

# Mirror neurons and the social nature of language: The neural exploitation hypothesis

Vittorio Gallese

*University of Parma, Parma, Italy*

This paper discusses the relevance of the discovery of mirror neurons in monkeys and of the mirror neuron system in humans to a neuroscientific account of primates' social cognition and its evolution. It is proposed that mirror neurons and the functional mechanism they underpin, embodied simulation, can ground within a unitary neurophysiological explanatory framework important aspects of human social cognition. In particular, the main focus is on language, here conceived according to a neurophenomenological perspective, grounding meaning on the social experience of action. A neurophysiological hypothesis—the “neural exploitation hypothesis”—is introduced to explain how key aspects of human social cognition are underpinned by brain mechanisms originally evolved for sensorimotor integration. It is proposed that these mechanisms were later on adapted as new neurofunctional architecture for thought and language, while retaining their original functions as well. By neural exploitation, social cognition and language can be linked to the experiential domain of action.

## INTRODUCTION

The neuroscientific study of social cognition is opening new perspectives for a better and fuller understanding of what it means to be human. Several aspects of social cognition are nowadays the topic of empirical investigation, particularly after the development of the powerful brain imaging technologies, enabling us to directly look at what happens inside our brains when engaged in a variety of perceptual, executive and cognitive tasks. This ever-growing accumulation of neuroscientific evidence has substantially broadened our knowledge of how the human brain works and suggested new perspectives for the understanding of social cognition. This undoubtedly positive balance, though, shouldn't obscure the risks inherent in a blind reliance upon the epistemic power of this sole approach (see Coltheart, 2006, for a radical criticism of brain

imaging in relation to our understanding of the mind). Especially so, if the brain imaging evidence is blindly used to validate a preconceived notion of what the human mind is and how it works.

As recently pointed out by Barrett, Henzi, and Rendall (in press), there are two opposed but equally potentially dangerous biases that may hinder our understanding of social cognition: (1) Anthropocentrism and the related anthropomorphism, by means of which we tend to project onto other species cognitive traits that we consider typical of our species; and (2) the opposite anti-anthropomorphism, according to which human traits are a priori uniquely human. By following the anti-anthropomorphism bias, many scholars in the cognitive sciences exclusively focus on clarifying differences between humans and other primates with respect to the use of propositional attitudes. According to this mainstream

**AQ1**

**AQ2**

Correspondence should be addressed to: Vittorio Gallese, Department of Neuroscience – Section of Physiology, University of Parma, I-43100 Parma, Italy. E-mail: vittorio.gallese@unipr.it

This work was supported by MIUR (Ministero Italiano dell'Università e della Ricerca) and by the EU grants NESTCOM and DISCOS.

view, humans have Theory of Mind (ToM), nonhuman primates do not.

This paradigm, still pervasive in contemporary cognitive science, is doomed to failure when trying to establish a direct link between our use of propositional attitudes and their supposed neural correlates. No one can deny that we use what we call “propositional attitudes.” However, it is far from clear that this is the sole or even principal character of human social cognition (see Barrett & Henzi, 2005; Barrett et al., in press; Gallese, 2001, 2006). It must be added that the chances that we will find boxes in our brain containing the neural correlates of beliefs desires and intentions *as such* probably amount to next to zero. I am afraid that such a search might look like an ill-suited form of reductionism leading us nowhere.

The research strategy of social cognitive neuroscience could perhaps benefit by considering the following points: (1) We should adopt a bottom-up approach, by thoroughly investigating the non-metarepresentational aspects of human social cognition, so far unduly minimized or even neglected. (2) The empirical investigation of human social cognition should be informed by an evolutionary perspective, hence complemented by the neurophysiological and psychological investigation of the functional mechanisms underpinning nonhuman primates’ social cognition. The only way to go beyond a mere correlative use of brain-imaging data acquired in humans consists in unveiling the neural mechanisms leading to the activation of different brain regions in different tasks. (3) By doing so, it might be established to what extent the apparently different social cognitive abilities and strategies adopted by different species of primates may be underpinned by similar functional mechanisms, which in the course of evolution acquire increasing complexity (see Sommerville & Decety, 2006, for a discussion of similar points).

The empirical data briefly reviewed in this paper on the discovery of mirror neurons and its implications in social cognition are examples of this approach and research strategy. I take these data as strong evidence in support of the crucial role played by action in shaping our cognitive social competence, language included.

By focusing on the experiential and situated aspects of human social cognition, that is, by adopting a neurophenomenological approach to the empirical investigation of social cognition, we may be capable of circumventing the abovementioned

biases and getting a more realistic appreciation of what human cognition is and how it relates in evolution with the social cognitive endowments of nonhuman primates. The data on the mirror neuron system (MNS) in monkeys and humans suggest that the ease with which we “mirror” the behavior of others, recognize others as similar to us, and directly comprehend their behavior—in other words, our implicit “intentional attunement” with others (Gallese, 2006)—might rely on a series of neural matching mechanisms that we have just started to uncover.

In the present paper I briefly review the properties of the MNS in monkeys and humans and then specifically focus on the role that the MNS (and the cortical motor system, in general) may play in a crucial aspect of social cognition: language. The recent research on the MNS in humans may shed light on the social nature of language, and provide neuroscientific grounding to aspects of language investigated by psycholinguistics like, among others, situation models and collaborative and interactive accounts of conversation, according to which the perception of shared environment and behaviors helps in maintaining alignment between conversational partners (see Clark & Wilkes-Gibbs, 1986; Pickering & Garrod, 2004).

## THE MIRROR NEURON SYSTEM FOR ACTIONS IN MONKEYS AND HUMANS: EMPIRICAL EVIDENCE

About fifteen years ago mirror neurons were discovered in the premotor cortex of the macaque monkey. These neurons discharge not only when the monkey executes goal-related hand and/or mouth actions like grasping objects, but also when observing other individuals (monkeys or humans) executing similar actions (Ferrari, Gallese, Rizzolatti, & Fogassi, 2003; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996). Neurons with similar mirroring properties, matching action observation and execution have also been discovered in a sector of the posterior parietal cortex reciprocally connected with area F5 (PF/PG mirror neurons; see Fogassi et al., 2005; Gallese, Fogassi, Fadiga, & Rizzolatti, 2002; Rizzolatti, Fogassi, & Gallese, 2001). It has been proposed that the MNS may underpin a direct form of action understanding (Gallese, Keysers, & Rizzolatti, 2004; Gallese et al., 1996; Rizzolatti & Craighero, 2004; Rizzo-

latti et al., 1996, 2001), by means of embodied simulation, a specific mechanism through which the brain/body system models its interactions with the world (Gallese, 2001, 2003a,b, 2005a,b, 2006). The discovery of mirror neurons has changed our views on the relations among action perception and cognition, and has boosted a renewed interest in the neuroscientific investigation of the social aspects of primate cognition.

Experiments by Umiltà et al. (2001) showed that F5 mirror neurons are also activated during the observation of partially hidden actions, when the monkey can predict the action outcome, even in the absence of the complete visual information about it. Macaque monkeys' mirror neurons therefore respond to acts made by others not exclusively on the basis of their visual description, but on the basis of the anticipation of the final goal-state of the motor act, by means of the activation of its motor neural representation in the observer's premotor cortex.

These data can hardly be reconciled with "minimalist" interpretations of mirror neurons, such as that proposed by Knoblich and Jordan (2002), according to which mirror neurons merely code "the perceived effect the action exerts on the object" (2002, p. 116). Furthermore, these data alone seem to contradict the notion that the functional mechanism at the basis of the activation of mirror neurons qualifies as a form of "direct perception" of the acts of others (see Gallagher, this issue). It is obvious that there must be a system that visually analyzes and describes the acts of others. A "direct perception" of the observed motor acts most likely describes the activation of extrastriate visual neurons sensitive to biological motion. However, the view that such "pictorial" analysis per se is sufficient to provide an understanding of the observed act must be questioned. Without reference to the observer's internal motor knowledge, this description is devoid of experiential meaning for the observing individual. Furthermore, the activation of mirror neurons in the experiment by Umiltà et al. (2001) testifies to something even more different from a "direct perception": it exemplifies a form of simulation-driven "motor inference."

In other experiments it has been shown that a particular class of F5 mirror neurons ("audio-visual mirror neurons") respond not only when the monkey *executes* and *observes* a given hand action, but also when it just *hears* the sound typically produced by the action (Kohler et al.,

2002). These neurons respond to the sound of actions and discriminate between the sounds of different actions, but do not respond to other similarly interesting sounds such as arousing noises, or monkeys' and other animals' vocalizations. Events as different as sounds, images, or voluntary acts of the body, are nevertheless mapped by the same network of audio-visual mirror neurons. The presence within a non-linguistic species of such neural matching system can be interpreted as the dawning of an embodied "conceptualization" mechanism, that is a mechanism that grounds meaning in the situated and experience-dependent systematic interactions with the world (see Gallese, 2003b; Gallese & Lakoff, 2005). The world becomes "our world" to the extent that it evokes and is subjected to our actions.

A major step forward in the research on the MNS consisted in the discovery that parietal mirror neurons not only code the goal of an executed/observed motor act, like grasping an object, but they also code the overall action intention (e.g., bringing the grasped object to the mouth or into a container; Fogassi et al., 2005). The MNS maps integrated sequences of goal-related motor acts (grasping, holding, bringing, placing, the different "words" of a "motor vocabulary"; see Rizzolatti et al., 1988) in order to obtain different and parallel intentional "action sentences," that is, temporally chained sequences of motor acts properly assembled to accomplish a more distal goal-state. The "motor vocabulary" of grasping-related neurons, by sequential chaining, reorganizes itself so as to map the fulfillment of an action intention. The overall action intention (to eat, to place the food or object) is the goal state of the ultimate goal-related motor act of the chain. These results seem to suggest—at least at such a basic level—that the "prior intention" of eating or placing the food is also coded by parietal mirror neurons (see de Vignemont & Haggard, this issue, for a different interpretation). Of course, this shouldn't imply that monkeys *explicitly* represent prior intentions as such.

Several studies have also demonstrated in the human brain the existence of a MNS matching action perception and execution (see Gallese, 2003a, 2006; Gallese et al., 2004; Rizzolatti & Craighero, 2004; Rizzolatti et al., 2001, for reviews). During action execution/observation there is strong bilateral activation of ventral premotor (BA 6 and BA 44) and posterior

A03

A04

parietal (BA 40) areas, the likely human homologue of the monkey areas in which mirror neurons were originally described. The MNS in humans shows a coarse but consistent somatotopic organization, with distinct cortical regions in the premotor and posterior parietal cortices being activated by the observation/execution of mouth-, hand-, and foot-related acts (Aziz-Zadeh, Wilson, Rizzolatti, & Iacoboni, 2006; Buccino et al., 2001). It has also been shown that the MNS in humans is directly involved in imitation of simple movements (Iacoboni et al., 1999), in imitative learning of novel and complex motor skills (Buccino et al., 2004b), in perception of facial communicative actions (Buccino et al., 2004a), and in understanding the intentions of the actions of others (Iacoboni et al., 2005).

The relevance for social psychology of the discovery of the MNS should be apparent. Social interaction, interpersonal coordination and joint actions require the capacity to understand and anticipate partners' behavior. The MNS seems to provide the right neurofunctional substrate to all these capacities. Furthermore, many interesting phenomena described by social psychologists, like the "chameleon effect"—the unconscious mimicry by the observer of postures, expressions, and behaviors of her/his social partners (Chartrand & Bargh, 1999)—with the MNS can find a neurophysiological explanation.

## THE MNS AND ITS RELEVANCE IN THE EVOLUTION OF SOCIAL COGNITION

If the presence of mirror neurons in different species of primates such as macaques and humans seem to favor, on the one hand, a continuist view of the evolution of social cognition, it is also true that, on the other, the very same evidence must be reconciled with the diversity and uniqueness of human (social) cognition. This is a major topic for future research.

It is likely that monkeys use their MNS to optimize their social interactions, by making sense of their conspecifics' behavior. The evidence collected so far suggests that the MNS is sophisticated enough to enable its exploitation for different social purposes. This matching mechanism can indeed support social facilitation in monkeys. The observation and hearing of noisy eating actions facilitates eating behavior in pigtailed macaque monkeys (Ferrari, Maiolini, Addressi, Fogassi, & Visalberghi, 2005). Another

study shows that pigtailed macaque monkeys recognize when they are imitated by a human experimenter (Paukner, Anderson, Borelli, Visalberghi, & Ferrari, 2005). Pigtailed macaques look more at an experimenter imitating the monkeys' object-directed acts than at an experimenter manipulating an identical object but not imitating their actions. Since both experimenters acted in synchrony with the monkeys, the monkeys based their looking preference not on temporal contingency, but by tracking the structural components of the experimenters' actions by means of motor simulation.

It has been repeatedly argued that macaque monkeys are not capable of *motor* imitation. Recent evidence by Subiaul, Cantlon, Holloway, and Terrace (2005) suggests that they are capable of *cognitive* imitation. Furthermore, the study by Paukner et al. (2005) shows that when observing the actions of others macaque monkeys do entertain the capacity to discriminate between very similar goal-related acts on the basis of their degree of similarity with the goal-related acts the monkeys themselves have just executed. This capacity seems as cognitively sophisticated as motor imitation, because it implies that monkeys are capable of monitoring their own actions and relating them to the actions of others.

The apparent inability of nonhuman primates (chimps included) to understand others as intentional agents (see Povinelli & Eddy, 1996; see also Povinelli & Vonk, 2003), given the presence of the MNS in nonhuman primates, has led scholars to dispute and argue against a role of the MNS in providing "sufficient basis for agentive understanding" (see Pacherie & Dokic, 2006, p. 106), or as playing—by means of motor simulation—a major role in social cognition (Jacob & Jeanerod, 2004). The chimps' inability to understand others as intentional agents, however, turned out to be only apparent in particular cooperative contexts. In fact, there is evidence that chimps when engaged in a *competitive* setting do indeed deduce what others know on the basis of where they are looking (Hare et al., 2000; Tomasello, Carpenter, Call, Behne, & Moll, 2005).

Even more importantly, it has been recently shown that *rhesus monkeys* can establish a cognitive link between seeing and knowing, by systematically choosing to steal food from the human competitor that could not see the food, while refraining from doing it when the human competitor could see it (Flombaum & Santos, 2006). Similarly, it has been shown that rhesus

monkeys choose to obtain food silently only in situations in which silence is crucial to remain undetected by a human competitor (Santos, Nissen, & Ferrugia, 2006).

These results show that nonhuman primates—including macaques—possess the ability to deduce what others know about the world on the basis of ostensive behavioral cues, like the direction of gaze. To what extent this capacity depends on the MNS will require further investigations. However, it is clear that the so far misconceived and underrated social cognitive abilities of non-human primates cannot constitute an argument against the relevance of the MNS for social cognition.

Monkeys most likely do not explicitly attribute mental states to others as a causal explanation of others' behavior. Many posit that in order to do that one needs language. To thoroughly understand social cognition we must therefore investigate the neurofunctional mechanisms at the basis of the faculty of language. Before doing that, however, we should clarify what we refer to when we speak of language. Human language for most of its history has just been spoken language. This suggests that language most likely evolved from dialogic speech in order to provide individuals with a more powerful and flexible social cognitive tool to share, communicate and exchange knowledge.

In the next sections I propose to look at the experiential groundings of human linguistic competence and emphasize the tight connection between meaning and action. I then show how the functional mechanism supposedly describing the function of the MNS—embodied simulation—can also ground several aspects of language.

### **A “NEUROPHENOMENOLOGICAL” LOOK AT LANGUAGE FACULTY: ACTION, EXPERIENCE AND THEIR EXPRESSION**

Speech is comparable to a gesture because what it is charged with expressing will be in the same relation to it as the goal is to the gesture which intends it. (Merleau-Ponty, 1960/1964, p. 89)

The intimate nature of language and the evolutionary process producing it still remain somehow elusive. Such elusiveness is determined by the complexity and multidimensional nature of lan-

guage. What do we refer to when we investigate the language faculty and its evolution? Barrett et al. (in press) have recently—persuasively, in my opinion—argued that apparent cognitive complexity in the social domain emerges from the interaction of brain, body and world, rather than being a mere outcome of the level of intrinsic cognitive complexity that primate species possess.

Viewing social cognition as an embodied and situated enterprise (see Anderson, 2003; Barsalou, 1999; Barrett & Henzi, 2005; Clark, 1997; Gallese, 2003; Lakoff & Johnson, 1980, 1999; Niedenthal, Barsalou, Winkielman, Krauth-Gruber, & Ric, 2005) offers the possibility of a new neuroscientific approach to language. Let us see why and how by first briefly introducing the perspective of phenomenology, which provides stimulating perspectives on the nature and structure of human experience and its connection to language, by putting bodily action at the center of the stage. By following the phenomenological perspective we learn that language is a social enterprise in which action plays a crucial role.

A caveat first. I want to emphasize that neuroscience's goal is not to validate or confute philosophical theories. However, when neuroscience aims at understanding personal-level issues like language and meaning, it cannot escape a serious confrontation with a discipline like philosophy that puts these topics at the core of its investigation. By means of such multidisciplinary dialogue, neuroscience can contribute to the building of a new philosophy of nature.

Probably one of Husserlian phenomenology's greatest merits is to have pointed out that every form of consciousness is intentional, that is, *consciousness of something*, and to have stressed how cognitive forms of intentionality are rooted in the aboutness and relatedness to the world of our bodily actions. The facticity of human experience is even more within the focus of Martin Heidegger, with his notion of being-in-the-world (1927/1962) and his distancing from Husserl's transcendental idealism. According to Heidegger, being and world are to be seen as a unitary phenomenon, intrinsically and ontologically connected. This perspective substantially blurs distinctions between subject and object and between internal and external realms.

In Heidegger's perspective, animals and humans profoundly differ with respect to their relationship with the world. Only humans fully possess a world, because only human existence has a true historical dimension, which, in turn,

AQ2

AQ7

AQ6

depends on language (Heidegger, 1929/1995). According to Heidegger, language is meaningful because it reveals and discloses possibilities of contextual actions (1927/1962). Meaning emerges from a peculiar historical world to which humans are connected through their daily interactions with it (Heidegger, 1925/1985). Hence language is ontologically of practical nature. As underlined by Costa (2006), terms like “concepts” and “thoughts,” according to Heidegger, are to be understood as originating from our practical experience of the world. This is what Heidegger implies by claiming that meaning has its roots in the ontology of being-in-the-world (1927/1962). Being-in-the-world precedes reflection.

Our understanding of the meaning of a word like “table” does not stem from our use of a linguistic game, which, at best, can specify when to apply a given word as a tag to a given object in the world. The meaning of “table” stems from its use, from what we can do with it, that is, from the multiple and interrelated possibilities for action it evokes.<sup>1</sup>

Neuroscience today shows that the scientific investigation of the “Körper” (the brain–body system) can shed light on the “Leib” (the lived body of experience), as the latter is the lived expression of the former. The neurophysiological aspects of action did not interest philosophers like Husserl and Heidegger, also because of the too mechanistic views purported by neurobiology at the beginning of last century. The phenomenological approach, though, clearly shows that meaning does not inhabit a pre-given Platonic world of ideal and eternal truths to which mental representations connect and conform. Phenomenology thus entertains a perspective partly compatible with many empirical results of contemporary cognitive neuroscience: Meaning is the outcome of our situated interactions with the world.

With the advent of language, and even more with the “discovery” of written language, meaning is amplified as it frees itself from being dependent upon specific instantiations of actual experience. Language connects all possible actions within a network expanding the meaning of individual situated experiences. Language evokes the totality of possibilities for action the world puts upon us, and structures action within a web of related meanings. By endorsing this perspec-

tive, it follows that if we confine language to its sole predicative use, we reify a consistent part of language’s nature. Our understanding of linguistic expressions is not solely an epistemic attitude; it is a way of being. Our way of being, in turn, depends on what we act, how we do it, and how the world responds to us.

The relationship between language and body is also emphasized by Maurice Merleau-Ponty (1960/1964). According to Merleau-Ponty, signification arouses speech as the world arouses the body. For the speaking subject to express a meaning is to become fully aware of it. In other words, the signifying intention of the speaker can be conceived as a gap to be filled with words. When we speak, by means of the shared neural networks activated by embodied simulation, we experience the presence of others in ourselves and of ourselves in others. This mirroring likely helps in filling the gap.

A further contribution to clarifying the relationship between language, action and experience comes from Paul Ricoeur’s hermeneutic phenomenology. According to Ricoeur, language is first and foremost *discourse*, and therefore the “mimetic bond between the act of saying and effective action is never completely severed” (1986/1991, p. XIV). The hermeneutic development of phenomenology in Ricoeur’s approach connects intentionality to meaning: the logical sense of language must be grounded in the broader notion of meaning that is coextensive with the notion of intentionality (Ricoeur, 1986/1991, p. 40). In *From Text to Action* (1986/1991) Ricoeur builds upon the historical dichotomy introduced in linguistics by de Saussure (1973/1974) and by Hjelmslev (1959) between *langue* and *speech*, or between *schema* and *use*, respectively, and draws an important distinction between the formal language studied by structural linguistics and discourse, and in particular its original form, speech. According to Ricoeur discourse is seen as an event, taking place in time to a speaker who speaks about something. By means of discourse, language acquires a situated world. It is in discourse that all meanings are transferred, hence “... disco not only has a world but has an other, another person, an interlocutor to whom it is addressed” (Ricoeur, 1986/1991, p. 78).

The action-related account of language proposed by phenomenology and its intersubjective framing suggest that the neuroscientific investigation of what language is and how it works should

<sup>1</sup> It is worth noting how long it took before a similar perspective emerged in the field of cognitive psychology (see Gibson, 1979; Glenberg, 1997; see also Gallese, 2003c)

begin from the domain of action. This investigation has already produced remarkable findings. The MNS provides a matching mechanism that seems to play an important role in social cognition, thus it looks like a very good candidate also for grounding the social nature of language. In the next sections I show that when processing language humans, by means of embodied simulation, activate the motor system at the different levels at which traditionally language can be described.<sup>2</sup> The first level, defined as “embodied simulation at the vehicle level,” pertains to phono-articulatory aspects of language. The second level, defined as “embodied simulation at the content level,” concerns the semantic content of a word, verb, or proposition. Finally, the relationship between action simulation and syntax will be briefly addressed.

AQ8

### EMBODIED SIMULATION AT THE VEHICLE LEVEL

It is now ascertained that Broca’s region, formerly considered an exclusive speech-production area, contains neurons activated by the execution/observation/imitation of oro-facial gestures and of hand acts. This region is known to be part of the MNS (Bookheimer, 2002; Nishitani, Schürmann, Amunts, & Hari, 2005; Rizzolatti & Craighero, 2004). In an elegant transcranial magnetic stimulation (TMS) experiment, Fadiga, Craighero, Buccino, and Rizzolatti (2002) showed that listening to phonemes induces an increase of the amplitude of motor-evoked potentials (MEPs) recorded from the tongue muscles involved in their execution. This result was interpreted as a motor resonance mechanism at the phonological level. These findings have been complemented by a TMS study by Watkins, Strafella, and Paus (2003), who showed that listening to and viewing speech gestures enhanced the amplitude of MEPs recorded from lip muscles. A recent fMRI study demonstrated the activation of motor areas devoted to speech production during passive listening to phonemes (Wilson, Saygin, Sereno, & Iacoboni, 2004). Finally, Watkins and Paus (2004) showed that during auditory speech perception, the increased size of the MEPs obtained by TMS over the face area of the primary motor cortex correlated with

cerebral blood flow increase in Broca’s area. This suggests that the activation of the MNS for facial gestures in the premotor cortex facilitates the primary motor cortex output to facial muscles, as evoked by TMS.

Not only speech perception, but also covert speech production activates the motor system. McGuigan and Dollins (1989) showed with EMG that tongue and lip muscles are activated in covert speech in the same way as during overt speech. An fMRI study by Wildgruber, Ackermann, Klose, Kardatzki, and Grodd (1996) showed primary motor cortex activation during covert speech. Finally, a recent study by Aziz-Zadeh, Cattaneo, Rochat, and Rizzolatti (2005) showed covert speech arrest after transient inactivation with repetitive TMS of the left primary motor cortex and left premotor BA 44.

The presence in Broca’s region of both hand and mouth motor representations can not only cast some light on the evolution of language (Arbib, 2005; Corballis, 2002, 2004; Fadiga & Gallese, 1997; Gentilucci & Corballis, 2006; Rizzolatti & Arbib, 1998), but also on its ontogeny in humans. A tight relationship between the development of manual and oral motor skills has been repeatedly documented in children. Goldin-Meadow (1999) proposed that speech production and speech-related hand gestures could be considered as outputs of the same process. Canonical babbling in 6- to 8-month-old children is accompanied by rhythmic hand movements (Masakata, 2001). Hearing babies born to deaf parents display hand actions with a babbling-like rhythm. Manual gestures anticipate early development of speech in children, and reportedly predict later success up to the two-word level (Iverson & Goldin-Meadow, 2005).

AQ9

The same relationship between manual and oral language-related gestures persists in adulthood. Several works by Gentilucci and colleagues (Gentilucci, 2003; Gentilucci, Benuzzi, Gangitano, & Grimaldi, 2001; Gentilucci, Santunione, Roy, & Stefanini, 2004a; Gentilucci, Stefanini, Roy, & Santunione, 2004b) have shown a close relationship between speech production and the execution/observation of arm and hand gestures. In one of these studies, Gentilucci et al. (2004a) showed that the execution/observation of the action of bringing an object to the mouth activates a mouth articulation posture likely related to food manipulation, which selectively influences speech production. This suggests that the system involved in speech production shares

<sup>2</sup> To what extent these levels can be conceived as distinctly mapped in the brain is not so obvious yet.

(and may derive from) the neural premotor circuit involved in the control of hand/arm actions.

In another related study, Gentilucci et al. (2004b) showed that different observed actions influence lip shaping kinematics and voice formants of the observer. The observation of grasping influences the first formant, which is related to mouth opening, while the observation of bringing to the mouth influences the second formant of the voice spectrum, related to tongue position. All of these effects are greater in children than in adults. When observing hand grasping the observer activates the normally subsequent motor act, that is, mouth grasping. When observing bringing to the mouth, chewing is activated. This in turn affects speech production. As proposed by Gentilucci et al. (2004b), this mechanism may have facilitated the evolutionary shift from a primitive arm gesture communication system to speech. The phono-articulatory aspects of speech production, in principle as remote as possible from meaning, show unexpected connections with the execution/observation of socially meaningful arm motor acts.

In a very recent paper, Bernardis and Gentilucci (2006) showed that word and corresponding-in-meaning communicative arm gestures influence each other when they are simultaneously emitted. The second formant in the voice spectra is higher when the word is pronounced together with the gesture. No modification in the second formant is observed when executing a meaningless arm movement involving the same joints. Conversely, the second formant of a pseudo-word is not affected by the execution of meaningful arm gestures. The same effects occur when gestures are observed. In sum, spoken words and symbolic communicative gestures are coded as a single signal by a unique communication system within the premotor cortex.

The involvement of premotor Broca's area in translating the representations of communicative arm gestures into mouth articulation gestures was recently confirmed by transient inactivation of BA 44 with repetitive TMS (Gentilucci, Bernardis, Crisi, & Volta, 2007). Since BA 44 is part of the MNS, it is likely to posit that through embodied simulation the communicative meaning of gestures is fused with the articulation of sounds required to express it in words. It appears that within premotor BA 44, "vehicle" and "content" of social communication are tightly intercon-

nected. This is consistent with some tenets of "constructionist" approaches to language, according to which *all* levels of linguistic descriptions involve pairing of forms with semantic/discourse functions (Goldberg, 2003).

## EMBODIED SIMULATION AT THE CONTENT LEVEL

The meaning of a sentence, regardless of its content, has been classically considered to be understood by relying on symbolic, amodal mental representations (Fodor, 1998; Pylyshyn, 1984). An alternative hypothesis assumes that the understanding of language relies on "embodiment" (Barsalou, 1999; Gallese, 2003c; Gallese & Lakoff, 2005; Glenberg, 1997; Glenberg & Robertson, 2000; Lakoff, 1987; Lakoff & Johnson, 1980, 1999; Pulvermüller, 1999, 2002).

According to the embodiment theory, the neural structures presiding over action execution should also play a role in understanding the semantic content of the same actions when verbally described. Empirical evidence shows this to be the case. Glenberg and Kaschak (2002) asked participants to judge if a read sentence was sensible or nonsense by moving their hand to a button requiring movement away from the body (in one condition) or toward the body (in the other condition). Half of the sensible sentences described action toward the reader and half away from the reader. Readers responded faster to sentences describing actions whose direction was congruent with the required response movement. This clearly shows that action contributes to sentence comprehension.

The most surprising result of this study, though, was that the same interaction between sentence movement direction and response direction was also found with abstract sentences describing transfer of information from one person to another such as, "Liz told you the story" vs. "You told Liz the story." These latter results extend the role of action simulation to the understanding of sentences describing abstract situations. Similar consistent results were recently published by other authors (Borghi, Glenberg, & Kaschak, 2004; Matlock, 2004).

A prediction of the embodiment theory of language understanding is that when individuals listen to action-related sentences, their MNS should be modulated. The effect of this modulation should influence the excitability of the



primary motor cortex, henceforth the production of the movements it controls. To test this hypothesis we carried out two experiments (Buccino et al., 2005). In the first experiment, by means of single pulse TMS, either the hand or the foot/leg motor areas in the left hemisphere were 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. Motor evoked potentials (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, as were MEPs recorded from foot muscles by listening to foot-action-related sentences.

In the second behavioral experiment participants had to respond with the hand or the foot while listening to sentences expressing hand and foot actions, as compared to abstract sentences. Coherently with the results obtained with TMS, reaction times of the two effectors were specifically modulated by the effector-congruent heard sentences. These data show that processing sentences describing actions activates different sectors of the motor system, depending on the effector used in the listened action.<sup>3</sup>

Several brain-imaging studies have shown that processing linguistic material in order to retrieve its meaning activates regions of the motor system congruent with the processed semantic content. Hauk, Johnsrude, and Pulvermüller (2004) showed in an event-related fMRI study that silent reading of *words* referring to face, arm or leg actions (e.g., lick, pick, kick) led to the activation of different sectors of the premotor–motor areas controlling motor acts of the body congruent with the referential meaning of the read action words. Tettamanti et al. (2005) showed that listening to *sentences* expressing actions performed with the mouth, the hand and the foot, produces activation of different sectors of the premotor cortex, depending on the effector used in the action-related sentence listened to by participants. These activated premotor sectors correspond, albeit only coarsely, with those active during the observation of hand, mouth and foot actions (Buccino et al., 2001).

<sup>3</sup> A discussion of the facilitatory or inhibitory nature of the specific modulation of the motor system during language processing is beyond the scope of this article, and therefore will not be dealt with here.

These results have been recently replicated and expanded by Aziz-Zadeh et al. (2006), who showed in the same group of participants that the same cortical regions activated by action observation were also activated by the understanding of action-related sentences.

The MNS is involved not only in understanding visually presented actions, but also in mapping acoustically or visually presented action-related sentences. It must be added, though, that the precise functional relevance of the MNS and embodied simulation in the process of language understanding remains unclear. Their involvement might simply reflect motor imagery induced by the understanding process, which, in turn, might occur somewhere upstream, within the supposedly “real linguistic part of the brain,” whatever it might be. The study of the spatio-temporal dynamic of language processing becomes crucial in settling this issue. ERP experiments on silent reading of face-, arm- and leg-related words showed category-specific differential activations ~200 ms after word onset. Distributed source localization performed on stimulus-triggered ERPs showed different somatotopically arranged activation sources, with a strongest inferior frontal source for face-related words, and a maximal superior central source for leg-related words (Pulvermüller, Härle, & Hummel, 2000). This early differential activation can be hardly reconciled with the “late motor imagery” hypothesis, which is more consistent with the embodied simulation account of language understanding.

This dissociation in brain activity patterns supports the idea of stimulus-triggered early lexico-semantic processes taking place within the premotor cortex. Pulvermüller, Shtyrov, and Ilmoniemi (2003) used magnetoencephalography (MEG) to investigate the time course of cortical activation underlying the magnetic mismatch negativity elicited by hearing a spoken action-related word. The results showed that auditory areas of the left superior-temporal lobe became active 136 ms after the information in the acoustic input was sufficient for identifying the word, and activation of the left inferior-frontal cortex followed after an additional delay of 22 ms.

In sum, although these results are far from being conclusive on the relevance of embodied simulation of action for language understanding, they show that simulation is specific, automatic, and has a temporal dynamic compatible with such

a function.<sup>4</sup> It should be added that several neuropsychological studies testify that frontal lesions, including those of the premotor cortex, produce deficits in the comprehension of action verbs (Bak & Hodges, 2003; Bak, O'Donovan, Xuereb, Boniface, & Hodges, 2001; Bak et al., 2006; Kemmerer & Tranel, 2000, 2003).

We certainly need more research. More in-activation studies on healthy subjects and the careful neuropsychological study of patients with focal brain lesions will tell us more about the validity of this hypothesis.

## EMBODIED SIMULATION AND SYNTAX

In the previous sections I have reviewed evidence showing the involvement of motor cortical circuits in various aspects of social cognition, and in particular in the multi-level processing of language. We should now frame what has been discussed so far about action and language within an evolutionary perspective, and, in so doing, introduce syntax.

Hauser, Chomsky, and Fitch (2002) proposed to differentiate two domains within the language faculty: a “narrow language faculty” (NLF), encompassing aspects that are specific to language, and a “broad language faculty” (BLF), inclusive of more general cognitive functions not unique to humans, but shared with nonhuman animals. According to Hauser et al. (2002), at the core of NLF is “recursion,” a specifically human computational mechanism at the basis of language grammar, which, nevertheless, might have evolved for functions other than language. The merit of this proposal consists in its greater evolutionary plausibility when compared with alternative discontinuist views, like those positing a linguistic “big-bang” out of which full-blown human language supposedly emerged (Bickerton, 1995). Pinker and Jackendoff (2005), though critical of the “recursion-only hypothesis,” praised the merit of abandoning a monolithic view of language.

If language is the most distinctively human component of social cognition, and if embodied simulation is indeed crucial in social cognition,

<sup>4</sup> In the present paper I exclusively focus on action. Other studies, though, also show the involvement of the sensorimotor system in the mapping of other abstract domains, like the case of time mapped onto spatial metaphors (see Boroditsky, 2000; Boroditsky & Ramscar, 2002).

syntax appears to be an ideal benchmark to test the relevance for human social cognition of this mechanism and of its neural underpinnings, the MNS. Syntax is a basic ingredient of the NLF, as defined by Hauser et al. (2002). According to the modular approach to syntax, syntactic processing is typically operated by a serial parsing encapsulated system, in which the initial phase of processing has only access to information about syntax. According to Fodor (1983, p. 77), “... To show that [the syntactic] system is penetrable (hence informationally unencapsulated), you would have to show that its processes have access to information that is not specified at any of the levels of representation that the language input system computes.”

Recent studies, *pace* Fodor, show that the syntactic system *is* indeed penetrable. Syntactic ambiguities are evaluated using non-linguistic constraints like real-world properties of referential context (e.g., the actions an object affords). Humans continuously define linguistically relevant referential domains by evaluating sentence information against the situation-specific affordances. These affordances are not encoded as part of the linguistic representation of a word or phrase. Listeners use information like action goals to anticipate upcoming referents. A recent study by Chambers, Tanenhaus, and Magnuson (2004) showed that syntactic decisions about ambiguous sentences are affected by the number of referential candidates that can afford the action evoked by the verb in the unfolding sentence. Even a key component of the supposed NLF is intimately intertwined with action and its embodied simulation.

Is there any evidence about the involvement of the ventral premotor cortex in processing syntax? Several fMRI studies show a clear relationship between the premotor cortex and the mapping of sequential events. Schubotz and von Cramon (2004) contrasted the observation of biological hand actions with that of abstract motion (movements of geometric shapes). In both conditions 50% of the stimuli failed to attain the normally predictable end state. The task of participants was to indicate whether the actions were performed in a goal-directed manner or not, and whether the abstract motions were performed regularly or not. Results showed that both conditions elicited significant activation within the ventral premotor cortex. In addition, the prediction of biological actions also activated BA 44/45, which is part of the MNS. Schubotz and von Cramon (2004)

concluded that their findings point to a basic premotor contribution to the representation or processing of sequentially structured events.

The premotor cortex participation to the mapping of sequential events appears to be even more specifically related to language, as fMRI studies have shown selective activation of premotor BA 44 during syntactic processing of natural language, like when detecting grammatical errors (Embick, Marantz, Miyashita, O'Neil, & Sakai, 2000; Newman, Just, Keller, Roth, & Carpenter, 2003), as well as during the acquisition of artificial linguistic grammars characterized by long-distance, non-local syntactic dependencies (Musso et al., 2003; Tettamanti et al., 2002; see also Friederici, 2004).

According to a widely endorsed view in linguistics, the human language faculty is grounded in the unique ability to process hierarchically structured recursive sequences, configured as “phrase structure grammar” (PSG). The human species is capable of mastering PSG, while apparently other nonhuman primate species are confined to the use of much simpler “finite state grammars” (FSG; see Hauser et al., 2002; Hauser & Fitch, 2004). An fMRI study by Friederici, Bahlmann, Heim, Schubotz, and Anwander (2006) showed that the premotor sector of the inferior frontal gyrus is specifically activated during the processing of an artificial grammar bearing the PSG structure.

On the basis of all these results it seems plausible to hypothesize that “PSG” is the output of a cortical premotor network originally evolved to control/represent the hierarchical structure of goal-related action. When in the course of evolution selective pressures led to the emergence of language, the same neural circuits in charge of controlling the hierarchy of goal-related actions might have been “exploited” to serve the newly acquired function of language syntax. A similar functional overlap between action and language acquisition is indeed present during development: Children parallel their capacity to master hierarchical complexity both in the domain of language and goal-related action (Greenfield, 1991).

My hypothesis can be tested with brain-imaging experiments. The prediction is that premotor regions of the inferior frontal gyrus should be activated by tasks involving the processing of complex PSG-like hierarchical structures, both in the domain of action and language.

## THE “NEURAL EXPLOITATION HYPOTHESIS”

Let us now turn to the wider implications of the MNS and embodied simulation for social cognition, by formulating the “neural exploitation hypothesis.” My main claim is that key aspects of human social cognition are underpinned by neural exploitation, that is, by the adaptation of neural mechanisms originally evolved for sensorimotor integration, later on also employed to contribute to the neurofunctional architecture of thought and language, while retaining their original functions as well (Gallese & Lakoff, 2005; see also Gallese, 2003c, 2007).

The execution of any complex coordinated action makes use of *at least* two cortical sectors—the premotor cortex and the motor cortex, linked by reciprocal neural connections. The motor cortex to a large extent controls individual synergies—relatively simple movements like extending and flexing the fingers, turning the wrist, flexing and extending the elbow, etc. The role of the premotor cortex is more complex: structuring simple motor behaviors into coordinated motor acts. The premotor cortex must thus provide a “phase structure” to actions and specify the right parameter values in the right phases, e.g., by activating the appropriate clusters of cortico-spinal neurons in the appropriate temporal order. This information is conveyed through neural connections by the premotor cortex to specific regions of the primary motor cortex. Similarly, as exemplified by the MNS, the same premotor circuitry controlling action execution instantiates the embodied simulation of the observed actions of others.

There is therefore a “structuring” neurofunctional architecture within the premotor system that can function according to two modes of operation. In the first operation mode, documented by some of the empirical evidence reviewed here, the circuit structures action execution and action perception, imitation, and imagination, with neural connections to motor effectors and/or other sensory cortical areas. When the action is executed or imitated, the cortico-spinal pathway is activated, leading to the excitation of muscles and the ensuing movements. When the action is observed or imagined, its actual execution is inhibited. The cortical motor network is activated (though, not in all of its components), but action is not produced, it is only simulated.

In the second mode of operation, the same system is decoupled from its action execution/perception functions and can offer its structuring output to non-sensorimotor parts of the brain (Gallese & Lakoff, 2005; Lakoff & Johnson, 1999), among which the dorsal prefrontal cortex most likely plays a pivotal role. When engaged in the second mode of operation, the neurofunctional architecture of the premotor system might contribute to the mastering of the hierarchical structure of language and thought.<sup>5</sup> According to the neural exploitation hypothesis, the “words” of the premotor vocabulary (Rizzolatti et al., 1988) are not only assembled and chained to form intentional “action sentences” (see the discussion of the MNS and action intentions); they can also be assembled and chained to structure language sentences and thoughts.

I am fully aware that at present this is pure speculation. It is certainly possible that Broca’s region and the ventral premotor cortex are multifunctional, and that the functional overlap testified by the activation of the same premotor cortical sectors during both syntax-related linguistic and action-related non-linguistic tasks is only apparent because of the poor spatial resolution of the currently available brain-imaging technology (see Grodzinsky, 2005, for a critique of the link between syntax and the motor system). However, it must be stressed that the neural exploitation hypothesis has the merit of offering elements for the neurofunctional grounding of the systematic relation observed between syntax and the activation of premotor sectors of the frontal cortex. We certainly can’t be satisfied by merely stating that syntax resides in Broca’s region without explaining why, that is, without a clear understanding of what makes Broca’s region a “syntax-committed” cortical area.

To make things even more difficult, one should reconcile the hypothesis on the cognitive con-

tinuity of social cognition and the role played by the MNS in its evolution in primates, with the apparent *discontinuity* among primate species in their capacity for processing complex recursive structures. My tentative suggestion is that one important difference between humans and non-human primates could be the higher level of recursivity attained in our species—among other neural systems—by the premotor cortex, of which the MNS is part. By considering the evidence reviewed above, the premotor system is likely one of the most important brain regions where this evolutionary process might have taken place. The neural exploitation hypothesis posits that the increased computational power and degree of recursivity attained by the human brain—and in particular by the premotor cortex of which the MNS is part—might have produced a qualitative leap forward in the capacity to process recursive structures.

Is, however, the computational divide between humans and other primates the only explanation? Is the presence/absence of the computational resources enabling PSG the only explanation of the uniqueness of human language and cognition? Probably not. Further elements must be taken into account. The evolution of social cognition isn’t a monotonic function, strictly correlating the chronological position a species occupies in phylogeny with its level of social cognitive sophistication. For example, it has recently been reported that European starlings (*Sturnus vulgaris*) recognize acoustic patterns defined by a recursive, self-embedding, context-free grammar. They are also able to classify new patterns defined by the grammar while excluding agrammatical patterns. The authors of this study (Gentner, Fenn, Margoliash, & Nusbaum, 2006) concluded that the capacity to classify sequences from recursive, centre-embedded grammars is not uniquely human.

A further example shows that dogs exhibit social communicative skills in tasks in which apes fail, like finding food on the basis of human pointing or gaze cues (Hare & Tomasello, 2005). The specific quality of the social connectedness among individuals of different species, and among different individuals of the same species within particular contexts, bears consequences for the natural selection of specific social cognitive skills, and for their actual expression. These examples urge great caution when claims about the uniqueness of human social cognition are made. The fact that a given cognitive trait is uniquely expressed

<sup>5</sup> Establishing a relation between the motor system and the structure of language is by no means a new idea. Lashley (1951) and Marsden (1984), for example, proposed a link between syntax and the action sequencing function of the basal ganglia. A discussion of the role played in syntax by subcortical motor centers like basal ganglia and cerebellum and their thalamo-cortical connections to the premotor cortex is beyond the limited scope of this paper. However, it is perhaps worth noting that the present hypothesis is—at least partly—compatible with the procedural hypothesis of grammar proposed by Ullman (2001) according to which aspects of grammar are subserved by a frontal/basal-ganglia procedural memory system that also underlies cognitive and motor skills.

by one particular species doesn't necessarily imply the qualitative uniqueness of the neural mechanisms underpinning its expression.

## CONCLUSIONS

The social cognitive endowments of our species are likely the evolutionary outcome of the natural selection of mechanisms that were not mind reading specific. The neural exploitation hypothesis is parsimonious, because it postulates that the quantitative upgrading of pre-existing neurofunctional architecture can produce a qualitative evolution of different cognitive social skills, language included.

The MNS has been invoked to explain many different aspects of social cognition, like imitation (see Rizzolatti et al., 2001), action and intention understanding (see Rizzolatti, Fogassi, & Gallese, 2006), mind reading (see Gallese, 2007; Gallese & Goldman, 1998), empathy (see de Vignemont & Singer, 2006; Gallese, 2003a,b; Sommerville & Decety, 2006) and its relatedness to aesthetic experience (see Freedberg & Gallese, in press), and language (see Arbib, 2005; Gallese & Lakoff, 2005; Rizzolatti & Arbib, 1998). The posited importance of the discovery of mirror neurons for a better understanding of social cognition, together with a sort of mediatic overexposure and trivialization, have stirred resistance, criticism and even a sense of irritation in some quarters of the cognitive sciences.

I think a clarification is in order. The relevance of the MNS in so many different aspects of social cognition does not stem from a specific endowment of these neural cells, as if mirror neurons were "magical neurons," so to speak. Mirror neurons derive their property from the specific input-output connections they entertain with other populations of neurons in the brain.

The MNS is involved in so many aspects of social cognition because the activation of the multiple and parallel cortico-cortical circuits instantiating mirror properties underpins a fundamental aspect of social cognition, that is, the multilevel connectedness among individuals within a social group. Such connectedness finds its phylogenetic and ontogenetic roots in the social sharing of situated experiences of action and affect. The MNS provides the neural basis of such sharing. Embodied simulation and the MNS certainly cannot provide a full and thorough account of our sophisticated social cognitive

skills. However, I believe that the evidence presented here indicates that embodied mechanisms involving the activation of the motor system, of which the MNS is part, do play a major role in social cognition, language included. A second merit of this hypothesis is that it enables the grounding of social cognition into the experiential domain of existence, so heavily dependent on action (Gallese, 2007; Gallese et al., 2004).

To imbue words with meaning requires a fusion between the articulated sound of words and the shared meaning of the experience of action. Embodied simulation does exactly that. Furthermore, and most importantly, the neural exploitation hypothesis holds that embodied simulation and the MNS provide the means to share communicative intentions and meaning, thus granting the parity requirements of social communication.

By attributing to action the crucial role it plays in experientially grounding the meanings we share with others, the neural exploitation hypothesis stresses that the multi-level comparative study of the premotor system of primate brains is a *necessary* starting point for a better understanding of social cognition, and, more generally, for a better understanding of who we are.

Manuscript received 13 February 2007

Manuscript accepted 30 April 2007

First published online day/month/year

## REFERENCES

- Anderson, M. L. (2003). Embodied cognition: A field guide. *Artificial Intelligence*, *149*, 91–130.
- Arbib, M. A. (2005). From monkey-like action recognition to human language: an evolutionary framework for neurolinguistics. *Behavioral and Brain Sciences*, *28*, 105–168.
- Aziz-Zadeh, L., Cattaneo, L., Rochat, M., & Rizzolatti, G. (2005). Covert speech arrest induced by rTMS over both motor and nonmotor left hemisphere frontal sites. *Journal of Cognitive Neuroscience*, *17*, 928–938.
- Aziz-Zadeh, L., Wilson, S. M., Rizzolatti, G., & Iacoboni, M. (2006). Congruent embodied representations for visually presented actions and linguistic phrases describing actions. *Current Biology*, *16*, 1818–1823.
- Bak, T. H., & Hodges, J. R. (2003). "Kissing and dancing"—a test to distinguish the lexical and conceptual contributions to noun/verb and object/action dissociations: Preliminary results in patients with frontotemporal dementia. *Journal of Neurolinguistics*, *16*, 169–181.

- Bak, T. H., O'Donovan, D. G., Xuereb, J. H., Boniface, S., & Hodges, J. R. (2001). Selective impairment of verb processing associated with pathological changes in Brodmann areas 44 and 45 in the motor neurone disease-dementia-aplasia syndrome. *Brain*, *124*, 103–130.
- Bak, T. H., Yancopoulou, D., Nestor, P. J., Xuereb, J. H., Spillantini, M. G., Pulvermuller, F., et al. (2006). Clinical, imaging and pathological correlates of a hereditary deficit in verb and action processing. *Brain*, *129*, 321–332.
- Barrett, L., & Henzi, P. (2005). The social nature of primate cognition. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *272*, 1865–1875.
- AQ2** Barrett, L., Henzi, P., & Rendall, D. (in press). Social brains, simple minds: does social complexity really require cognitive complexity? *Proceedings of the Royal Society of London. Series B: Biological Sciences*.
- Barsalou, L. W. (1999). Perceptual symbol systems. *Behavioral Brain Science*, *22*, 577–609.
- Bernardis, P., & Gentilucci, M. (2006). Speech and gesture share the same communication system. *Neuropsychologia*, *44*, 178–190.
- Bickerton, D. (1995). *Language and human behavior*. Seattle, WA: University of Washington Press.
- Bookheimer, S. (2002). Functional MRI of language: New approaches to understanding the cortical organization of semantic processing. *Annual Review of Neuroscience*, *25*, 151–188.
- Borghi, A. M., Glenberg, A. M., & Kaschak, M. P. (2004). Putting words in perspective. *Memory and Cognition*, *32*, 863–873.
- Boroditsky, L. (2000). Metaphoric structuring: understanding time through spatial metaphors. *Cognition*, *75*, 1–28.
- Boroditsky, L., & Ramscar, M. (2002). The roles of body and mind in abstract thought. *Psychological Science*, *13*, 185–188.
- 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., Lui, F., Canessa, N., Patteri, I., Lagravinese, G., Benuzzi, F., et al. (2004a). Neural circuits involved in the recognition of actions performed by nonconspicuous: An fMRI study. *Journal of Cognitive Neuroscience*, *16*, 114–126.
- 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.
- Buccino, G., Vogt, S., Ritzl, A., Fink, G. R., Zilles, K., Freund, H.-J., et al. (2004b). Neural circuits underlying imitation learning of hand actions: an event-related fMRI study. *Neuron*, *42*, 323–334.
- Chambers, C. G., Tanenhaus, M. K., & Magnuson, J. S. (2004). Actions and affordances in syntactic ambiguity resolution. *Journal of Memory and Language*, *30*, 687–696.
- Chartrand, T. L., & Bargh, J. A. (1999). The chameleon effect: The perception-behavior link and social interaction. *Journal of Personality & Social Psychology*, *76*, 893–910.
- Clark, A. (1997). *Being there: Bringing brain, body, and world together again*. Cambridge, MA: MIT Press.
- Clark, H. H., & Wilkes-Gibbs, D. (1986). Referring as a collaborative process. *Cognition*, *22*, 1–39.
- Corballis, M. C. (2002). *From hand to mouth: The origins of language*. Princeton, NJ: Princeton University Press.
- Corballis, M. C. (2004). FOXP2 and the mirror system. *Trends in Cognitive Science*, *8*, 95–96.
- Costa, V. (2006). *Esperire e parlare. Interpretazione di Heidegger*. Milano, Italy: JACA Book.
- de Saussure, F. (1973/1974). *Course in general linguistics* (Trans. W. Baskins). London: Fontana/Collins.
- de Vignemont, F., & Singer, T. (2006). The emphatic brain: how, when, and why? *Trends in Cognitive Science*, *10*, 435–441.
- Embick, D., Marantz, A., Miyashita, Y., O'Neil, W., & Sakai, K. L. (2000). A syntactic specialization for Broca's area. *Proceedings of the National Academy of Sciences USA*, *97*, 6150–6154.
- 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., & Gallese, V. (1997). Action representation and language in the brain. *Theoretical Linguistics*, *23*, 267–280.
- 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.
- Ferrari, P. F., Maiolini, C., Addessi, E., Fogassi, L., & Visalberghi, E. (2005). The observation and hearing of eating actions activates motor programs related to eating in macaque monkeys. *Behav. Brain Res.*, *161*, 95–101.
- Flombaum, J. L., & Santos, L. R. (2006). Rhesus monkeys attribute perceptions to others. *Current Biology*, *15*, 447–452.
- Fodor, J. (1983). *The modularity of mind*. Cambridge, MA: MIT Press.
- Fodor, J. (1998). *Concepts*. Oxford, UK: Oxford University Press.
- Fogassi, L., Ferrari, P. F., Gesierich, B., Rozzi, S., Chersi, F., & Rizzolatti, G. (2005). Parietal lobe: From action organization to intention understanding. *Science*, *302*, 662–667.
- Freedberg, D., & Gallese, V. (in press). Motion, emotion and empathy in aesthetic experience. *Trends in Cognitive Science*.
- Friederici, A. D. (2004). Processing local transitions versus long-distance syntactic hierarchies. *Trends in Cognitive Science*, *8*, 245–247.
- Friederici, A. D., Bahlmann, J., Heim, S., Schubotz, R. I., & Anwander, A. (2006). The brain differentiates human and non-human grammars: functional localization and structural connectivity. *Proceedings of the National Academy of Sciences USA*, *103*, 2458–2463.

**AQ14****AQ13**

- Gallese, V. (2001). The “shared manifold” hypothesis: from mirror neurons to empathy. *Journal of Consciousness Studies*, 8(5–7), 33–50.
- Gallese, V. (2003a). The manifold nature of interpersonal relations: The quest for a common mechanism. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, 358, 517–528.
- Gallese, V. (2003b). The roots of empathy: The shared manifold hypothesis and the neural basis of inter-subjectivity. *Psychopathology*, 36(4), 171–180.
- Gallese, V. (2003c). A neuroscientific grasp of concepts: From control to representation. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, 358, 1231–1240.
- Gallese, V. (2005a). Embodied simulation: from neurons to phenomenal experience. *Phenomenology and the Cognitive Sciences*, 4, 23–48.
- Gallese, V. (2005b). “Being like me”: self–other identity, mirror neurons and empathy. In S. Hurley & N. Chater (Eds.), *Perspectives on imitation: From cognitive neuroscience to social science* (Vol. 1, pp. 101–118). Cambridge, MA: MIT Press.
- AQ14** Gallese, V. (2006). Intentional attunement: A neurophysiological perspective on social cognition and its disruption in autism. *Experimental Brain Res. Cog. Brain Res.*, 1079, 15–24.
- Gallese, V. (2007). Before and below theory of mind: Embodied simulation and the neural correlates of social cognition. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 362, 659–669.
- AQ15** Gallese, V., Eagle, M. N., & Migone, P. (2007). Intentional attunement: Mirror neurons and the neural underpinnings of interpersonal relations. *Journal of the American Psychoanalytic Association*, 55(1), 131–176.
- Gallese, V., Fadiga, L., Fogassi, L., & Rizzolatti, G. (1996). Action recognition in the premotor cortex. *Brain*, 119, 593–609.
- Gallese, V., Fogassi, L., Fadiga, L., & Rizzolatti, G. (2002). Action representation and the inferior parietal lobule. In W. Prinz & B. Hommel (Eds.), *Attention and performance XIX* (pp. 247–266). Oxford, UK: Oxford University Press.
- Gallese, V., & Goldman, A. (1998). Mirror neurons and the simulation theory of mind-reading. *Trends in Cognitive Science*, 12, 493–501.
- Gallese, V., Keysers, C., & Rizzolatti, G. (2004). A unifying view of the basis of social cognition. *Trends in Cognitive Science*, 8, 396–403.
- Gallese, V., & Lakoff, G. (2005). The brain’s concepts: The role of the sensorimotor system in reason and language. *Cognitive Neuropsychology*, 22, 455–479.
- AQ16** Gallese, V., & Umiltà, M. A. (2006). Cognitive continuity in primate social cognition. *Biological Theory*, 1, 25–30.
- Gentilucci, M. (2003). Grasp observation influences speech production. *European Journal of Neuroscience*, 17, 179–184.
- Gentilucci, M., Benuzzi, F., Gangitano, M., & Grimaldi, S. (2001). Grasp with hand and mouth: a kinematic study on healthy subjects. *Journal of Neurophysiology*, 86, 1685–1699.
- AQ10** Gentilucci, M., Bernardis, P., Crisi, G., & Volta, R. D. (2006). Repetitive transcranial magnetic stimulation of Broca’s area affects verbal responses to gesture observation. *Journal of Cognitive Neuroscience*, 18, 1059–1074.
- AQ14** Gentilucci, M., & Corballis, M. C. (2006). From manual gesture to speech: A gradual transition. *Neurosci Biobehav Rev.*, 30, 949–960.
- Gentilucci, M., Santunione, P., Roy, A. C., & Stefanini, S. (2004a). Execution and observation of bringing a fruit to the mouth affect syllable pronunciation. *European Journal of Neuroscience*, 19, 190–202.
- Gentilucci, M., Stefanini, S., Roy, A. C., & Santunione, P. (2004b). Action observation and speech production: study on children and adults. *Neuropsychologia*, 42, 1554–1567.
- Gentner, T. Q., Fenn, K. M., Margoliash, D., & Nusbaum, H. C. (2006). Recursive syntactic pattern learning by songbirds. *Nature*, 440, 1204–1207.
- Gibson, J. (1979). *The ecological approach to visual perception*. Hillsdale, NJ: Lawrence Erlbaum Associates, Inc.
- Glenberg, A. M. (1997). What memory is for. *Behavioral and Brain Sciences*, 20, 1–55.
- Glenberg, A. M., & Kaschak, M. P. (2002). Grounding language in action. *Psychonomic Bulletin & Review*, 9, 558–565.
- Glenberg, A. M., & Robertson, D. A. (2000). Symbol grounding and meaning: A comparison of high-dimensional and embodied theories of meaning. *Journal of Memory and Language*, 43, 379–401.
- Goldberg, A. E. (2003). Constructions: A new theoretical approach to language. *Trends in Cognitive Science*, 7, 219–224.
- Goldin-Meadow, S. (1999). The role of gesture in communication and thinking. *Trends in Cognitive Science*, 3, 419–429.
- Greenfield, P. M. (1991). Language, tools, and brain: The ontogeny and phylogeny of hierarchically organized sequential behavior. *Behavioral and Brain Sciences*, 14(4), 531–550.
- Grodzinsky, Y. (2006). The language faculty, Broca’s region, and the mirror system. *Cortex*, 42, 464–468.
- Hare, B., & Tomasello, M. (2005). Human-like social skills in dogs? *Trends in Cognitive Science*, 9, 439–444.
- Hauk, O., Johnsrude, I., & Pulvermüller, F. (2004). Somatotopic representation of action words in human motor and premotor cortex. *Neuron*, 41(2), 301–307.
- Hauser, M. D., Chomsky, N., & Fitch, W. T. (2002). The faculty of language: What is it, who has it, and how did it evolve? *Science*, 298, 1569–1579.
- Hauser, M. D., & Fitch, W. T. (2004). Computational constraints on syntactic processing in a non-human primate. *Science*, 303, 377–380.
- Heidegger, M. (1962). *Being and time* (Trans. J. Macquarrie & E. Robinson). New York: Harper & Row. (Originally published 1927)
- Heidegger, M. (1985). *History of the concept of time* (Trans. Theodore Kisiel). Bloomington, IN: Indiana University Press. (Originally published 1925)
- Heidegger, M. (1995). *The fundamental concepts of metaphysics. World, finitude, solitude* (Trans. W. McNeill & N. Walker). Bloomington, IN: Indiana University Press. (Originally published 1929)

- Hjelmslev, J. (1959). *Essais linguistiques*. Copenhagen, Denmark: Linguistic Circle of Copenhagen.
- Iacoboni, M., Molnar-Szakacs, I., Gallese, V., Buccino, G., Mazziotta, J., & Rizzolatti, G. (2005). Grasping the intentions of others with one's own mirror neuron system. *PLoS Biology*, 3, 529–535.
- Iacoboni, M., Woods, R. P., Brass, M., Bekkering, H., Mazziotta, J. C., & Rizzolatti, G. (1999). Cortical mechanisms of human imitation. *Science*, 286, 2526–2528.
- AQ14** Iverson, J. M., & Goldin-Meadow, S. (2005). Gesture paves the way for language development. *Psychol. Sci.*, 16, 367–371.
- Jacob, P., & Jeannerod, M. (2004). The motor theory of social cognition: a critique. *Trends in Cognitive Neuroscience*, 9, 21–25.
- Kemmerer, D., & Tranel, D. (2000). A double dissociation between linguistic and perceptual representations of spatial relationships. *Cognitive Neuropsychology*, 17, 393–414.
- Kemmerer, D., & Tranel, D. (2003). A double dissociation between the meanings of action verbs and locative prepositions. *Neurocase*, 9, 421–435.
- Knoblich, G., & Jordan, J. S. (2002). The mirror system and joint action. In M. I. Stamenov & V. Gallese (Eds.), *Mirror neurons and the evolution of brain and language* (pp. 115–124). Amsterdam: John Benjamins.
- Kohler, E., Keysers, C., Umiltà, M. A., Fogassi, L., Gallese, V., & Rizzolatti, G. (2002). Hearing sounds, understanding actions: Action representation in mirror neurons. *Science*, 297, 846–848.
- Lakoff, G. (1987). *Women, fire, and dangerous things: What categories reveal about the mind*. Chicago: University of Chicago Press.
- Lakoff, G., & Johnson, M. (1980). *Metaphors we live by*. Chicago: University of Chicago Press.
- Lakoff, G., & Johnson, M. (1999). *Philosophy in the flesh*. New York: Basic Books.
- Lashley, K. S. (1951). The problem of serial order in behavior. In L. A. Jeffress (Ed.), *Cerebral mechanisms in behavior* (pp. 112–146). New York: Wiley.
- Marsden, C. D. (1984). Which motor disorder in Parkinson's disease indicates the true motor function of the basal ganglia? In *Functions of the basal ganglia* (Ciba Foundation Symposium, 108, pp. 225–241). London: Pittman.
- AQ9** Masataka, N. (2001). Why early linguistic milestones are delayed in children with Williams syndrome: late onset of hand banging as a possible rate-limiting constraint on the emergence of canonical babbling. *Developmental Science*, 4, 158–164.
- Matlock, T. (2004). Fictive motion as cognitive simulation. *Memory and Cognition*, 32, 1389–1400.
- McGuigan, F. J., & Dollins, A. B. (1989). Patterns of covert speech behavior and phonetic coding. *Pavlovian Journal of Biological Science*, 24, 19–26.
- Musso, M., Moro, A., Glauche, V., Rijntjes, M., Reichenbach, J., Buchel, C., et al. (2003). Broca's area and the language instinct. *Nature Neuroscience*, 6, 774–781.
- Newman, S. D., Just, M. A., Keller, T. A., Roth, J., & Carpenter, P. A. (2003). Differential effects of syntactic and semantic processing on the subregions of Broca's area. *Cognitive Brain Research*, 16, 297–307.
- Niedenthal, P. M., Barsalou, L. W., Winkielman, P., Krauth-Gruber, S., & Ric, F. (2005). Embodiment in attitudes, social perception, and emotion. *Personality and Social Psychology Review*, 9, 184–211.
- Nishitani, N., Schurmann, M., Amunts, K., & Hari, R. (2005). Broca's region: From action to language. *Physiology*, 20, 60–69.
- Pacherie, E., & Dokic, J. (2006). From mirror neurons to joint action. *Cognitive Systems Research*, 7, 101–112.
- Paukner, A., Anderson, J. R., Borelli, E., Visalberghi, E., & Ferrari, P. F. (2005). Macaques (*Macaca nemestrina*) recognize when they are being imitated. *Biol. Lett.*, 1, 219–222.
- Pickering, M. J., & Garrod, S. (2004). Toward a mechanistic psychology of dialogue. *Behavioral Brain Science*, 27, 169–226.
- Pinker, S., & Jackendoff, R. (2005). The faculty of language: what's special about it? *Cognition*, 95, 201–236.
- Povinelli, D., & Vonk, J. (2003). Chimpanzee minds: Suspiciously human? *Trends in Cognitive Science*, 7, 157–160.
- Povinelli, D. J., & Eddy, T. J. (1996). What young chimpanzees know about seeing. *Monogr Soc Res Child Dev.*, 61, 1–152.
- Pulvermüller, F. (1999). Word in the brain's language. *Behavioral Brain Sciences*, 22, 253–336.
- Pulvermüller, F. (2002). *The neuroscience of language*. Cambridge, UK: Cambridge University Press.
- Pulvermüller, F., Härle, M., & Hummel, F. (2000). Neurophysiological distinction of verb categories. *Neuroreport*, 11, 2789–2793.
- Pulvermüller, F., Shtyrov, Y., & Ilmoniemi, R. J. (2003). Spatio-temporal patterns of neural language processing: an MEG study using minimum-norm current estimates. *NeuroImage*, 20, 1020–1025.
- Pylshyn, Z. W. (1984). *Computation and cognition: Toward a foundation for cognitive science*. Cambridge, MA: MIT Press.
- Ricouer, P. (1991). *From text to action. Essays in hermeneutics, II* (Trans. K. Blamey & J. B. Thompson). Evanston, IL: Northwestern University Press. (Originally published 1986)
- Rizzolatti, G., & Arbib, M. A. (1998). Language within our grasp. *Trends in Neuroscience*, 21, 188–194.
- Rizzolatti, G., Camarda, R., Fogassi, M., Gentilucci, M., Luppino, G., & Matelli, M. (1988). Functional organization of inferior area 6 in the macaque monkey: II. Area F5 and the control of distal movements. *Experimental Brain Research*, 71, 491–507.
- Rizzolatti, G., & Craighero, L. (2004). The mirror neuron system. *Annual Review of Neuroscience*, 27, 169–192.
- Rizzolatti, G., Fadiga, L., Gallese, V., & Fogassi, L. (1996). Premotor cortex and the recognition of motor actions. *Cognitive Brain Research*, 3, 131–141.
- Rizzolatti, G., Fogassi, L., & Gallese, V. (2001). Neurophysiological mechanisms underlying the understanding and imitation of action. *Nature Neuroscience Reviews*, 2, 661–670.



- Rizzolatti, G., Fogassi, L., & Gallese, V. (2006). Mirrors in the mind. *Scientific American*, 295(5), 54–61.
- Santos, L. R., Nissen, A. G., & Ferrugia, J. A. (2006). Rhesus monkeys, *Macaca mulatta*, know what others can and cannot hear. *Animal Behavior*, 71, 1175–1181.
- Schubotz, R. I., & von Cramon, D. Y. (2004). Sequences of abstract nonbiological stimuli share ventral pre-motor cortex with action observation and imagery. *Journal of Neuroscience*, 24, 5467–5474.
- AQ14** Sommerville, J. A., & Decety, J. (2006). Weaving the fabric of social interaction: articulating developmental psychology and cognitive neuroscience in the domain of motor cognition. *Psychon Bull Rev.*, 13, 179–200.
- Subiaul, F., Cantlon, J. F., Holloway, R. L., & Terrace, H. S. (2004). Cognitive imitation in rhesus macaque. *Science*, 305, 407–410.
- Tettamanti, M., Alkadhi, H., Moro, A., Perani, D., Kollias, S., & Weniger, D. (2002). Neural correlates for the acquisition of natural language syntax. *NeuroImage*, 17, 700–709.
- Tettamanti, M., Buccino, G., Saccuman, M. C., Gallese, V., Danna, M., Scifo, P., et al. (2005). Listening to action-related sentences activates fronto-parietal motor circuits. *Journal of Cognitive Neuroscience*, 17, 273–281.
- Tomasello, M., Carpenter, M., Call, J., Behne, T., & Moll, H. (2005). Understanding and sharing intentions: the origins of cultural cognition. *Behav Brain Sci.*, 28, 675–691.
- Ullman, M. T. (2001). A neurocognitive perspective on language: The declarative/procedural model. *Nature Reviews Neuroscience*, 2, 717–726.
- 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*, 32, 91–101.
- Watkins, K. E., & Paus, T. (2004). Modulation of motor excitability during speech perception: the role of Broca’s area. *Journal of Cognitive Neuroscience*, 16, 978–987.
- Watkins, K. E., Strafella, A. P., & Paus, T. (2003). Seeing and hearing speech excites the motor system involved in speech production. *Neuropsychologia*, 41(8), 989–994.
- Wildgruber, D., Ackermann, H., Klose, U., Kardatzki, B., & Grodd, W. (1996). Functional lateralization of speech production at primary motor cortex: An fMRI study. *Neuroreport*, 7, 2791–2795.
- Wilson, S. M., Saygin, A. P., Sereno, M. I., & Iacoboni, M. (2004). Listening to speech activates motor areas involved in speech production. *Nature Neuroscience*, 7, 701–702.

UNCORRECTED PROOF