Motor Cognition and Its Role in the Phylogeny and Ontogeny of Action Understanding

Vittorio Gallese, Magali Rochat,
and Giuseppe Cossu
University of Parma

Corrado Sinigaglia
University of Milan

Social life rests in large part on the capacity to understand the intentions behind the behavior of others. What are the origins of this capacity? How is one to construe its development in ontogenesis? By assuming that action understanding can be explained only in terms of the ability to read the minds of others—that is, to represent mental states—the traditional view claims that a sharp discontinuity occurs in both phylogeny and ontogeny. Over the last few years this view has been challenged by a number of ethological and psychological studies, as well as by several neurophysiological findings. In particular, the functional properties of the mirror neuron system and its direct matching mechanism indicate that action understanding may be primarily based on the motor cognition that underpins one's own capacity to act. This article aims to elaborate and motivate the pivotal role of such motor cognition, providing a biologically plausible and theoretically unitary account for the phylogeny and ontogeny of action understanding and also its impairment, as in the case of autistic spectrum disorder.

Keywords: action understanding, motor cognition, mirror neurons, autism, social cognition

Fundamental among social abilities is the capacity to accurately detect and understand the intentional conduct of others, to anticipate their upcoming actions, and to appropriately adjust one's own behavior. The phylogenetic origins of this capacity and its development in ontogenesis are matters of hot debate in both comparative and developmental psychology.

From an evolutionary perspective, the traditional view claims the existence of a sharp cognitive discontinuity between humans and nonhuman primates. Humans supposedly understand others by means of their capacity to *mind read*—that is, to attribute a causal role to internal mental states. All other animal species would be confined to the observable causal aspects of reality—that is, they would be basically just *behavior readers*. From an ontogenetic perspective, theories differ about how and when the supposed mind-reading ability emerges during infant cognitive development.

Recent findings in cognitive neuroscience shed light on the existence of a common neural mechanism that could account for action and intention understanding abilities in both humans and nonhuman primates. These findings have revealed that the motor cortex, long confined to the role of mere action programming and execution, in fact plays a crucial role in complex cognitive abilities such as the understanding of the intentions and goals of actions.

In the present article, we introduce a new notion of the phylogenetic and ontogenetic origin of action understanding that capitalizes upon the motor system. We call it the *motor cognition hypothesis*.[1] We posit that motor cognition provides both human and nonhuman primates with a direct, prereflexive understanding of biological actions that match their own action repertoire. Motor cognition finds its neural substrate in brain areas involved in matching action perception and action execution (the mirror neuron system [MNS]). A consequence of our hypothesis is that action understanding is tightly related to the motor expertise individuals acquire during their development.

The present article is exclusively focused on the role played by the motor system in the phylogeny and ontogeny of the understanding of action goals and intentions. We are aware that social cognition cannot be reduced to motor-based action understanding; however, the discussion of the crucial role played by emotions and affect in social cognition is beyond the scope of the present article.

We first consider the problem of social cognition from a broader phylogenetic perspective. Neuroscientific evidence relating to the existence and functions of a neural mechanism that underpins action understanding abilities in macaque monkeys and humans is introduced and discussed. Recent evidence about its development in ontogeny in humans is also reviewed and discussed. We then address evidence from research in developmental psychology on ontogenetic aspects of intentional understanding and relate this

[1] Our hypothesis is in line with the attribution of a crucial role played by the motor system in cognitive functions, originally put forward by Marc Jeannerod (1999, 2007) and Giacomo Rizzolatti (Rizzolatti et al., 1988, 2000) and further discussed by Decety and Grèzes (1999) and Gallese (2000), among others.

empirical evidence to the results of neuroscientific investigation. Finally, we introduce a new perspective on the origin of intentional understanding, the motor cognition hypothesis, and discuss its relevance for understanding autistic spectrum disorder (ASD).

The motor cognition hypothesis provides a radical alternative perspective to the mainstream view endorsed by classic cognitive science and by many who work on the philosophy of mind. This new perspective is more plausible from both an evolutionary and a neurobiological point of view, as it provides a neurophysiological groundwork for our understanding of how human social cognition may have evolved. Furthermore, the new perspective sheds light on the ontogeny of social cognition and its developmental derangement, as in ASD.

Social Cognition and Its Phylogenetic Bases

Just like humans, nonhuman primates are social beings living in highly cohesive groups. The basic requirement of primate group living is associated with a particularly sharp sensitivity to subtle social cues (Humphrey, 1976), such as visual (Dasser, 1988; Humphrey, 1974) and acoustic (Snowdon, 1986) discrimination of others. Following Dunbar (1992), who posited that the development of sophisticated cognitive skills resulted from the pressure of the social group's increased complexity, we argue that nonhuman primates exhibit several complex social behaviors, such as gaze following, deception, and reconciliation, that are apparently very similar to human behavior.

Others have argued that the main difference between human and nonhuman primates' social cognition is the degree of intentional understanding—that is, what causes a goal-directed action. According to a mainstream view, humans have the unique ability to go below the behavior's surface, to infer mental states such as intentions, beliefs, and desires that might drive the current or future agents' behavior (Povinelli & Eddy, 1996; Tomasello & Call, 1997), whereas nonhuman primates' knowledge is thought to rely on the extraction of procedural rules from observable environmental regularities (W. Köhler, 1927; Povinelli, 2000; Visalberghi & Tomasello, 1998). Tomasello and Call (1997), initially echoing the position of Povinelli and Eddy (1996), proposed that nonhuman primates basically learn to understand and predict an imminent action by learning to associate given antecedent behaviors with particular consequences in recurrent contextual situations. Povinelli and Giambrone (2001) claimed that even if both human and nonhuman primates are endowed with a common system for processing the intentional structure of action by detecting the statistical regularities of others' behavior, this ability neither precedes nor scaffolds the uniquely human capacity to conceive and reason about intentions as mental states.

In our account, the main problem with this view stems from the fact that mind reading is taken as the sole and primary way to achieve intentional understanding. Our point is that in both phylogeny and ontogeny, before and below this metarepresentational ability is motor cognition. In fact, the traditional conception of nonhuman primates as mere behavior readers, essentially unable to interpret movements in terms of intentional actions, has been challenged recently. Chimps' inability to understand others' behavior as intentional is only apparent when tested in cooperative contexts. When chimps are engaged in competitive settings, they can understand what others know on the basis of where they are

looking (Hare, Call, Agnetta, & Tomasello, 2000; Tomasello, Carpenter, Call, Behne, & Moll, 2005). Furthermore, Call, Hare, Carpenter, and Tomasello (2004) reported that chimpanzees succeed in discriminating between an intentionally teasing action and an unintentionally clumsy one performed by a human. Of the utmost importance, it has been shown that rhesus monkeys can establish a cognitive link between seeing and knowing; they systematically chose to steal food from the human competitor who could not see the food, while refraining from doing so when the human competitor could see it (Flombaum & Santos, 2005). Similarly, rhesus monkeys seek to harvest food silently only in situations in which silence is crucial for remaining undetected by a human competitor (Santos, Nissen, & Ferrugia, 2006).

All of these experiments reveal that nonhuman primates—probably even rhesus macaques—are endowed with the ability to understand the intentional meaning of others' behavior by relying on visible behavioral cues. These data do not demonstrate that nonhuman primates entertain metarepresentations of intentions, but rather that they might directly understand others' behavior as intentional by detecting the intrinsic goal relatedness upon which motor behavior is organized and mapped. These studies, therefore, strongly challenge the traditional dichotomous account of primate social cognition based on a sharp evolutionary discontinuity between behavior readers (nonhuman primates) and mind readers (humans) (Gallese, 2007; Gallese & Umiltà, 2006). Apparent cognitive complexity in the social domain emerges from the interaction of brain, body, and world, rather than being a mere consequence of the level of intrinsic cognitive complexity that a primate species possesses (Barrett, Henzi, & Rendall, 2007).

Neuroscientific investigations have recently revealed in both monkeys and humans the neural mechanism underlying the capacity for understanding the actions of others. This issue is the focus of the next sections.

The MNS for Actions in Monkeys

Studies of single neuron recording in the ventral premotor cortex (area F5) of macaque monkeys have revealed the existence of a class of motor neurons, the *mirror neurons*, that discharge during both the execution and the observation of goal-directed motor acts (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996). Further experiments revealed neurons with similar motor act observation- and execution-matching properties in sectors of the inferior parietal lobule (PF/PFG mirror neurons; see Fogassi et al., 2005; Gallese, Fogassi, Fadiga, & Rizzolatti, 2002; Rizzolatti & Craighero, 2004), reciprocally connected with area F5 (Petrides & Pandya, 1984; Rizzolatti & Luppino, 2001; Rizzolatti, Luppino, & Matelli, 1998). The relevance of these findings stems from the fact that, for the first time, a neural mechanism allowing direct matching between the sensory (visual and/or auditory) perception and the motor execution of a motor act had been identified. This matching system provides a parsimonious solution to the problem of translating the results of the visual analysis of an observed movement—in principle, devoid of meaning for the observer—into something that the observer is able to understand to the extent that it refers to his or her own motor knowledge. It has been proposed that the MNS, by matching observed, implied (Umiltà et al., 2001), or heard (E. Kohler et al., 2002) goal-directed motor acts onto their motor

representation in the observer's motor system, allows a direct form of action understanding (Gallese et al., 1996; Rizzolatti et al., 1996; Rizzolatti & Gallese, 1997) through a mechanism of embodied simulation (Gallese, 2001, 2003a, 2003b, 2006, 2007).

A major step forward in research on the MNS was the discovery that parietal mirror neurons, besides coding the goal of a single executed or observed motor act like grasping an object, code the overall action intention as well (e.g., bringing the grasped object to the mouth or into a container; Fogassi et al., 2005). For the sake of clarity, we define motor acts here as goal-related series of movements. Motor goal relatedness is a necessary and sufficient condition for characterizing a series of movements as having the status of a motor act and being identifiable as a specific motor act. Motor acts are chained together to display a motor intention, which is constituted by a specific motor goal hierarchy (e.g., grasping to bring to the mouth vs. grasping to throw). The MNS maps integrated sequences of goal-directed motor acts (grasping, holding, bringing, placing—defined as the different "words" of a motor "vocabulary"; see Rizzolatti et al., 1988; Rizzolatti, Fogassi, & Gallese, 2000), clustering them into syntactically separate and parallel intentional "action sentences." This motor syntax generates hierarchically clustered, temporally chained sequences of motor acts properly assembled to accomplish more distal goal states. The motor vocabulary of grasping-related neurons is syntactically reorganized by a specific sequential chaining tailored to map the fulfillment of the action intention. The overall action intention (to eat, to hide the food or object, etc.) is the goal state of the larger chain of goal-related motor acts.

These results seem to suggest, at least at a basic level, that the core intention of eating or placing food in the mouth is also coded by parietal mirror neurons. Needless to say, this does not imply that monkeys explicitly represent intentions as such.

The MNS for Actions in Humans

Neurophysiological and brain-imaging studies have provided indirect evidence for the existence of a similar MNS involving homologous cortical areas in the human brain (for a review, see Gallese, Keysers & Rizzolatti, 2004; Rizzolatti & Craighero, 2004). Several fMRI studies have demonstrated that the observation of actions activates the lower part of the precentral gyrus plus the posterior part of the inferior frontal gyrus and the rostral part of the inferior parietal lobule, brain regions described as "forming the core of human mirror system" (Rizzolatti & Craighero, 2004, p. 176). Diamond (2006) proposed that the MNS probably would not be exclusively in premotor areas, but would also be in a border region that spans the anterior premotor cortex and posterior lateral prefrontal cortex. According to Diamond, this region would be critical for deducing abstract rules about how physically separate things might be conceptually related. Even though such a thesis could be in principle appealing, we believe that the shift from motor goals and intentions to abstract rules is beyond the functional properties of the MNS, at least on the basis of the currently available evidence.

Buccino et al. (2001) has demonstrated that the MNS is somatotopically organized. The same regions within premotor and posterior parietal cortices that are normally active when humans execute mouth-, hand-, and foot-related acts are also activated when we observe the same motor acts executed by others.

It is interesting that several brain-imaging studies have shown that the intensity of MNS activation during action observation depends on the similarity between the observed actions and the participants' action repertoire (Buccino, Lui, et al., 2004; Calvo-Merino, Glaser, Grèzes, Passingham, & Haggard, 2005; Calvo-Merino, Grèzes, Glaser, Passingham, & Haggard, 2006). The MNS in humans is directly involved in the imitation of simple movements (Iacoboni et al., 1999), the imitation learning of complex skills (Buccino, Vogt, et al., 2004), the perception of communicative actions (Buccino, Lui, et al., 2004), and the detection of action intentions (Iacoboni et al., 2005).

In the Iacoboni et al. (2005) study, participants witnessed three kinds of videos portraying grasping hand actions without a context, the context only (a scene containing objects), and grasping hand actions embedded in contexts. In the third condition, the context suggested the intention associated with the grasping action (either drinking or cleaning up). Actions embedded in contexts, compared with the other two conditions, yielded a significant signal increase in the posterior part of the inferior frontal gyrus and the adjacent sector of the ventral premotor cortex where hand actions are represented. Thus, premotor mirror areas—areas active during the execution and the observation of motor acts—that were previously thought to be involved only in action recognition are actually involved in understanding the "why" of action—that is, the intention behind it.

Another result from the study by Iacoboni et al. (2005) lends further support to the motor hypothesis of intentional understanding. After the scanning session, all participants were debriefed about the actions they had witnessed. Independent of whether they were explicitly instructed to determine the intention of the observed actions of others or not, participants all correctly identified the action intentions of others. It is important that the different instructions given to the two groups did not affect the activation of premotor mirror areas. This means that, at least for simple actions, detection of intentions occurs by default and is underpinned by the mandatory activation of an embodied simulation mechanism (Gallese, 2005, 2006, 2007).

The results of Iacoboni et al. (2005) suggest that most of the time, at least at the level of simple intentional actions, even humans may not explicitly represent intentions as such when understanding them in others. Action intentions are not just propositional constructs. They are embedded within the intrinsic intentionality of action, its intrinsic relatedness to an end state, a goal. By means of embodied simulation, when witnessing others' behavior, their intentions can be directly grasped without the need of representing them in propositional form.[2]

The Ontogeny of the MNS

One crucial issue not yet clarified is how the MNS develops in ontogeny. To what extent is the mirroring mechanism described in this article innate, and how is it shaped and modeled during development? The answer to these questions is that we simply do not yet know.

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[2] For a discussion of the role of the mirror neuron mechanism and embodied simulation in actual mentalizing processes, see Gallese (2007) and Sinigaglia (in press).

As Claes von Hofsten (2007) recently wrote, early in life cognition is anchored to action at an interindividual level. From a functional perspective, cognitive development has to do with expanding the prospective control of actions. We know that motor skills mature much earlier and continue their development far longer than previously thought (Diamond, 2000). Compelling evidence shows that neonates are able to visually control their hand movements. For example, von Hofsten (1982) demonstrated that the newborn is endowed with a rudimentary form of eye–hand coordination. Van der Meer (1997) showed that newborns can purposely control their arm movements to meet external demands and that the development of visual control of arm movement is under way soon after birth. Even more interesting, recent evidence shows that hand motor control is remarkably sophisticated well before birth. Zoia et al. (2007) measured the kinematics of fetal hand movements. The results showed that the spatial and temporal characteristics of fetal movements were by no means uncoordinated or unpatterned. By the 22nd week of gestation, fetal hand movements show kinematic patterns that depend on the goal of the different motor acts fetuses perform. These results led Zoia et al. (2007) to argue that 22-week-old fetuses show a surprisingly advanced level of motor planning already compatible with the execution of intentional actions.

Should these findings be further confirmed and extended, one might speculate that during prenatal development specific connections may develop between the motor centers controlling mouth and hand goal-directed behaviors and brain regions that will become the recipients of visual input after birth (see also Anokhin's [1964] seminal insights on systemogenesis). Such connectivity could provide functional templates (e.g., specific spatiotemporal patterns of neural firing) to areas of the brain that, once reached by visual information, would be ready to specifically respond to the observation of biological motion like hand or facial gestures. In other words, neonates and infants, by means of specific connectivity developed during the late phase of gestation between motor and "to-become-visual" regions of the brain, would be ready to imitate the gestures they see performed by adult caregivers and would be endowed with the neural resources that enable rich interpersonal behaviors like turn taking, protoconversations, affective attunement, and the like, which characterize our postnatal life from its very beginning. This hypothesis could be empirically tested by having neonates engage in mouth and/or hand motor activity when blindfolded. The prediction is that such motor activity would induce activation of posterior visual areas.

The earliest indirect evidence available to date of an MNS in infants comes from a study by Shimada and Hiraki (2006) that demonstrated by means of near infrared spectroscopy the presence of an action execution and observation matching system in 6-month-old human infants. It is interesting that this study showed that the sensory–motor cortex of infants (but not that of adult participants) was also activated during the observation of a moving object on a TV screen. These findings suggest that during the early developmental stages, even nonbiological moving objects are anthropomorphized by being mapped onto motor representations pertinent to the observers' acquired motor skills.

It can be hypothesized that an innate rudimentary MNS is already present at birth, which can then be flexibly modulated by motor experience and gradually enriched by visuomotor learning. Indeed, such a system could be an ideal candidate for the neural underpinning of neonatal facial imitation, originally described in humans by Meltzoff and Moore (1977) and subsequently described in chimpanzees (Myowa-Yamakoshi, Tomonaga, Tanaka, & Matsuzawa, 2004) and macaque monkeys (Ferrari et al., 2006). Furthermore, it has been shown that congenitally limb-deficient human adults activate the MNS when entertaining phantom limb movement sensations (Brugger, Kollias, Muri, Crelier, & Hepp-Reymond, 2000) or when viewing limb movements performed by others (Gazzola et al., 2007). As recently proposed by Lepage and Théoret (2007), the development of the MNS can be conceptualized as a process whereby the child learns to refrain from acting out the automatic matching mechanism that links action perception and execution. Such development could be viewed as a process leading from mandatory reenactment to a covert simulation of the observed motor acts, most likely through the maturation of prefrontal inhibiting mechanisms.

The Ontogenesis of Action and Intention Understanding

The ability to attribute mental states to others has been explained by some authors by introducing the notion of a theory of mind module (ToM; Premack & Woodruff, 1978). This ability has been thought to develop gradually during the first 3–5 years of life, grounded on some ToM precursor abilities such as joint attention and understanding the meaning of gaze direction. ToM is considered to be full-blown when infants pass the false-belief task (Baron-Cohen, Leslie, & Frith, 1985)—that is, when they understand that others' behavior is driven by their own representation of the world and that such representation might not accurately reflect reality or might be different from their own (Baron-Cohen et al., 1985; Wimmer and Perner, 1983).

It is noteworthy that according to those standard cognitive tests, a mature ToM coincides with the emergence of relatively advanced linguistic competence. Indeed, authors like Hauser, Chomsky, and Fitch (2002) have stated that recursivity constitutes the core principle underlying both language grammar and metarepresentation. In line with this view, Karmiloff-Smith (1992) and Ruffman, Slade, Rowlandson, Rumsey, and Granham (2003) have argued that in providing reflective thinking, language enables representations about mental states. Studies of deaf children suggest a correlation between delayed language (American Sign Language) acquisition and delayed understanding of false beliefs (de Villiers, 2003, 2005).

The issue of whether the ability to reason about other minds could precede the maturation of language skills or even be present in nonverbal species has been addressed by a series of developmental and comparative psychology studies. For example, the looking time experiment of Onishi and Baillargeon (2005) seems to indicate a covert ability of 15-month-old infants to predict an actor's behavior on the basis of his or her true or false beliefs. Southgate, Senju, and Csibra (2007) showed that 25-month-old infants correctly anticipate an actor's actions even when those actions can be predicted only by attributing a false belief to the actor. Furthermore, Warneken and Tomasello (2006) showed that 18-month-old infants understand others' goals and help others to achieve them in a variety of different situations.

These studies suggest that infants display sophisticated social cognitive abilities well before they develop sophisticated language abilities. However, what most concerns us here is the fact that

infants are able to understand goal-related actions already during the first year of life without relying on either language or full-blown metarepresentational abilities (Hamlin, Wynn, & Bloom, 2007; Tomasello and Haberl, 2003). In fact, there is wide agreement that the ability to detect action goals during the first year of life does not involve mentalizing (i.e., any form of attribution of propositional attitudes, such as beliefs and desires). In spite of this consensus (for a different proposal, see Kuhlmeier, Wynn, & Bloom, 2003), the mechanism thought to be at the basis of this kind of nonmentalistic action understanding is still an object of controversy.

According to some theorists, specialized developmental mechanisms that are in place at birth (Baron-Cohen, 1994; Leslie, 1994; Premack, 1990) allow infants to interpret actions as goal directed very early in life. Innate sensitivity to ostensive behavioral cues like animacy, self-propelled motion, temporal contingency, and equifinal variations of action would enable infants to ascribe goal directedness to the actions of a wide range of entities, largely encompassing their experience-related knowledge.

Gergely and Csibra's teleological stance hypothesis (Csibra, Birò, Koòs, & Gergely, 2003; Csibra, Gergely, Birò, Koòs, & Brockbank, 1999; Gergely, Nàdasdy, Csibra, & Bìrò, 1995) posits that by 9 months of age, infants are capable of a "normative evaluation of actions based on the principle of rational action" (Csibra & Gergely, 2007, p. 70). This allows infants to construe an action in terms of its goal directedness when the agent reaches the goal through the most efficient means, given the contextual constraints. The authors argue that this inference is based on the observed action or action sequence, the goal, and the current situational constraints without requiring any mentalizing. The presence of the rationality principle scaffolds the further development of an intentional or mentalistic stance when infants' cognition becomes sufficiently flexible to represent fictional and counterfactual states (Csibra et al., 2003).

Another theoretical view in developmental psychology stresses the intrinsic link between action understanding and experience. Following Piaget (1953), some scholars emphasize the constructional effect of observational and self-agentive experience on infants' understanding of the goals of actions (Sommerville & Woodward, 2005). In particular, infant research employing habituation–dishabituation paradigms have shown that: (a) Infants are sensitive to the action goals of others even at 3 months of age, but only when facilitated by previous motor experience (Sommerville, Woodward, & Needham, 2005); (b) 10-month-old infants identify the goal of action sequences to the extent that they can perform them (Sommerville & Woodward, 2005); and (c) 6-month-old infants are sensitive to the action goals of others only when performed by a human agent (Woodward, 1998). In addition, it has been recently shown that infants produce proactive goal-directed eye movements when observing a goal-directed placing action only to the extent they can perform it (Falck-Ytter, Gredeback, & von Hofsten, 2006).

Meltzoff (1988, 1995) proposed that human infants are endowed with the ability to detect cross-modal equivalences between their own sensory experiences and the actions of others. The recognition of postures and patterns of movement leads to the apprehension that others are intentional agents like the self. According to Meltzoff (2007a, 2007b), the equivalence between self and others allows bidirectional learning to occur in which infants understand others' acts through their own motor experience and can vicariously learn the consequences of a new action by seeing it executed by another person.

We believe that the results of Sommerville and Woodward (2005) and Falck-Ytter et al. (2006), as well as Meltzoff's viewpoint, suggest that in the case of specific goal-related interactions (such as hand–object interactions typical for reaching and grasping), it is simpler and more plausible to construe infants' understanding of intentions in terms of their own motor knowledge than to call on a pure-reason-based inferential system such as that assumed by Gergely and Csibra's teleological stance hypothesis. Rather, they suggest that the rationality principle that rules the teleological interpretation of action constrains the intentional attribution of infants to the most efficient of the possible motor behaviors in a given situation, thus identifying goal relatedness with efficacy. This may be useful in cases where the goal relatedness of the observed movement can be measured only in terms of "the shortest path" or "shortest time." However, in the case of motor acts such as reaching and grasping, goal relatedness cannot be reduced to mere physical (e.g., kinematic) efficacy, because it presupposes specific modalities of hand–mouth object interaction.

A very recent looking-time study with rhesus macaques, carried out with the same experimental paradigm used by Gergely and Csibra with human infants, has shown that the tested animals were able to detect the efficacy of the observed hand motor act only when the act belonged in their motor repertoire or was at least compatible with their motor expertise (Rochat, Serra, Fadiga, & Gallese, 2008; see also Wood, Glynn, & Hauser, 2008). These results provide the first evidence for the presence through phylogeny of the ability to evaluate the contextual adequacy of an action directed to a particular motor goal. As primates situated at a lower level of the evolutionary scale seem to skillfully evaluate only observed motor acts that they can actually perform themselves, it may be proposed that a basic form of action evaluation and understanding relies on the visuomotor matching mechanism typical of mirror neurons.

Moreover, the discovery that goal relatedness is the functional organizing principle of primates' motor systems provides a neurophysiological counterpart to the above-mentioned psychological findings, lending support to a motor account of the development of intentional understanding.

The Motor Cognition Hypothesis

The mainstream view on action and intention understanding holds that humans, when understanding others, start from the observation of behaviors and biological motion whose intentions are quite opaque without rather elaborate inferential reasoning and which thus have to be interpreted and explained in mental terms. This explanatory process is referred to as mind reading—that is, the attribution to others of internal mental states, mapped in the mind of the observer as internal representations in propositional format. These representations supposedly play a causal role in determining how the observed behavior is to be understood.

We challenge this purely mentalistic view of intersubjectivity. We posit that what forms the basis of our capacity (and the capacity of nonhuman primates) to understand the intentions behind others' behavior is a more basic functional mechanism that exploits the intrinsic functional organization of the motor system.

Indeed, the motor system in primates is organized in terms of goal-directed motor acts (e.g., series of movements directed to a particular goal, like grasping, tearing, or manipulating an object) and not in terms of movements (e.g., variation of the articulation position with no specific goal; see Rizzolatti et al., 1988, 2000). Goal-directed motor acts are the nuclear building blocks around which action is produced, perceived, and understood.

Primates constantly use their distal effectors—for example, their hands and mouth—to explore, exploit, modify, know about, and to various degrees communicate about the external world. Neuroscientific investigation during the last few decades has shed light on the neurophysiological mechanisms underpinning such abilities and in particular on the cortical neural circuits controlling grasping and manipulative behaviors. In primates, a central role in grasping is played by a circuit formed by the inferior parietal lobule (area AIP in particular) and the inferior part of the ventral premotor cortex (area F5). This last area sends its output to the hand field of the primary motor cortex (F1/M1). Some neurons in F5 discharge when the monkey grasps an object using different effectors—for example the right hand, the left hand, or the mouth. On the basis of this finding, it has been suggested that these neurons code the goal of the motor act of grasping (Rizzolatti et al., 1988, 2000).

A formal, quantitative testing of this proposal was recently carried out by Umiltà et al. (2008), in which hand-related neurons were recorded from premotor area F5 and primary motor cortex (area F1) in monkeys trained to grasp objects using two different tools: normal pliers and "reverse pliers." These tools require opposite movements to grasp an object: With normal pliers the hand has to first open and then close, as when grasping with the bare hand, whereas with reverse pliers the hand has to first close and then open. The use of the two tools enabled researchers to dissociate the neural activity related to hand movement per se from that related to the goal of the motor act.

All recorded neurons in area F5 and half of the neurons recorded from the primary motor cortex discharged in relation to accomplishing the goal of grasping (i.e., when the tool closed on the object), regardless of whether in this phase the hand was opened or closed—that is, regardless of the movements employed to accomplish the goal. The data of Umiltà et al. (2008) indicate that goal coding is at the basis of the organization of grasping (and presumably other motor acts) in area F5 and even to a minor extent in the primary motor cortex. Goal coding is not an abstract, merely mentalistic property. Goal coding appears to be a distinctive functional feature upon which the cortical motor system of nonhuman (and human) primates is organized. Furthermore, in the same study it was shown that when F5 mirror neurons discharge, the goal of the motor act is specified both when they are activated during action execution and when they discharge in response to an observed action. The findings of Umiltà et al. (2008) strongly corroborate the hypothesis that the activation of the MNS is not the result of top-down action and intention understanding, which according to a mainstream view would supposedly occur upstream from the motor system (Goldman, 2006). The activation of the MNS is intrinsically constitutive of action and intention understanding, at least at the level of basic actions.

These discoveries open a new perspective on the origins of social understanding. They emphasize the crucial role played by the motor system in providing the building blocks upon which more sophisticated social cognitive abilities can be built. What is

more important, these neurophysiological findings provide a neurofunctional basis for interpreting the ever-growing evidence coming from developmental psychology research on the role played by experience-based motor knowledge in shaping the development of social cognitive skills. The motor cognition hypothesis also provides a refreshingly new approach to understanding the developmental breakdown of social cognition as in ASD.

Motor Cognition and Its Breakdown in the Case of Autism

The clinical condition of ASD provides a unique observation point for scrutinizing the ontogenesis of social cognition at the crucial intersection between action and intention. Children with autism display a striking inability to relate themselves to other people in ordinary ways; according to Kanner (1943), this represents the fundamental feature of autism. However, in the same seminal article, Kanner reported that "almost all mothers . . . recalled their astonishment at the children's *failure to assume at any time an anticipatory posture* preparatory to being picked up" (italics in original; Kanner, 1943, p. 242). Yet the relevance of motor disorders in autism was downplayed for decades, owing to the fact that the varieties of motor impairments in autistic children were eclipsed by the children's overwhelming lack of social and emotional reciprocity. Furthermore, no theoretical framework was available in the early studies on motor impairment that could reliably intersect the failure of anticipatory postures, stereotyped behavior, imitation deficits, clumsy gait, and other motor impairments with the impairments of sociability and communication.

These difficulties notwithstanding, it became increasingly clear that motor disorders were a core component of ASD. In a detailed review by Rogers and Pennington (1991), the two authors put forward strong evidence for an imitation deficit in autism, thus leading them to postulate a developmental model of autism in which "early cascading social–communicative impairments" might stem from an early deficit in motor imitation. Subsequent research further increased the robustness of the motor hypothesis (Williams, Whiten, & Singh, 2004; see Gernsbacher, Sauer, Geye, Schweigert, & Hill Goldsmith, 2008; for a review, see Rogers & Williams, 2006). Yet, until quite recently, explanatory hypotheses about the motor impairment in children with autism were, at best, purely tentative, because the underlying mechanisms remained obscure. Furthermore, it has never been in dispute that the most striking, self-evident features of ASD are the impairments (displayed with various degrees of severity) of the capacity to establish meaningful social communication and bonds, to establish visual eye contact with others, to share attention with others, and to understand others' intentions, emotions, and sensations (Dawson et al., 2002). Not surprisingly, a dominant paradigm in the study of autism portrayed the aloneness of these children as the consequence of a defective theory of mind, a sort of "mindblindness" (Baron-Cohen, 1995). Recent advances in neurophysiology, however, challenge this view and shed new light on the relation between ASD and impaired motor cognition.

Unlike typically developing children, children with autism use motor strategies that basically rely on feedback information rather than on feed-forward modes of control. Such motor disturbance prevents children with autism from adopting antic-

ipatory postural adjustments (Schmitz, Martineau, Barthélemy, & Assaiante, 2003). Additional aspects of the motor domain, such as action simulation, mimicry, and imitation, have been recently explored by a number of studies, all confirming a deep impairment of core mechanisms of motor cognition in children with autism.

Two recent studies, for instance, employing different techniques—EEG (Oberman et al., 2005) and transcranial magnetic stimulation (Théoret et al., 2005)—suggest that individuals with ASD might be suffering an action simulation deficit induced, perhaps, by a dysfunction of their MNS. The study by Oberman et al. (2005) showed that ASD individuals, contrary to healthy controls, did not show mu frequency suppression over the sensory–motor cortex during action observation. The study by Théoret et al. (2005) showed that, again contrary to healthy controls, ASD individuals did not show transcranial-magnetic-stimulation-induced hand muscle facilitation during hand action observation.

A further indication of motor cognitive deficits in ASD is exemplified by imitation deficits. Children with autism have problems in both symbolic and nonsymbolic imitative behaviors (imitating the use of objects, imitating facial gestures, and vocal imitation; Rogers, 1999; for review, see Rogers & Williams, 2006). These deficits characterize both high- and low-functioning forms of ASD. Imitative deficits are apparent not only in comparison with healthy subjects but also in comparison with mentally retarded nonautistic subjects. As previously proposed (Williams et al., 2004; Williams, Whiten, Suddendorf, & Perrett, 2001), imitation deficits in autism could stem from the incapacity to establish a motor equivalence between demonstrator and imitator, most likely due to a malfunctioning of the mirror neuron system, and/or because of disrupted emotional–affective regulation of the same system (Gallese, 2003b, 2006; Oberman & Ramachandran, 2007). It has been proposed that motor deficits would prevent children with autism from reproducing the observed motor acts (Diamond, 2000).

Dapretto et al. (2006) investigated the neural correlates of the capacity to imitate the facial expressions of basic emotions in high-functioning ASD individuals. The results of this fMRI study showed that during observation and imitation, unlike control subjects, children with autism did not show activation of the MNS in the pars opercularis of the inferior frontal gyrus. Activity in this area inversely correlated with symptom severity in the social domain. McIntosh, Reichman-Decker, Winkielman, and Wilbarger (2006) recently showed that individuals with ASD, unlike healthy controls, do not show automatic mimicry of the facial expression of basic emotions, as revealed by EMG recordings, although they can voluntarily do it upon request.

Some behavioral articles have recently challenged this view, either arguing against a general imitation impairment and a global MNS deficit in children with ASD (Bird, Leighton, Press, & Heyes, 2007; Hamilton, 2008; Hamilton, Brindley, & Frith, 2007) or claiming that specific impairments in imitation skills should not be attributed to a malfunctioning MNS (Leighton, Bird, Charman, & Heyes, 2008).

In particular, Bird et al. (2007) demonstrated that ASD individuals exhibit faster response times when performing movements that match an ongoing observed opening or closing hand move-

ment. We challenge the idea that such evidence tells us anything about the real involvement of motor cognition in imitation, because the stimuli and required behaviors consisted only of mere bodily movements and not of goal-related motor acts. The article by Leighton et al. (2008) showed that high-functioning adults with ASD were equally impaired on imitative as well as nonimitative versions of the same pen-and-cups task. However, such a double deficit, in our opinion, does not refute the putative role of the MNS in imitation tasks, but instead shows that ASD individuals suffer motor deficits beyond purely imitative impairments (see Diamond, 2000). We take such evidence as compatible with our motor cognition hypothesis.

Finally, Hamilton et al. (2007) reported that high-functioning ASD children showed the same behaviors as typically developing children when imitating goal-related finger movements and hand motor grasping acts, and showed even better performance on gesture recognition tasks than typically developing children. These results seem to raise a problem for a unitary account of the role of imitation deficits in ASD, although Hamilton (2008) did find that children with ASD were impaired in mimicry, thus revealing a deficit in one area of motor "resonance." As to why individuals with ASD showed better performance in gesture recognition than typically developing children, it is worth noting that it can in principle be imputed to a nonmotor strategy based on the inspection of purely visual cues, thus relying on the semantic relation between the context and the way the hand looks.

A recent article by Bernier, Dawson, Webb, and Murias (2007) not only reports imitative deficits in individuals with ASD but also reports a positive correlation between the severity of such deficits and reduced attenuation of the mu rhythm over motor cortex during action observation, thus suggesting a relation between imitation deficits and a malfunctioning MNS in individuals with ASD.

The theoretical relevance of motor cognition in action understanding has been clarified by the recent elegant series of experiments by Cattaneo et al. (2008). Participants were typically developing children and high-functioning children with autism who were required to both execute and observe two different actions: grasping with the right hand a food item placed on a plate, bringing it into the mouth, and eating it; or grasping a piece of paper placed on the same plate, and putting it into a box. During the execution and observation conditions of both actions, the activity of the mouth-opening mylohyoid muscle (MH) of participants was recorded using EMG surface electrodes. The results showed that during the execution and observation of the eating action, a sharp increase of MH activity was recorded in typically developing children, starting well before the food was grasped. No increase of MH activity was present during the observation of the placing action. This means that one of the muscles responsible for the action's final goal (opening the mouth to eat a piece of food) was already activated during the initial phases of the action sequence. The motor system anticipated the final goal (eating), thus directly mapping the action intention, both when the action was executed and when others were observed doing it. In contrast, high-functioning children with autism showed much later activation of the MH muscle during eating action execution and no activation at all during eating action observation. These results indicate that children with autism are impaired in smoothly chaining sequential motor acts within a reaching-to-grasp-to-eat intentional action

sequence. This impairment is then mirrored in the action observation condition and most likely accounts for their difficulty in directly understanding the intention of the observed action when executed by others.

Finally, a recent study (Cossu et al., 2008) has simultaneously investigated the imitation of meaningful and meaningless actions with and without objects; the production of meaningful actions from visual and verbal cues, respectively; and the comprehension of pantomimes by choosing the corresponding visual (from alternative pictures) and verbal targets (from the name spoken by the examiner). Fifteen high-functioning children with autism (mean age 9.4 years) were selected, along with two much younger control groups (4 to 5 years and 5 to 6 years). The results showed that each child with autism failed all 10 of the tasks presented: neither imitation, production, nor comprehension of the presented actions reached the degree of accuracy observed even in much younger typically developing children. This study indicates that the whole architecture of motor cognition is developmentally impaired in children with autism.

Hence, converging evidence from a variety of studies suggests that a dysfunction of motor cognition might be at the basis of some of the social cognitive impairments seen in ASD individuals. In contrast to what a long-standing mainstream account of autism contends (see Baron-Cohen, 1995; Baron-Cohen et al., 1985)— that the lack of social understanding of individuals with ASD is due to their inability to theorize about the minds of others—we contend that theorizing is most likely the only compensatory strategy available to them. Many of the social–cognitive impairments manifested by individuals with ASD are rooted in their incapacity to organize and directly grasp the intrinsic goal-related organization of motor behavior.

Conclusions

The evidence reviewed above from different fields of research such as ethology, developmental psychology, and neuroscience supports a common account of action understanding. The hypothesis being proposed here posits that the ability to understand others' intentional behavior relies primarily on the motor cognition that underpins one's own capacity to act. Goal coding is first a distinctive functional feature upon which the cortical motor system of primates is organized. Goal-directed motor acts are the nuclear building blocks around which action is produced, perceived, and understood. Taking advantage of the motor system's functional organization in terms of motor goals and motor intentions, the mirror neuron matching mechanism enables a direct comprehension of the actions of others. Such comprehension is prereflexively accomplished because the behavior of others consists of goal-directed motor acts and is recognized as such by virtue of the activation in the observer's brain of the neurons presiding over the motor accomplishment of that same act. The motor cognition hypothesis emphasizes the crucial role of the motor system in the phylogeny and ontogeny of basic aspects of social cognition and sheds new light on some of the social impairments seen in individuals with autism.

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