The Human Mirror Neuron System and Embodied Representations

Lisa Aziz-Zadeh and Richard B. Ivry

Abstract Mirror neurons are defined as neurons in the monkey cortex which respond to goal oriented actions, whether the behavior is self-generated or produced by another. Here we briefly review this literature and consider evidence from behavioral, neuropsychological, and brain imaging studies for a similar mirror neuron system in humans. Furthermore, we review functions of this system related to action comprehension and motor imagery, as well as evidence for speculations on the system's ties with conceptual knowledge and language.

The relationship between the control of movement and our perception of the actions produced by others has become the subject of considerable study over the past 20 years. This relationship has been spurred by a shift in thinking about the function of the motor system as involved in the control of action, rather than movement and the discovery of the mirror neuron system (Gallese et al., 1996; Jeannerod, 1999). Various lines of evidence have been pursued to delineate the anatomy and functional domain of this so-called "mirror network". At the neuronal level, mirror neurons are defined as those that fire during specific goal-related behaviors, regardless of whether the behavior is self-generated or produced by another agent. At the system level, a distributed set of neural regions has been identified that are engaged during tasks involving either the production or perception of action. The excitement in the neuroscience community over the mirror network stems from the notion that this system may provide biologically plausible mechanisms for the development of conceptual knowledge, through embodied processes that allow for interpreting the movements of others and comprehending the intent of their actions.

In this chapter, we will focus on the mirror neuron system, examining the evidence from behavioral, neuropsychological, and brain imaging studies.

R.B. Ivry (✉)
Department of Psychology, 3210 Tolman Hall, University of California, Berkeley, CA 94720-1650, USA
e-mail: ivry@berkeley.edu

This review will explore how the mirror neuron concept has proven useful for understanding links between perception and action. Moreover, we will consider broader implications for the representation of conceptual knowledge. Indeed, mirror neurons have been viewed as essential components for the most unique human behavior: the use of language to enhance and facilitate social communication.

Common Coding of Perception and Action in the Motor System

To begin our review of the mirror neuron system, we first consider the anatomy and physiology of the motor system in primates. Similar to what has occurred in the study of perceptual systems, the motor system appears to be a complex medley of areas, with multiple maps of the body. Indeed, while vision scientists are fond of claiming that 50% of the cortex is involved in visual perception, a similar argument could be made regarding the motor system when one recognizes that frontal cortex is devoted to the translation of goals into actions and movements, with substantial contributions from parietal cortex. What these chauvinistic statements underscore is the fact that it is simplistic to divide brain structure by task domain. A computational perspective makes clear that divisions between perception and action are artificial and, in fact, misguided.

Identification of mirror region though comparative anatomy

Matelli and his colleagues examined the primate motor cortices using cytrochrome oxidase activity (Matelli et al., 1985). Using this methodology, six strips of different enzymatic activity were revealed, each strip corresponding to one area, or what are referred to as F1-F6 (Fig. 1). We focus our attention on area F5, the region where mirror properties were discovered. Neurons in F5 are activated during both hand and mouth movements (Gentilucci et al., 1988) and become active during specific goal-directed actions.

For human cortex, BA 44 is hypothesized to be homologous to macaque area F5. The human frontal and superior central sulcus are considered homologous to the macaque superior arcuate sulcus. The areas that lie rostral to the precentral sulcus would therefore correspond to areas F2 and F7 in the macaque (reviewed in (Geyer et al., 2000)). The ascending branch of the human inferior precentral sulcus and the inferior frontal sulcus correspond to the macaque inferior arcuate sulcus (AI). The descending branch of the human inferior precentral sulcus corresponds to the inferior precentral dimple (IPD) in the macaque monkey; thus the homology between BA 44 and F5. Further support for this hypothesis comes from cytoarchitectonic analyses. Unlike neighboring BA 45, BA 44 is agranular, similar to F5.
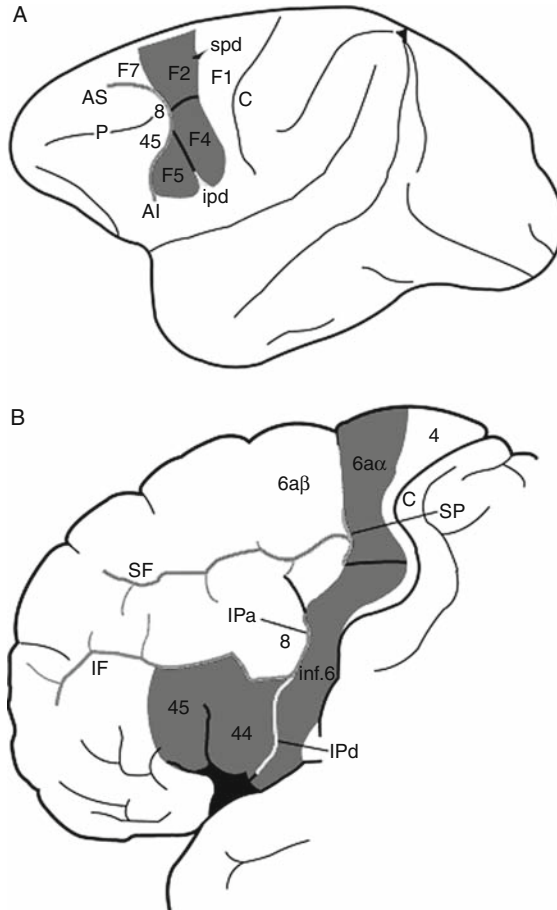
Fig. 1 Monkey and human brain homologies. **A.** Primate Brain. **B.** Human Brain (Geyer et al. (2000)). The superior arcuate sulcus (AS) is thought to be homologous to the superior frontal sulcus (SF) in humans. The inferior arcuate sulcus (AI) is homologous to the inferior frontal sulcus (IF). Ipd = inferior precentral dimple. C = central sulcus. F5 is hypothesized to be homologous to human Brodmann Area 44

Canonical and Mirror Neurons in Area F5

While motor and sensory properties of premotor cortex have been explored in many primate and human studies (Penfield and Rasmussen, 1950; Riehle and Requin, 1989), Rizzolatti and colleagues have systematically examined the relationship between these two domains over the past decade, focusing on the representation of actions and their goals. In a typical study, the monkey would view different objects. On some trials, the animal would reach for the object

(action production); on others, the animal would observe the experimenter manipulate the object (action observation) or view the object passively as a visual control (Gallese et al., 1996).

These studies revealed two distinct classes of neurons: *canonical neurons* and *mirror neurons*. Canonical neurons are primarily found along the posterior bank of the arcuate sulcus (F5ab) and are associated with the execution of motor actions. They also respond when the animal is presented with graspable objects. These neurons show some degree of specificity for particular actions, with this specificity consistent for movement as well as for objects associated with these movements. For example, a canonical neuron that responds when the animal produces a precision grip will also be activated when the animal views a small object that would require a similar action. Likewise, those that fire while seeing a large object also fire during whole hand prehension (Gallese et al., 1996). Unlike mirror neurons, they are not active while watching someone else perform the action. Thus, one might infer that canonical neurons represent a possible action that might be performed by the monkey. When the object is manipulated by another agent, this possibility becomes unlikely.

Mirror neurons are active when either the animal produces the action or when observing another agent produce the action. Interestingly, these neurons are not active during presentation of the object under conditions in which movement is precluded (by instructions) or when the object is manipulated by a tool. Simple emotionally meaningful gestures also fail to excite mirror neurons. Hence only direct action with an object is effective. As with canonical neurons, mirror neurons are action specific, coding for actions such as grasping, gripping, etc., and do not require actual observation of the action. The neuron will also fire even when the action is produced in the dark, arguing against a direct dependency on visual feedback. The activation of mirror neurons during action observation occurs in the absence of subthreshold activation of the motor pathways. Indeed, during action observation alone, primary motor cortex neurons (F1) do not become active. While mirror neurons were first identified in F5c, which is located on the convexity of area F5, more recent work has reported their presence in other frontal and parietal areas (Gallese et al., 2001; Fogassi et al., 2005; Nelissen et al., 2005).

Gallese et al. examined the relationship between the visual and motor responses of the mirror neurons. Some neurons require a close correspondence between the motor and perceptual properties (e.g. extracting food with the index finger). For other neurons, the relationship between perception and action is more abstract. A neuron might show relatively high specificity during movement (e.g., only when grasping an object), but fire when that object is either grasped or manipulated in different ways by another agent. Other neurons are activated by the goal of the observed action, regardless of how it is achieved (Gallese et al., 1996). For example, neurons of this type can be activated during action observation by different effectors (e.g., mouth and hand), as long as the manner in which the goal was achieved is similar (e.g., grasping for the purpose of eating).

Mirror neurons in F5 respond to an action even when the goal of the action is occluded from the monkey's vision. For example, they will fire when the monkey is shown that there is an apple behind a screen and the experimenter is seen reaching for it, but the final grasping of the object is obscured from the monkey's view. By contrast, these cells do not fire if the monkey knows that there is no object behind the screen, even when the actor mimes the same action. Thus, the neurons code for specific goal-oriented actions, or some aspect of intentionality (Umilta et al., 2001).

A dramatic demonstration of the goal-based coding of mirror neurons comes from studies in which physiological recordings were made when the monkey was presented with the sounds made by actions (Kohler et al., 2002). A subset of neurons that fired when the animal crushed a peanut shell or observed this same action performed by the experimenter, were also active when only the sound of the peanut being cracked was presented. Thus, some mirror neurons are multi-sensory, or perhaps modality-independent.

Perception-Action Representations in Other Cortical Areas

Despite its strong response to visual input, area F5 in the monkey brain is not directly linked to the occipital areas (Fig. 2). Instead, the predominant input to this region is from the inferior parietal (IP) lobule (Rizzolatti et al., 1981; Pandya and Yeterian, 1984). The rostral half of the lateral bank of the intra-parietal sulcus (IPS) has been found to include neurons that are excited by actions of the hand (Taira et al., 1990, as referenced in Gallese et al., 1996). Some of these have similar properties as canonical neurons (Sakata et al., 1995),
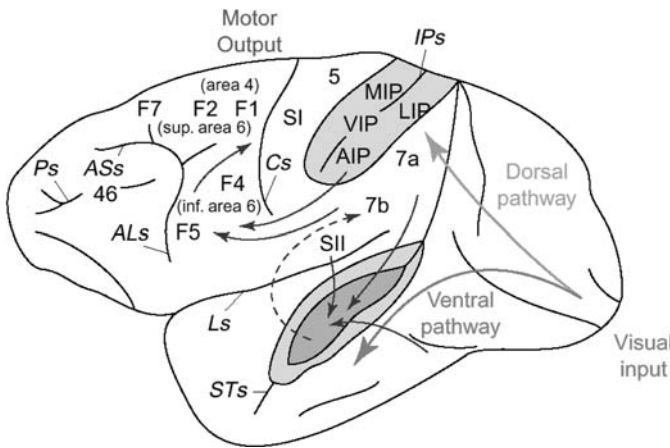

Fig. 2 Fronto-parietal regions within the monkey brain and pathways. Cs = central sulcus; IPs = inferior parietal sulcus; STs = superior temporal sulcus; ASs = Arcuate sulcus

being selective for the size and shape of the object, as well as the action with which the object is manipulated. Other neurons, especially in inferior parietal lobule are active during both action execution and observation, suggesting similar mirror-like properties in the parietal lobe (Fogassi et al., 1996; Fogassi and Gallese, 2000; Fogassi et al., 2005; Nelissen et al., 2005).

An interesting contrast can be made between neurons with mirror-like properties in parietal and premotor regions. First, neurons in the anterior intraparietal (AIP) cortex are more likely to respond during the visual presentation of objects than F5 neurons. Second, while almost all F5 neurons respond during movement, only a subset of AIP neurons are more active when the animal produces the action compared to passive viewing. Thus, purely visually driven neurons are present in AIP.

Neurons sensitive to the interaction of hands with objects have also been identified in the lower bank of the superior temporal sulcus (STS) (Perrett et al., 1990). These neurons are similar to F5 mirror neurons in that they generalize to different variations of the same action, don't respond when similar movements are produced in the absence of objects (or meaningful goals), and respond during observed actions.

Mirror Neuron System in the Human Brain

The human mirror system has been the subject of considerable investigation in the past decade. As noted above, early investigations involved intracortical recordings during neurosurgery (Ojemann, 1981). More recent studies have involved neurologically healthy individuals, using non-invasive techniques to examine physiological processes. These studies indicate a fronto-parietal mirror network in humans, with links to the superior temporal sulcus (STS) (Fig. 3). We provide just a few examples here of this rather extensive literature (Molnar-Szakacs et al., 2002; Rizzolatti and Craighero, 2004; Fadiga et al., 2005; Iacoboni, 2005).

Fadiga and colleagues (1995) used transcranial magnetic stimulation (TMS) to record motor evoked potentials (MEP) during action observation (e.g. lifting the arm). They hypothesized that if the human premotor cortex is sensitive to observation of that action, then the primary motor cortex, only a synapse away, should also be excited, even if the excitation is subthreshold. Thus, TMS was used as a probe of motor cortex excitability. As predicted, MEPs elicited by TMS applied over the primary motor cortex were significantly greater during action observation compared to when the object was observed alone. Since this initial study, there are now numerous brain imaging studies indicating mirror areas including Brodmann area 44, the premotor cortex, and the inferior parietal lobule to be activated during action observation (Fadiga et al., 1995; Grafton et al., 1996; Rizzolatti et al., 1996; Grezes et al., 1998; Binkofski et al., 1999; Iacoboni et al., 1999; Nishitani and Hari, 2000; Buccino et al., 2001;
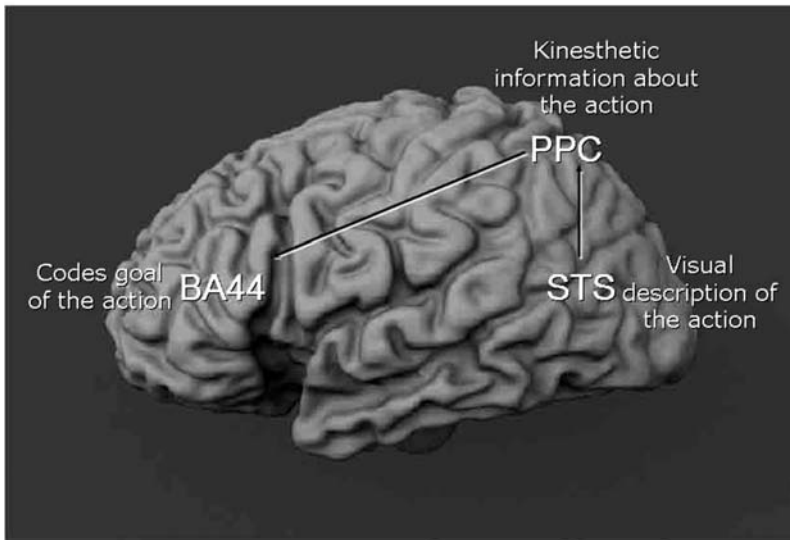
Neural Architecture for Action Representation

Fig. 3 A section of some of the neuronal pathways important for action representation (Iacoboni, 2005). Black lines represent input from the visual cortex. Some more connections not shown here: output from BA 44 to the premotor cortex, as well as input to the system from the prefrontal cortex and sensory motor areas

Aziz-Zadeh et al., 2002; Grezes et al., 2003; Johnson-Frey et al., 2003; Koski et al., 2003; Molnar-Szakacs et al., 2004; Iacoboni et al., 2005; Aziz-Zadeh et al., 2006a).

The degree to which action observation activates motor areas is dependent on the level of the skill of the observer. In one such study, skilled dancers, specializing in either classical ballet or capoiera, watched videos of ballet or capoiera (Calvo-Merino et al., 2005). "Mirror" areas, namely the premotor cortex, intraparietal sulcus, superior temporal sulcus, and superior parietal lobule, were activated more strongly when these experts viewed movements they were extensively trained to perform compared to videos of movements that fell outside their expertise. Because both dance techniques involve movement of similar muscles, these results indicate that the human mirror system is sensitive to higher levels of action organization and influenced by training in a particular motor skill.

The mirror network has also been shown to be modulated by contextual/intentional differences between stimuli (Iacoboni et al., 2005). Participants either watched a hand grasp a cup as part of a larger context (e.g., to drink, to clean) or watched the same action without a background context. Greater

activation of the ventral premotor cortex was observed when actions occurred within the appropriate context. Thus, context, which provides the goal of the action (e.g. to eat or clean) and from which the intentions of the actor may be deciphered, can modulate the degree of engagement of the mirror network.

A few studies have explored activity in the mirror network to auditory stimuli. Motor evoked potentials (MEPs) recorded from muscles controlling the lips or tongue following TMS of the left motor cortex were modulated when people listen to different syllables (Fadiga et al., 2002). In another study, MEPs were recorded from the left or right hand while participants listened to bimanual action sounds (typing, tearing paper), a leg action sound (walking) or a control sound (thunder). Listening to hand action sounds facilitated MEPs, but only when the left hemisphere hand area was stimulated; no changes were found with right hemisphere stimulation (Aziz-Zadeh et al., 2004). Support for an auditory mirror system in the left hemisphere was also found in a recent fMRI study. The left premotor cortex was significantly activated to sounds of hand and mouth actions in a somatotopic fashion as compared to control sounds (Gazzola et al., 2006).

A left lateralized activation of an auditory mirror system is in contrast to bilateral changes that have been reported during action observation (Aziz-Zadeh et al., 2006a). The neural system for vocalization is evolutionarily the oldest lateralized system (Corballis, 2002). Perhaps this pre-existing lateralization in the brain biased a similar left hemisphere shift for an auditory component of the mirror system. Putting the lateralized findings together, it appears that the human mirror system may have different levels of abstraction for actions in each hemisphere. In the left hemisphere, actions may be coded more abstractly or in an amodal manner. Right hemisphere action coding may be more modality specific and limited. This multimodality of the left hemisphere human mirror system may provide features that make it well suited for facilitating the emergence of language (Hauser et al., 2002).

Functional Roles for the Perception-Action Coupling

Intimate links between perception and action have been recognized to capture fundamental aspects of human cognition. These include action representation, intention understanding, simulation theory, motor imagery, empathy, imitation, and aspects of language including speech perception and the representation of conceptual knowledge. A number of thoughtful reviews on this topic can be found in the recent literature (Gallese, 2003; Gallese et al., 2004; Rizzolatti and Craighero, 2004; Blakemore and Frith, 2005; Iacoboni, 2005). Here, we briefly review some of these ideas, focusing on aspects related to action representation and language.

Ideomotor Action Theory

As is so often the case, William James anticipated current thinking when he stated, "Every representation of a movement awakens in some degree the actual movement which is its object". He postulated that a movement "image" was created through visual observation as well as from the proprioceptive information received during action execution. Through association, the motor "image" was then invoked whenever we thought of a movement, or what he called "ideomotor action" (James, 1890).

Greenwald (1970) extended these ideas, proposing that voluntary movements were represented as images of their sensory feedback. Since visual feedback is an important part of most actions, action observation plays a central role in the multimodal representation of actions. In this manner, strong links are created between action observation and action production. As such, we should observe compatibility effects between the two domains. That is, stimuli with high ideomotor compatibility activate the response image, which then activates the corresponding response. This notion has been adopted to account for imitation (Brass et al., 2001). In an imitation task, the "stimulus" is the actor who first performs the action.

Prinz and colleagues have promoted a similar view of the relationship between actions and their consequences (Hommel et al., 2001). In this model, stimuli and responses share a common representation and this representation is one of an abstract action or "action concept". Because of their common representation, when the response code is activated, the stimulus/sensory code is activated as well. Conversely, when the stimulus/sensory code is activated, the response code is activated.

This perspective is consistent with the ubiquitous finding of compatibility effects in behavioral studies (reviewed in Kornblum and Lee, 1995); see (Hommel et al., 2001) for an alternative perspective). To give one example, Aziz-Zadeh et al. (2005) used a simple reaction time task where the "go" stimulus was a left hand, a right hand, or a control stimulus flashed to either the left or right visual field (LVF/RVF). Responses were significantly facilitated when the left hand appeared in the LVF/right hemisphere or right hand stimuli appeared in the RVF/left hemisphere. This data indicate ideomotor compatibility is maintained within each hemisphere, even when no decision about the stimulus is necessary.

The perspective of ideomotor action theory, thus, is of an abstract representation that integrates sensory and motor representations. The functional role for the mirror neuron can be seen as one variant of an ideomotor hypothesis, albeit with a greater specification of the underlying neural mechanisms.

Motor Imagery

Motor imagery also appears to share many features observed during actual movement. The duration of imagined actions is similar to that of actually

executing the action (Decety et al., 1989; Ochipa et al., 1997) and the time required to mentally imagine unnatural movements exceeds that required to imagine natural movements, consistent with the actual performance of each (Parsons, 1994). Premotor areas (Rizzolatti et al., 2002) and occasionally the primary motor areas are active during motor imagery (Rueckert et al., 1994; Porro et al., 1996; Dechent et al., 2004). Damage to the latter, however, does not disrupt the ability to predict the time required to complete actions such as a sequence of finger movements or visually guided reaching movements; rather, an inability to accurately imagine the duration of these actions was associated with parietal damage (Sirigu et al., 1996).

Does mental imagery utilize unspecific factors such as intention or readiness to move, or does imagery entail the internal simulation of the action? When people imagine producing an action, there is increased corticospinal excitability similar to that observed during actual motor execution. For example, MEPs elicited by TMS were systematically modulated when people imagined flexion or extension movements (Fadiga et al., 1999). This effector-specific effect is similar to that observed during action execution (Humphrey, 1986). Thus, consistent with what has been observed in studies of visual imagery, motor imagery would appear to engage circuits used in action production.

Action Comprehension

A core notion of the mirror neuron hypothesis is the idea that the motor system is not involved in movement but in action. This view emphasizes the importance of the goal in defining motor output. As emphatically argued by Rizzolatti, "Unlike movement, action is defined by a goal and by expectancy. Movements are the final outcome of action and are programmed and controlled as such only when action is set (Rizzolatti et al., 2000)". Through its links between action and perception, the mirror system provides a mapping of external reality onto our own internal representations.

Canonical neurons may be important for linking a particular object with the actions necessary to interact with it (Fadiga et al., 2000). Thus, even in tasks not requiring any movement, activation is premotor cortex is frequently observed when people view 3D objects (Grafton et al., 1997). This activation can be seen as the preparation for "potential" interactions with objects. Even if the inter-action does not occur, the activation may be a component of the semantic knowledge about the object. Understanding what an object is may involve engaging representations of how we interact with that object (Fadiga et al., 2000; Kellenbach et al., 2003; Boronat et al., 2005).

The firing of mirror neurons, by contrast, seems to generate an internal representation of the observed action. This internal representation may provide a simulation model of understanding another's actions. By mapping someone's actions onto our own motor representations, we can decipher that person's

goals (Gallese, 2003; Gallese et al., 2004). These representations might be further abstracted given their multimodal nature. Thus mirror neurons in the F5 region may serve as "motor concepts" for a potential action, coding the concept of a particular goal (i.e. "grasping", "chewing", etc.). This lexicon of "motor concepts" may be shared by mirror and canonical neurons: canonical neurons select the "concept" by observing an object while mirror neurons select the "concept" by observing an action. We will return to this idea when we discuss conceptual representation.

The mirror neuron hypothesis focuses on the idea that neural activity in premotor regions during action observation (or listening to the sounds associated with an action) is an essential part of how that action comes to be understood. An alternative view is that this activity is epiphenomenal, arising from strong connections between this region and "higher-level" regions that support multimodal representations of action goals. These connections should be highly developed from the many times that an individual has thought about a particular action and then produced a movement to achieve that action. When watching another person perform a movement, comprehension might require the engagement of these higher-level areas, with the premotor activity arising from a form of priming, even if it is not essential for comprehension itself. This is a tricky question, especially since we do not have a good definition of what constitutes a "higher-area". For the present purposes, though, it is useful to focus on the causality question with respect to premotor cortex, especially since this region has played such a prominent role in the mirror neuron literature.

Lesion methods have proven to be a powerful tool for assessing functional hypotheses. Specifically, the mirror neuron hypothesis as commonly stated would lead to the expectation that lesions of premotor cortex would produce impairments in action comprehension? We are unaware of any primate studies that have reported such deficits. This question, however, has been asked in a number of neuropsychological studies, with inconclusive results. Heilman and his colleagues tested patients with apraxia due to left hemisphere lesions on various tasks involving action comprehension. The patients were divided into two groups, those with posterior lesions and those with anterior lesions. The latter would likely include premotor cortex, although there was no detailed reports of the neuropathology. While the two groups were preselected to be similarly affected on motor tasks, only the patients with posterior lesions were impaired on the action comprehension tests (Heilman et al., 1982; Rothi et al., 1985). These results are consistent with the traditional model of praxis proposed by Liepmann (reviewed in (Leiguarda and Marsden, 2000) in which left parietal lobe supports common representations for action production and comprehension (see also (Kertesz and Ferro, 1984; De Renzi et al., 1986).

However, two recent studies have shown that action comprehension may be compromised in patients with lesions to frontal premotor areas. Tranel and his colleagues investigated conceptual representation for actions in 90 patients with lesions to various sites in the left or right hemisphere. The retrieval of knowledge for actions was measured by asking participants to evaluate action

attributes from viewing pictures of actions and compare and match pictured actions. Based on a lesion overlap method, they reported the highest incidence of impairment was correlated with damage to left premotor/prefrontal cortex, the left parietal region, and the white matter underneath the left posterior middle temporal region (Tranel et al., 2003). A similar pattern of deficit was reported in a study in which aphasic patients were tested for their comprehension of visually or verbally presented actions (Saygin et al., 2004): patients with lesions of premotor or parietal areas were impaired on these tasks, although lesions in premotor areas were more predictive of deficits.

Taken together, these last two studies indicate that action comprehension deficits can be observed in patients with premotor lesions. The fact that similar deficits are found in patients with parietal lesions (and that there are other reports in which patients with anterior lesions performed normally, (see (Wang and Goodglass, 1992; Schnider et al., 1997) makes it difficult to draw strong conclusions from this work. We recognize that even if mirror-related activity in premotor cortex were found to not be essential for action comprehension, the mirror neuron idea would not be refuted. The focus could now shift to other regions such as parietal cortex, another area in which common activity is observed during action production and action comprehension (Fogassi et al., 2005).

Speech Perception and Production

The theoretical motivation for considering links between action and perception was perhaps most cogently articulated by proponents of the motor theory of speech perception (Lieberman et al., 1967). The starting point for this theory was the recognition of the tremendous variability in the acoustic signal that arises due to between-individual variation in the articulatory apparatus, and more importantly, the effects coarticulation have on the acoustic stream. To overcome this variability, proponents of the motor theory of speech perception suggested that invariance lies in the underlying articulatory act. Specifically, perception involves the process of determining the articulatory gestures that would produce the acoustic signal. Thus, the motor theory of speech perception can be viewed as a particularly strong form of a mirror neuron hypothesis. In this theory, perception is dependent on the ability to map acoustic representations onto their corresponding motoric gestures. Indeed, this theory motivated some of the earliest evidence suggesting premotor involvement in perception: Cortical stimulation over selected sites in premotor cortex (including Broca's area) led to disruption of orofacial muscles and also phoneme identification (Ojemann, 1981). More recently, activation in a common premotor area was observed when participants produced or perceived syllables (Wilson et al., 2004).

The motor theory of speech perception was proposed to account for how consideration of motoric aspects of language production may be essential for

comprehending the sounds of language. An even broader problem concerns the dependence of language in a more general way on the motor system. Can language as a symbolic system be separated from language as a motor act? Or is the dependence of these subsystems so intertwined that abolishing one necessarily abolishes the other?

One way to explore this issue is to consider what happens to covert speech during transient lesions of motor areas through the use of repetitive TMS (rTMS). rTMS over Broca's area, as well as over both left and right mouth motor cortices, can induce overt speech arrest (Stewart et al., 2001). Is a similar pattern observed during covert speech? To explore this question, Aziz-Zadeh et al. applied rTMS over two left frontal lobe sites, one over a mouth premotor site and the other over Broca's area in the posterior part of the inferior frontal gyrus. Corresponding right hemisphere sites were also stimulated. Participants were asked to report the number of syllables in visually presented words. The stimuli were controlled for length to ensure that the participants had to generate acoustic representations to successfully perform the task. Counting, either overtly or covertly was slower following rTMS of either left hemisphere site. In contrast, stimulation of the premotor right hemisphere site only produced arrest during the overt condition. This dissociation suggests that, in addition to Broca's area, the left hemisphere premotor regions may be essential for the fluid use of internal language even when motor output is not required (Aziz-Zadeh et al., 2005).

Embodied Semantics

The focus of much of the research on mirror neurons has been to explore links between action and perception in general, and, more specifically, to understand how action comprehension may arise by reference to our own motor capabilities. While these are certainly important problems, this work alone does not account for the much broader interest in mirror neurons evident in the current cognitive neuroscience literature. Ramachandran has provocatively suggested that, "The discovery of mirror neurons in the frontal lobes of monkeys. . . is the single most important 'unreported' (or at least, unpublicized) story of the decade. I predict that mirror neurons will do for psychology what DNA did for biology: they will provide a unifying framework and help explain a host of mental abilities that have hitherto remained mysterious and inaccessible to experiments (Ramachandran, 2000)." The promise expressed here and underlying much of the current theorizing is that mirror neurons may hold a key to understanding the neural basis of conceptual knowledge.

This idea builds on the psychological construct of embodied semantics. By this view, the perception-action representations developed during action production and comprehension are also essential for developing the conceptual representations required to understand language. Thus, to understand the

sentence "Grasp the cup" would require activation of motoric, or more accurately, mirror-neuron based representations that would be engaged when grasping a coffee cup or observing another individual perform this act. Moreover, such conceptual representations would reflect the same form of goal-based specificity observed during action production and comprehension. That is, the concept "grasping" would be represented by motor areas that control grasping actions whereas the concept "kicking" would be represented by motor areas that are involved in actions involving the lower limbs.

The thesis of embodied semantics potentially applies to many kinds of concepts; for instance, concepts associated with visual color could be represented in part by visual color processing areas in the brain, such as V4. Given the robust activations of premotor cortex during action observation, much of the work to date on embodied semantics has been directed towards investigating the neural correlates of concepts associated with actions (e.g. kicking, grasping, biting, etc.). Hauk et al. (2004) found adjacent activations for words related to each effector and actual movement of those effectors (see also, Tettamanti et al., 2005). Similarly, Aziz-Zadeh et al. (2006b) compared activation patterns when participants watched short video clips of goal-directed actions or read short phrases describing these same actions. Within premotor cortex, activation patterns were similar in the two conditions, including showing the expected shift across different effectors (Fig. 4).

Of course our use of language is not limited to descriptions of concrete actions. Indeed, the power of language is that it can be used in a generative manner to describe abstract concepts. Metaphors provide one such example of how language is used for abstract thought: The reader can appreciate that we've played with a lot of ideas in this chapter, without thinking this to mean that the authors are a pair of children frolicking in a pile of toys. A prominent theory of metaphor comprehension, however, builds on the idea of embodied semantics. In particular, many metaphors are extensions of concrete concepts (Lakoff and
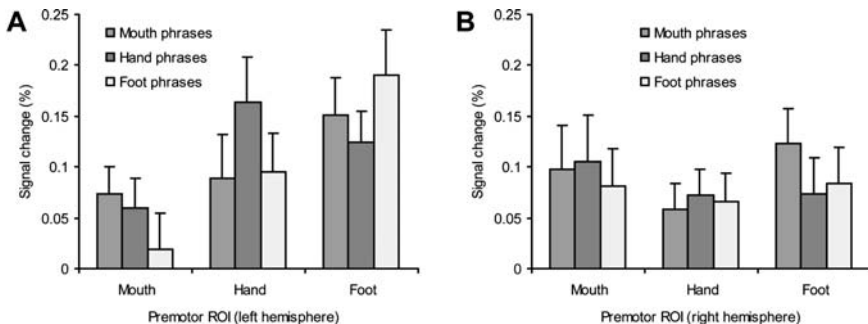

Fig. 4 A. In the left hemisphere, phrases related to foot actions significantly activate the region of the premotor cortex most activated by observation of foot actions. The same is true for the hand and the mouth. **B.** No significant patterns are observed in the right hemisphere (Aziz-Zadeh et al., 2006b)

Johnson, 1999). Thus, the abstract notion of playing with ideas is based in the embodied notion that playing with toys can involve shuffling objects about to create new forms. Mirror neurons in their generalized form, offers one mechanism for how conceptual knowledge, even for abstract entities such as metaphors, might be instantiated (see Gallese and Lakoff, 2005; Feldman and Narayanan, 2004).

Empirical evaluation of this broader view is the focus of study in a number of labs. To date, the few studies on embodied semantics have focused on relatively concrete action phrases (e.g. "grasping the pen"). There is, however, one intriguing result that has emerged in the initial studies of language comprehension, especially when compared to studies of action comprehension. Whereas, action observation has been shown to increase primary motor cortex excitability in an effector (or goal-based) manner, similar effects are not found during action-based linguistic processing. Indeed, the few studies to date suggest the opposite: motor cortex during linguistic comprehension may be inhibited in an effector-specific manner.

Consider a recent study (Buccino et al., 2005) in which single-pulse TMS was applied over the motor cortex while participants listened to short phrases describing actions related to the hand or foot (e.g. 'he sewed the skirt'). The stimulator was placed to target either the hand or foot area, allowing the researchers to measure motor-evoked potentials (MEPs) of the targeted effector. Interestingly, the magnitude of the MEPs for each effector was lower when the participants heard a sentence involving that effector (Fig. 5). For example, during stimulation of the hand area, MEPs were smaller for hand related phrases. Consistent with the TMS results, reaction times were slower when the effector used to make the response (either hand or foot) was the target of the TMS pulses.
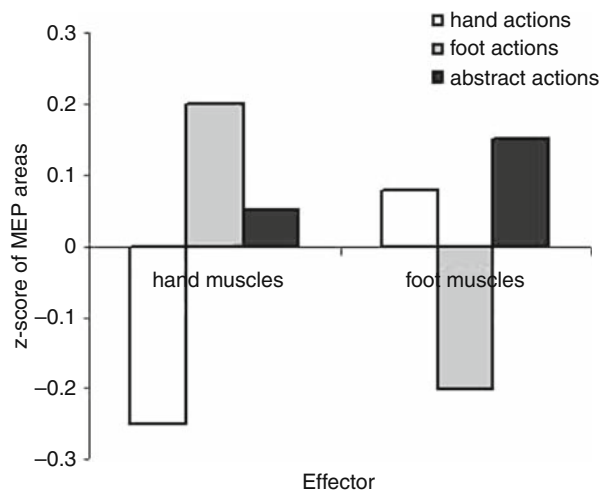

Fig. 5 Mean motor evoked potentials (MEPs) following intra-subject normalization recorded from both hand muscles (opponens pollicis and first dorsal interosseus) and foot/leg muscles (tibialis anterior and gastrocnemius). All recording were made while participants listed to different types of sentences (hand action, foot action, abstract control) (Buccino et al., 2005)

A related study makes clear how difficult it can be to disentangle different hypotheses. Pulvermuller and colleagues (Pulvermuller et al., 2005) stimulated the hand or foot areas in the left hemisphere while participants made lexical decisions on visually presented words related to either leg actions (e.g. kick) and or arm actions (e.g. pick). During stimulation of the hand area, reaction times to lexical decision of hand words were faster than to foot words. Similarly, during stimulation of the foot area, reaction times to lexical decision of foot words were faster than to hand words. The authors proposed that the TMS led to effector-specific facilitation and thus, faster RTs. It is important to note, though, that this conclusion would be opposite that drawn by Buccino et al. (2005).

However, an alternative interpretation of the Pulvermuller et al. (2005) results can be developed if one thinks of the effects of single pulse TMS in the more traditional manner of adding focal noise. Suppose the TMS pulses added noise in an effector-specific manner within motor cortex, effectively taking the targeted subregion off-line while the participants performed the language task. By this hypothesis, the effector-specific reduction in RTs on the lexical decision task would occur because the motor cortex region associated with that effector is functionally silenced. This interpretation would be consistent with the results of Buccino et al. (2005), suggesting again that linguistic processing of action concepts may lead to transient inhibition of motor cortex regions representing the effector(s) used to perform those actions.

This hypothesis needs to be reconciled with two other key findings in the mirror neuron literature. First, as reviewed previously, TMS studies of action observation and action imagery have shown effector-specific facilitation. For example, observing a hand action leads to increased MEPs in the hand area (Aziz-Zadeh et al., 2002). fMRI studies also have shown effector-specific increases of activation within motor cortex. It is unclear why the comprehension of observed or imagined actions would require the support of effector-specific representations in motor cortex, whereas these same representations must be inhibited when similar actions are described with words.

Second, the hypothesis that motor cortex is inhibited in an effector-specific manner by action words stands in contrast to fMRI results regarding the modulation of activity in premotor cortex during language comprehension tasks (Tettamanti et al., 2005; Aziz-Zadeh et al., 2006b). These imaging studies show that activity increases in an effector-specific manner, which are interpreted as reflecting the recruitment of embodied representations of the described actions.

One answer to these two puzzles may be developed by considering language typically involves more general and abstract representations than motor processing. Consider "grasping". In the primary motor cortex, the representation of a grasp likely requires specific muscles, used to produce a specific grip and force to interact with a particular object. The word "grasping", however does not code these specifics. Perhaps specific representations conveyed by the primary motor cortex need to be inhibited to allow the development of more abstract conceptual representations (Buccino et al., 2005). That is, inhibition

may be required to help support the distinction between the general representation of an action or concept in secondary areas from the actualization of a movement in primary sensory-motor areas (Gallese and Lakoff, 2005).

Conclusions: Looking into the mirror and beyond to the future

One important contribution of the work described here is the shift in how we now think about the sensory-motor areas with respect to the links between perception and action. The mirror neuron hypothesis makes explicit that it is too simplistic to use dichotomies that speak of brain regions as perceptual or motor. Secondary motor areas, and perhaps even primary areas, are engaged during perception, and large sectors of brain areas typically associated with perception are influenced by our intentions or possibilities for action.

We have noted some issues that have tended to be glossed over in much of the literature on mirror neurons. There has been an avalanche of imaging papers describing activations in premotor and motor cortex during perceptual tasks, as well as studies in animals and humans demonstrating physiological changes in these regions during action comprehension. However, few studies have tried to directly examine the causal role of this activity in perception. We know that processing extends into premotor and motor areas during action observation; but the extent to which these areas contribute to action comprehension remains unclear.

Nonetheless, as noted previously, mirror-like properties extend beyond premotor cortex. This work underscores fundamental ideas concerning the intimate relationship between perception and action, and outlines biologically-plausible models for understanding the emergence of conceptual knowledge from both phylogenetic and ontogenetic perspectives (Feldman, 2006). Evolutionarily, and developmentally, the ability to understand the actions and intentions of other individuals results from our individual capability to engage in similar behavior and thought. This idea is at the essence of the more general notion of embodied cognition.

It seems that we are at a position where it would be wise to take stock. As the evidence accumulates demonstrating the close relationship of perception and action, it is useful to consider the status of alternative theories. The mirror neuron hypothesis is counter to at least two general ideas. First, many models of brain function tended to compartmentalize functions along task domains such as perception and motor control. Second, with the emergence of cognitive science, symbolic processing models were developed that could perform complex functions without notions of embodiment. Do these models, with appropriate modification, remain viable in the face of the neuroscientific advances? And more important, what empirical tests can distinguish between different frameworks? It may well be that as our models of embodied cognition become fleshed out, the differences with non-embodied models may be reduced.

Literature

Aziz-Zadeh, L., Cattaneo, L., Rochat, M. and Rizzolatti, G., 2005. Covert speech arrest induced by rTMS over both motor and nonmotor left hemisphere frontal sites. J Cogn Neurosci. 17, 928–938.

Aziz-Zadeh, L., Koski, L., Zaidel, E., Mazziotta, J. and Iacoboni, M., 2006a. Lateralization of the human mirror neuron system. J Neurosci. 26, 2964–2970.

Aziz-Zadeh, L., Maeda, F., Zaidel, E., Mazziotta, J. and Iacoboni, M., 2002. Lateralization in motor facilitation during action observation: a TMS study. Exp Brain Res. 144, 127–131.

Aziz-Zadeh, L., Wilson, S. M., Rizzolatti, G. and Iacoboni, M., 2006b. Congruent Embodied Representations for Visually Presented Actions and Linguistic Phrases Describing Actions. Curr Biol. 16, 1818–1823.

Aziz-Zadeh, L., Iacoboni, M., Zaidel, E., Wilson, S. and Mazziotta, J., 2004. Left hemisphere motor facilitation in response to manual action sounds. Eur J Neurosci. 19, 2609–2612.

Binkofski, F., Buccino, G., Stephan, K. M., Rizzolatti, G., Seitz, R. J. and Freund, H. J., 1999. A parieto-premotor network for object manipulation: evidence from neuroimaging. Exp Brain Res. 128, 210–213.

Blakemore, S. J. and Frith, C., 2005. The role of motor contagion in the prediction of action. Neuropsychologia. 43, 260–267.

Boronat, C. B., Buxbaum, L. J., Coslett, H. B., Tang, K., Saffran, E. M., Kimberg, D. Y. and Detre, J. A., 2005. Distinctions between manipulation and function knowledge of objects: evidence from functional magnetic resonance imaging. Brain Res Cogn Brain Res. 23, 361–373.

Brass, M., Bekkering, H. and Prinz, W., 2001. Movement observation affects movement execution in a simple response task. Acta Psychol (Amst). 106, 3–22.

Buccino, G., Binkofski, F., Fink, G. R., Fadiga, L., Fogassi, L., Gallese, V., Seitz, R. J., Zilles, K., Rizzolatti, G. and Freund, H. J., 2001. Action observation activates premotor and parietal areas in a somatotopic manner: an fMRI study. Eur J Neurosci. 13, 400–404.

Buccino, G., Riggio, L., Melli, G., Binkofski, F., Gallese, V. and Rizzolatti, G., 2005. Listening to action-related sentences modulates the activity of the motor system: a combined TMS and behavioral study. Brain Res Cogn Brain Res. 24, 355–363.

Calvo-Merino, B., Glaser, D. E., Grezes, J., Passingham, R. E. and Haggard, P., 2005. Action observation and acquired motor skills: an FMRI study with expert dancers. Cereb Cortex. 15, 1243–1249.

Corballis, M. C., 2002. From Hand to Mouth: The Origins of Language. Princeton University Press, New Jersey.

De Renzi, E., Faglioni, P., Scarpa, M. and Crisi, G., 1986. Limb apraxia in patients with damage confined to the left basal ganglia and thalamus. J Neurol Neurosurg Psychiatry. 49, 1030–1038.

Decety, J., Jeannerod, M. and Prablanc, C., 1989. The timing of mentally represented actions. Behav Brain Res. 34, 35–42.

Dechent, P., Merboldt, K. D. and Frahm, J., 2004. Is the human primary motor cortex involved in motor imagery? Brain Res Cogn Brain Res. 19, 138–144.

Fadiga, L., Buccino, G., Craighero, L., Fogassi, L., Gallese, V. and Pavesi, G., 1999. Corticospinal excitability is specifically modulated by motor imagery: a magnetic stimulation study. Neuropsychologia. 37, 147–158.

Fadiga, L., Craighero, L., Buccino, G. and Rizzolatti, G., 2002. Speech listening specifically modulates the excitability of tongue muscles: a TMS study. Eur J Neurosci. 15, 399–402.

Fadiga, L., Craighero, L. and Olivier, E., 2005. Human motor cortex excitability during the perception of others' action. Curr Opin Neurobiol. 15, 213–218.

Fadiga, L., Fogassi, L., Gallese, V. and Rizzolatti, G., 2000. Visuomotor neurons: Ambiguity of the discharge or 'motor' perception? International Journal of Psychophysiology. 35, 165–177.

Fadiga, L., Fogassi, L., Pavesi, G. and Rizzolatti, G., 1995. Motor facilitation during action observation: a magnetic stimulation study. J Neurophysiol. 73, 2608–2611.

Feldman, J. and Narayanan, S., 2004. Embodied meaning in a neural theory of language. Brain Lang. 89, 385–392.

Feldman, J. A., 2006. From molecule to metaphor: A neural theory of language. MIT Press, Cambridge, MA.

Fogassi, L., Ferrari, P. F., Gesierich, B., Rozzi, S., Chersi, F. and Rizzolatti, G., 2005. Parietal lobe: from action organization to intention understanding. Science. 308, 662–667.

Fogassi, L. and Gallese, V., 2000. The neural correlates of action understanding in non-human primates. In: Stamenor, M. I. and Gallese, V. (Eds.), Mirror neurons and the evolution of brain and language. John Benjamins Publishing Company, Philadelphia.

Fogassi, L., Gallese, V., Fadiga, L., Luppino, G., Matelli, M. and Rizzolatti, G., 1996. Coding of peripersonal space in inferior premotor cortex (area F4). J Neurophysiol. 76, 141–157.

Gallese, V., 2003. The roots of empathy: the shared manifold hypothesis and the neural basis of intersubjectivity. Psychopathology. 36, 171–180.

Gallese, V. and Lakoff, G., 2005. The brains concepts: The role of the sensory-motor system in reason and language. Cognitive Neuropsychology. 22, 455–479.

Gallese, V., Fadiga, L., Fogassi, L. and Rizzolatti, G., 1996. Action recognition in the premotor cortex. Brain. 119, 593–609.

Gallese, V., Fogassi, L., Fadiga, L. and Rizzolatti, G., 2001. Action representation and the inferior parietal lobule. In: Prinz, W. and Hommel, B. (Eds.), Attention & Performance XIX. Common mechanisms in perception and action. Oxford University Press, Oxford, pp. 334–355.

Gallese, V., Keysers, C. and Rizzolatti, G., 2004. A unifying view of the basis of social cognition. Trends Cogn Sci. 8, 396–403.

Gazzola, V., Aziz-Zadeh, L. and Keysers, C., 2006. Empathy and the somatotopic auditory mirror system in humans. Curr Biol. 16, 1824–1829.

Gentilucci, M., Fogassi, L., Luppino, G., Matelli, M., Camarda, R. and Rizzolatti, G., 1988. Functional organization of inferior area 6 in the macaque monkey. I. Somatotopy and the control of proximal movements. Exp Brain Res. 71, 475–490.

Geyer, S., Matelli, M., Luppino, G. and Zilles, K., 2000. Functional neuroanatomy of the primate isocortical motor system. Anat Embryol (Berl). 202, 443–474.

Grafton, S. T., Arbib, M. A., Fadiga, L. and Rizzolatti, G., 1996. Localization of grasp representations in humans by positron emission tomography. 2. Observation compared with imagination. Exp Brain Res. 112, 103–111.

Grafton, S. T., Fadiga, L., Arbib, M. A. and Rizzolatti, G., 1997. Premotor cortex activation during observation and naming of familiar tools. Neuroimage. 6, 231–236.

Greenwald, A. G., 1970. Sensory feedback mechanism in performance control: With special reference to the ideomotor mechanism. Psychological Review. 77, 73–99.

Grezes, J., Armony, J. L., Rowe, J. and Passingham, R. E., 2003. Activations related to "mirror" and "canonical" neurones in the human brain: an fMRI study. Neuroimage. 18, 928–937.

Grezes, J., Costes, N. and Decety, J., 1998. Top-down effect of strategy on the perception of human biological motion: A PET investigation. Cognitive Neuropsychology. 15, 553–582.

Hauk, O., Johnsrude, I., Pulvermuller, F., 2004. Somatotopic representation of action words in human motor and premotor cortex. Neuron. 41, 301–307.

Hauser, M. D., Chomsky, N. and Fitch, W. T., 2002. The faculty of language: what is it, who has it, and how did it evolve? Science. 298, 1569–1579.

Heilman, K. M., Rothi, L. J. and Valenstein, E., 1982. Two forms of ideomotor apraxia. Neurology. 32, 342–346.

Hommel, B., Musseler, J., Aschersleben, G. and Prinz, W., 2001. The Theory of Event Coding (TEC): a framework for perception and action planning. Behav Brain Sci. 24, 849–878; discussion 878–937.

Humphrey, D. R., 1986. Representation of movements and muscles within the primate precentral motor cortex: historical and current perspectives. Fed Proc. 45, 2687–2699.

Iacoboni, M., 2005. Neural mechanisms of imitation. Curr Opin Neurobiol.

Iacoboni, M., Molnar-Szakacs, I., Gallese, V., Buccino, G., Mazziotta, J. C. and Rizzolatti, G., 2005. Grasping the Intentions of Others with One's Own Mirror Neuron System. PLoS Biol. 3, 1–7.

Iacoboni, M., Woods, R. P., Brass, M., Bekkering, H., Mazziotta, J. C. and Rizzolatti, G., 1999. Cortical mechanisms of human imitation. Science. 286, 2526–2528.

James, W., 1890. The principles of psychology. MacMillan, New York.

Jeannerod, M., 1999. The 25th Bartlett Lecture. To act or not to act: perspectives on the representation of actions. Q J Exp Psychol A. 52, 1–29.

Johnson-Frey, S. H., Maloof, F. R., Newman-Norlund, R., Farrer, C., Inati, S. and Grafton, S. T., 2003. Actions or hand-object interactions? Human inferior frontal cortex and action observation. Neuron. 39, 1053–1058.

Kellenbach, M. L., Brett, M. and Patterson, K., 2003. Actions speak louder than functions: the importance of manipulability and action in tool representation. J Cogn Neurosci. 15, 30–46.

Kertesz, A. and Ferro, J. M., 1984. Lesion size and location in ideomotor apraxia. Brain. 107, 921–933.

Kohler, E., Keysers, C., Umilta, M. A., Fogassi, L., Gallese, V. and Rizzolatti, G., 2002. Hearing sounds, understanding actions: action representation in mirror neurons. Science. 297, 846–848.

Kornblum, S. and Lee, J. W., 1995. Stimulus-response compatibility with relevant and irrelevant stimulus dimensions that do and do not overlap with the response. J Exp Psychol Hum Percept Perform. 21, 855–875.

Koski, L., Iacoboni, M., Dubeau, M. C., Woods, R. P. and Mazziotta, J. C., 2003. Modulation of cortical activity during different imitative behaviors. J Neurophysiol. 89, 460–471.

Lakoff, G. and Johnson, M., 1999. Philosophy in the flesh: The embodied mind and its challenge to western thought. Basic Books, New York.

Leiguarda, R. C. and Marsden, C. D., 2000. Limb apraxias: higher-order disorders of sensorimotor integration. Brain. 123 (Pt 5), 860–879.

Lieberman, A. M., Cooper, F. S., Shankweiler, D. P. and Studdert-Kennedy, M., 1967. Perception of the speech code. Psychol Rev. 74, 431–461.

Matelli, M., Luppino, G. and Rizzolatti, G., 1985. Patterns of cytochrome oxidase activity in the frontal agranular cortex of the macaque monkey. Behav Brain Res. 18, 125–136.

Molnar-Szakacs, I., Iacoboni, M., Koski, L. and Mazziotta, J. C., 2004. Functional Segregation within Pars Opercularis of the Inferior Frontal Gyrus: Evidence from fMRI Studies of Imitation and Action Observation. Cereb Cortex. pp. 986–994.

Molnar-Szakacs, I., Iacoboni, M., Koski, L., Maeda, F., Dubeau, M. C., Aziz-Zadeh, L., Mazziotta, J. C., 2002. Action observation in the pars opercularis: Evidence from 58 subjects studied with fMRI. J Cognitive Neurosci. F118.

Nelissen, K., Luppino, G., Vanduffel, W., Rizzolatti, G. and Orban, G. A., 2005. Observing others: multiple action representation in the frontal lobe. Science. 310, 332–336.

Nishitani, N. and Hari, R., 2000. Temporal dynamics of cortical representation for action. Proc Natl Acad Sci U S A. 97, 913–918.

Ochipa, C., Rapcsak, S. Z., Maher, L. M., Rothi, L. J., Bowers, D. and Heilman, K. M., 1997. Selective deficit of praxis imagery in ideomotor apraxia. Neurology. 49, 474–480.

Ojemann, G. A., 1981. Interrelationships in the localization of language, memory and motor mechanism in human cortex and thalamus. In: Thompson, B. (Ed.), New perspectives in cerebral localization. Raven Press, New York, pp. 157–175.

Pandya, D. N. and Yeterian, E. H., 1984. Proposed neural circuitry for spatial memory in the primate brain. Neuropsychologia. 22, 109–122.

Parsons, L. M., 1994. Temporal and kinematic properties of motor behaviour reflected in mentally simulated action. Journal of Experimental Psychology. 20, 709–730.

Penfield, W. and Rasmussen, T., 1950. A clinical study of localization of function. Cerebral cortex of man. Macmillan, New York.

Perrett, D. I., Harries, M. H., Mistlin, A. J. and Hietanen, J. K., 1990. Social signals analyzed at the single cell level: Someone is looking at me, something touched me, something movedp. International Journal of Comparative Psychology. 4, 25–55.

Porro, C. A., Francescato, M. P., Cettolo, V., Diamond, M. E., Baraldi, P., Zuiani, C., Bazzocchi, M. and di Prampero, P. E., 1996. Primary motor and sensory cortex activation during motor performance and motor imagery: a functional magnetic resonance imaging study. J Neurosci. 16, 7688–7698.

Pulvermuller, F., Hauk, O., Nikulin, V. V. and Ilmoniemi, R. J., 2005. Functional links between motor and language systems. Eur J Neurosci. 21, 793–797.

Ramachandran, V. S., 2000. Mirror neurons and imitation learning as the driving force behind "the great leap forward" in human evolution. In: Edge: Reality Club Lecture). http://www.edge.org/3rd_culture/bios/ramachandran.html.

Riehle, A. and Requin, J., 1989. Monkey primary motor and premotor cortex: single-cell activity related to prior information about direction and extent of an intended movement. J Neurophysiol. 61, 534–549.

Rizzolatti, G. and Craighero, L., 2004. The mirror-neuron system. Annu Rev Neurosci. 27, 169–192.

Rizzolatti, G., Fadiga, L., Matelli, M., Bettinardi, V., Paulesu, E., Perani, D. and Fazio, F., 1996. Localization of grasp representations in humans by PET: 1. Observation versus execution. Exp Brain Res. 111, 246–252.

Rizzolatti, G., Fogassi, L. and Gallese, V., 2002. Motor and cognitive functions of the ventral premotor cortex. Curr Opin Neurobiol. 12, 149–154.

Rizzolatti, G., Fogassi, L., Gallese, V., 2000. Cortical mechanisms subserving object grasping and action recognition: A new view on the cortical motor functions. In: Gazzaniga, M. S. (Ed.), The New Cognitive Neurosciences. MIT Press, Cambridge.

Rizzolatti, G., Scandolara, C., Matelli, M. and Gentilucci, M., 1981. Afferent properties of periarcuate neurons in macaque monkeys. II. Visual responses. Behav Brain Res. 2, 147–163.

Rothi, L. J., Heilman, K. M. and Watson, R. T., 1985. Pantomime comprehension and ideomotor apraxia. J Neurol Neurosurg Psychiatry. 48, 207–210.

Rueckert, L., Appollonio, I., Grafman, J., Jezzard, P., Johnson, R., Jr., Le Bihan, D. and Turner, R., 1994. Magnetic resonance imaging functional activation of left frontal cortex during covert word production. J Neuroimaging. 4, 67–70.

Sakata, H., Taira, M., Murata, A. and Mine, S., 1995. Neural mechanisms of visual guidance of hand action in the parietal cortex of the monkey. Cereb Cortex. 5, 429–438.

Saygin, A. P., Wilson, S. M., Dronkers, N. F. and Bates, E., 2004. Action comprehension in aphasia: linguistic and non-linguistic deficits and their lesion correlates. Neuropsychologia. 42, 1788–1804.

Schnider, A., Hanlon, R. E., Alexander, D. N. and Benson, D. F., 1997. Ideomotor apraxia: behavioral dimensions and neuroanatomical basis. Brain Lang. 58, 125–136.

Sirigu, A., Duhamel, J. R., Cohen, L., Pillon, B., Dubois, B. and Agid, Y., 1996. The mental representation of hand movements after parietal cortex damage. Science. 273, 1564–1568.

Stewart, L., Walsh, V., Frith, U. and Rothwell, J. C., 2001. TMS produces two dissociable types of speech disruption. Neuroimage. 13, 472–478.

Tettamanti, M., Buccino, G., Saccuman, M. C., Gallese, V., Danna, M., Scifo, P., Fazio, F., Rizzolatti, G., Cappa, S. F. and Perani, D., 2005. Listening to action-related sentences activates fronto-parietal motor circuits. J Cogn Neurosci. 17, 273–281.

Tranel, D., Kemmerer, D., Damasio, H., Adolphs, R. and Damasio, A. R., 2003. Neural correlates of conceptual knowledge for actions. Cognitive Neuropsychology. 20, 409–432.

Umilta, M. A., Kohler, E., Gallese, V., Fogassi, L., Fadiga, L., Keysers, C. and Rizzolatti, G.,
    2001. I know what you are doing. a neurophysiological study. Neuron. 31, 155–165.
Wang, L. and Goodglass, H., 1992. Pantomime, praxis, and aphasia. Brain Lang. 42,
    402–418.
Wilson, S. M., Saygin, A. P., Sereno, M. I. and Iacoboni, M., 2004. Listening to speech
    activates motor areas involved in speech production. Nat Neurosci. 7, 701–702.