking perception and action: An ideomotor approach. In H.-J. Freund, M. Jeannerod, M. Hallett, & R. Leiguarda (Eds.), *Higher-order motor disorders* (pp. 79–104). Oxford, UK: Oxford University Press.
- Kohler, E., Keysers, C., Umiltà, M. A., Fogassi, L., Gallese, V., & Rizzolatti, G. (2002, August 2). Hearing sounds, understanding actions: Action representation in mirror neurons. *Science*, *297*, 846–848.
- Koski, L., Wohlschläger, A., Bekkering, H., Woods, R. P., Dubeau, M.-C., Mazziotto, J. C. et al. (2002). Modulation of motor and premotor activity during imitation of target-directed actions. *Cerebral Cortex*, *12*, 847–855.
- Kosslyn, S. M., & Matt, A. M. C. (1977). If you speak slowly, do people read your prose slowly? Person-particular speech recoding during reading. *Bulletin of the Psychonomic Society*, *9*, 250–252.
- Lamm, C., Fischer, M. H., & Decety, J. (2007). Predicting the actions of others taps into one's own somatosensory representations: A functional MRI study. *Neuropsychologia*, *45*, 2480–2491.
- Laureys, S., Pellas, F., Van Eeckhout, P., Ghorbel, S., Schnakers, C., Perrin, F., et al. (2005). The locked-in syndrome: What is it like to be conscious but paralyzed and voiceless? In S. Laureys (Ed.), *Progress in Brain Research* (Vol. 150, pp. 495–511). Amsterdam: Elsevier/North Holland.
- Lewis, J. W., Phinney, R. E., Brefczynski-Lewis, J. A., & DeYoe, E. A. (2006). Lefties get it “right” when hearing tool sounds. *Journal of Cognitive Neuroscience*, *18*, 1314.
- Lieberman, A. M., Cooper, F. S., Shankweiler, D. P., & M. Studdert-Kennedy (1967). Perception of the speech code. *Psychological Review*, *74*, 431–461.
- Lieberman, A. M., & Mattingly, I. G. (1985). The motor theory of speech perception revised. *Cognition*, *21*, 1–36.
- Lindemann, O., Steneken, P., Van Schie, H. T., & Bekkering, H. (2006). Semantic activation in action planning. *Journal of Experimental Psychology: Human Perception and Performance*, *32*, 633–643.
- Longcamp, M., Tanskanen, T., & Hari, R. (2006). The imprint of action: Motor cortex involvement in visual perception of handwritten letters. *NeuroImage*, *33*, 681–688.
- Martin, A., Wiggs, C. L., Ungerleider, L. G., & Haxby, J. V. (1996). Neural correlates of category-specific knowledge. *Nature*, *379*, 649–652.
- Masson, M. E. J., Bub, D. N., & Newton-Taylor, M. (2008). Language-based access to gestural components of conceptual knowledge. *Quarterly Journal of Experimental Psychology*, *61*, 869–882.

- Milner, A. D., & Goodale, M. A. (2006). *The visual brain in action*. Oxford, UK: Oxford University Press. (Original work published 1995).
- Müsseler, J., & Hommel, B. (1997). Blindness to response-compatible stimuli. *Journal of Experimental Psychology: Human Perception and Performance*, *23*, 861–872.
- Myung, J., Blumstein, S. E., & Sedivy, J. C. (2006). Playing on the typewriter, typing on the piano: Manipulation knowledge of objects. *Cognition*, *98*, 223–243.
- Nazir, T. A., Boulenger, V., Roy, A., Silber, B., Jeannerod, M., & Paulignan, Y. (2008). Language-induced motor perturbations during the execution of a reaching movement. *Quarterly Journal of Experimental Psychology*, *61*, 933–943.
- Nishitani, N., & Hari, R. (2002). Viewing lip forms: Cortical dynamics. *Neuron*, *36*, 1211–1220.
- Nuku, P., Lindemann, O., Bekkering, H., & Fischer, M. H. (2007). *Joint attention in action observation: Inferring another's action intentions modulates visual attention*. Manuscript submitted for publication.
- Phillips, J. C., & Ward, R. (2002). S–R correspondence effects of irrelevant visual affordance: Time course and specificity of response activation. *Visual Cognition*, *9*, 540–558.
- Pickering, M. J., & Garrod, S. (2007). Do people use language production to make predictions during comprehension? *Trends in Cognitive Sciences*, *11*, 105–110.
- Pisella, L., Grea, H., Tilikete, C., Vighetto, A., Desmurget, M., Rode, G., et al. (2000). An “automatic pilot” for the hand in human posterior parietal cortex: Toward reinterpreting optic ataxia. *Nature Neuroscience*, *3*, 729–736.
- Poizner, H., Klima, E. S., & Bellugi, U. (1987). *What the hands reveal about the brain*. Cambridge, MA: MIT Press.
- Pratt, J., Kingstone, A., & Khoe, W. (1997). Motor-based vs. attention-based theories of inhibition of return. *Perception and Psychophysics*, *59*, 964–971.
- Preissl, H., Pulvermüller, F., Lutzenberger, W., & Birbaumer, N. (1995). Evoked potentials distinguish between nouns and verbs. *Neuroscience Letters*, *197*, 81–83.
- Pulvermüller, F. (2005). Brain mechanisms linking language and action. *Nature Reviews Neuroscience*, *6*, 576–582.
- Pulvermüller, F., Hauk, O., Nikulin, V. V., & Ilmoniemi, R. J. (2005a). Functional links between motor and language systems. *European Journal of Neuroscience*, *21*, 793–797.
- Pulvermüller, F., Lutzenberger, W., & Preissl, H. (1999). Nouns and verbs in the intact brain: Evidence from event-related potentials and high-frequency cortical responses. *Cerebral Cortex*, *9*, 498–508.
- Pulvermüller, F., Shtyrov, Y., & Ilmoniemi, R. (2005b). Brain signatures of meaning access in action word recognition. *Journal of Cognitive Neuroscience*, *17*, 884–892.
- Rayner, K. (1998). Eye movements in reading and information processing: 20 years of research. *Psychological Bulletin*, *124*, 372–422.
- Richardson, D. C., Spivey, M. J., & Cheung, J. (2001). Motor representations in memory and mental models: The embodied zork. In J. D. Moore & K. Stenning (Eds.), *Proceedings of the 23rd Annual Meeting of the Cognitive Science Society* (pp. 867–872). Mahwah, NJ: Lawrence Erlbaum Associates.
- Rizzolatti, G., & Craighero, L. (2004). The mirror-neuron system. *Annual Reviews Neuroscience*, *27*, 169–192.
- Rizzolatti, G., Fogassi, L., & Gallese, V. (2001). Neurophysiological mechanisms underlying imitation and the understanding of action. *Nature Reviews Neuroscience*, *2*, 661–670.
- Rosenbaum, D. A. (2005). The Cinderella of psychology: The neglect of motor control in the science of mental life and behavior. *American Psychologist*, *60*, 308–317.
- Rotman, G., Troje, N. F., Johansson, R. S., & Flanagan, J. R. (2006). Eye movements when observing predictable and unpredictable actions. *Journal of Neurophysiology*, *96*, 1358–1369.
- Saygin, A. P., Wilson, S. M., Dronkers, N., & Bates, E. (2004). Action comprehension in aphasia: Linguistic and non-linguistic deficits and their lesion correlates. *Neuropsychologia*, *42*, 1788–1804.
- Schenk, T. (2006). An allocentric rather than perceptual deficit in patient DF. *Nature Neuroscience*, *9*, 1369–1370.
- Schneider, G. (1969). Two visual systems: Brain mechanisms for localization and discrimination are dissociated by tectal and cortical lesions. *Science*, *163*, 895–902.
- Shepard, R. N. (1984). Ecological constraints in internal representation. *Psychological Review*, *91*, 417–447.
- Shepard, R. N. (1994). Perceptual-cognitive universals as reflections of the world. *Psychonomic Bulletin & Review*, *1*, 2–28.

- Shintel, H., Nusbaum, H., & Okrent, A. (2006). Analog acoustic expression in speech communication. *Journal of Memory and Language*, *55*, 167–177.
- Shtyrov, Y., Hauk, O., & Pulvermüller, F. (2004). Distributed neuronal networks for encoding category-specific semantic information: The mismatch negativity to action words. *European Journal of Neuroscience*, *19*, 1083–1092.
- Sommerville, J. A., & Decety, J. (2006). Weaving the fabric of social interaction: Articulating developmental psychology and cognitive neuroscience in the domain of motor cognition. *Psychonomic Bulletin & Review*, *13*, 179–200.
- Speer, N. K., Zacks, J. M., Reynolds, J. R., & Hedden, R. A. (2005, November). *Neural activity during reading reflects changes in the situation described by the text*. Paper presented at the Society for Neuroscience Annual Meeting, Washington, DC.
- Spivey, M. J., & Geng, J. J. (2001). Oculomotor mechanisms activated by imagery and memory: Eye movements to absent objects. *Psychological Research*, *65*, 235–241.
- Stock, A., & Stock, C. (2004). A short history of ideomotor action. *Psychological Research*, *68*, 176–188.
- Taylor, L. J., & Zwaan, R. A. (2008). Motor resonance and linguistic focus. *Quarterly Journal of Experimental Psychology*, *61*, 896–904.
- Tomasello, M. (2003). *Constructing a language: A usage-based theory of language acquisition*. Cambridge, MA: Harvard University Press.
- Tucker, M., & Ellis, R. (2001). The potentiation of grasp types during visual object categorization. *Visual Cognition*, *8*, 769–800.
- Tucker, R., & Ellis, M. (2004). Action priming by briefly presented objects. *Acta Psychologica*, *116*, 185–203.
- Umiltà, M. A., Kohler, E., Gallese, V., Fogassi, L., Fadiga, L., Keysers, C., et al. (2001). I know what you are doing: A neurophysiological study. *Neuron*, *31*, 155–165.
- Ungerleider, L. G., & Mishkin, M. (1982). Two cortical visual systems. In M. Ingle, M. Goodale, & R. Mansfield (Eds.), *Analysis of visual behavior* (pp. 549–586). Cambridge, MA: MIT Press.
- Urgesi, C., Moro, V., Candidi, M., & Aglioti, M. S. (2006). Mapping implied body actions in the human motor system. *The Journal of Neuroscience*, *26*, 7942–7949.
- Wolpert, D. M., Doya, K., & Kawato, M. (2003). A unifying computational framework for motor control and social interaction. *Philosophical Transactions of the Royal Society*, *358*, 593–602.
- Zwaan, R. A. (1996). Processing narrative time shifts. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *22*, 1196–1207.
- 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* (Vol. 44, pp. 35–62). New York: Academic Press.
- Zwaan, R. A., & Kaschak, M. P. (in press). Language comprehension as a means of “re-situating” oneself. In P. Robbins & M. Aydede (Eds.), *The Cambridge handbook of situated cognition*. Cambridge, UK: Cambridge University Press.
- Zwaan, R. A., Langston, M. C., & Graesser, A. C. (1995). The construction of situation models in narrative comprehension: An event-indexing model. *Psychological Science*, *6*, 292–297.
- Zwaan, R. A., Magliano, J. P., & Graesser, A. C. (1995). Dimensions of situation-model construction in narrative comprehension. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *21*, 386–397.
- Zwaan, R. A., & Radvansky, G. A. (1998). Situation models in language comprehension and memory. *Psychological Bulletin*, *123*, 162–185.
- Zwaan, R. A., & Rapp, D. N. (2006). Discourse comprehension. In M. A. Gernsbacher & M. J. Traxler (Eds.), *Handbook of psycholinguistics* (pp. 725–764). San Diego, CA: Elsevier.
- Zwaan, R. A., & Taylor, L. J. (2006). Seeing, acting, understanding: Motor resonance in language comprehension. *Journal of Experimental Psychology: General*, *135*, 1–11.