

Cognitive Critique



HOW DO WE UNDERSTAND THE ACTIONS OF OTHERS? BY MENTAL SIMULATION, NOT MIRRORING

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ABSTRACT

Assigning meaning to the actions of other subjects is an essential aspect of everyday social communication. A major contribution in understanding the brain mechanism supporting recognition of others' actions was the discovery of 'mirror neurons', which are activated both when a monkey grasps an object and when he observes other subjects executing the same grasps. However, our recent findings indicate that the system responsible for understanding the actions of other subjects encompasses the entire brain circuitry that supports action execution, rather than just the part of cortex containing 'mirror neurons'. These findings contradict the widely held notion

that 'mirror neurons' alone code the meaning of observed actions performed by other subjects, and instead support the theory that we decode others' actions by activating our own action system, i.e. by mentally simulating the observed acts.

THEORY OF MIND

Interpreting other people's actions and intentions, a common everyday practice in social settings, relies on mind-reading, which is the ability to assign mental states to fellow human beings. This ability of awareness of the probable content of other people's mind, the so called *Theory of Mind*, was originally thought to depend upon human linguistic capacities. However, there is evidence that nonhuman primates also have the capacity to understand the intentions that presumably motivate others' behavior (Premack and Woodruff 1978). Several independent reports of intentional deception in nonhuman primates support that they can act according to a manipulative Machiavellian strategy. For example, a monkey hides the available food, and pretends there is no food around when a hungry conspecific approaches (Byrne and Whiten 1988).

There are two major theories accounting for primates' ability to predict and explain behavior by attributing mental states to others: the *theory theory (TT)* and the *simulation theory (ST)*. Whereas TT depicts mind-reading as a detached theoretical activity (Carruthers and Smith 1996), ST portrays mind-reading as an attempt to simulate the mental life of the target agent (Gordon 1986; Heal 1986). The TT maintains that our capacity to understand the behavior of others arises from theoretical reasoning in accordance with causal laws of behavior. According to TT, we pull the mental concepts used in understanding behavior out of a body of implicit knowledge we all possess. In contrast, the ST claims that our capacity to explain and predict the behavior of other agents is based on our ability to use our own mental processes to simulate their mental states. According to ST, our ability to interpret others' behavior in terms of desires intentions and goals, to guess the probable content of their minds, is based on our ability to run cognitive simulations, to impersonate others' mental life, to pretend to be in their shoes. Thus the difference between TT and ST is the difference between theoretical reasoning and practical simulation.

The ST explains our ability to understand and predict the mental states of others and the causes of their behavior, to empatheti-

cally embody their feelings, and to re-enact our own past. Mental simulation of others' behavior is thought to enable sharing of experiences between individuals, and thus to serve social interaction. To avoid semantic confusion, I should mention that in cognitive neurosciences the term *mental simulation* is used in a wide sense to describe the process of internally rehearsing on other's actions, sensations, emotions and other cognitive operations. In this paper, I mainly focus on mental simulation in the domain of action. I focus on the microscale of recognition of simple actions rather than the macroscale of prediction of complex behavior, which is the scale of reference of philosophers involved in the *mind-reading* debate. Presumably, action-simulation is a prerequisite of more complex cognitive simulations. Before we can simulate the thought processes of others, we need to understand their mental states as well as their actions. Before we can explain why a person performed a certain action, we must characterize the action. Thus, understanding the actions of others by action-simulation is a prerequisite for more complex cognitive simulations. Consequently, the neuroscientific and the philosophical accounts of mental-simulation processes can be integrated to provide a global simulation-based explanation of our understanding of other minds. Mental processes become clarified as we gain knowledge about their biological basis, and there is no doubt that we would all benefit from a common glossary.

A crucial postulate of ST is that the same mechanisms support the intelligent control of actions and the comprehension of intelligent actions. This dual-responsibility requires a shared underlying neural network. Our experimental results in the University of Crete (Raos et al. 2004, 2007; Evangelidou et al. 2009; Kilintari et al. 2010) demonstrate that several primary and supplementary sensory-motor areas of the frontal and occipital cortex, as well as many parietal and occipito-temporal association cortical areas of the monkey brain are assigned the double-responsibility of action-generation and action-perception. Thus, our experimental results complement the ST.

BINDING SENSORY WITH MOTOR REPRESENTATIONS

Early influential theories of human perception and cognition included the motor theory of perception proposed by William James, the developmental emergence of cognition out of sensory-motor abilities proposed by Jean Piaget, and the perception through affordanc-

es in the ecological psychology of James Gibson. Later, in the early decades of cognitive science *propositional* forms of knowledge were suggested. Cognitive scientists first began to view the mind as an abstract information processor. The executive and perceptual systems were considered irrelevant for understanding the *central* cognitive processes. Jerry Fodor argued that central cognition is not modular, although its connections to the world are (Fodor 1983). At that time, artificial intelligence was dominated by computer models of abstract symbol processing.

Nowadays, *embodied cognition* and *mental simulation* theories seem more related to the early psychological than to the early cognitive theories. The embodied cognition approach implies that the mind must be understood as intimately related to a physical body that interacts with the world, rather than as an ungrounded symbol-processing entity (Wilson 2002). This approach attempts to provide continuity between cognitively simpler creatures and modern humans. The mental simulation approach explains how we represent a wider range of events by also using our bodily resources. It thus explains how we represent not just what we ourselves do but also what someone else is doing.

The classical picture of perception-for-action processing that has emerged over the past few decades can be summarized as follows. The presentation of a stimulus triggers several processes. *Early* processes are exclusively driven by input information derived from the stimulus; some *later* ones are controlled by input information from both stimulus and memory; and *even later* ones control movement. The percept emerges from binding its distributed features first, and then the action follows. On this classical view, perception and action are qualitatively different, and must occur in strict sequence. There is no action in perception, and there is no perception in action.

However, an action such as grasping an object with one hand, for example, does not simply involve perception of the object and generation of the correct grip. It also involves perceptual memory related to the object's features and affordances, action-memory related to the intended shaping of the hand for efficient grasping, and additional perceptual-memory related to the anticipated visual and somatosensory consequences of the intended movement. The interaction between (i) sensory-related information derived from the stimulus and recalled from memory, which is required for (a) identification of the stimulus and evaluation of its graspability, and

for (b) prediction of the sensory consequences of its manipulation, and (ii) certain executive features, such as the coordinates of reaching and the requirements of grasping, imply combined representations of perception and action at the level of execution of an action. According to our neuroimaging results (Raos et al. 2004, 2007; Evangelidou et al. 2009; Kilintari et al. 2010), these combined sensory-motor representations are activated both for the generation of an action and for its observation/perception. These results indicate that mental imagery of execution of action (mental rehearsal, or mental re-enactment) occurs during action-perception/recognition, and suggest sharing of sensory-motor representations also at the level of action-cognition. As will be discussed in following sections, our biological data support the notion that generation and recognition of one and the same action are represented in the same neural domain. Apparently, for both generation and recognition of the same action, shared contextual information selects the appropriate shared sensory-motor networks. Furthermore, there is neurobiological evidence (Haggard et al. 2003; Keysers et al. 2004; Avenanti et al. 2005; Blakemore et al. 2005; Bufalari et al. 2007) that not only understanding others' actions, but also understanding others' sensations, emotions (empathy) and intentions rely on neural mechanisms underlying actual sensations and actions, and share sensory-motor representations with the actual experiences. Thus there appears to be a binding of neural codes across sensory and motor domains, as well as across imaginary and actual domains. This binding of codes across domains is important because basic neuroscience and cognitive theories progress by unifying sets of laws.

Since it is difficult to discuss cognitive systems without referring to established theoretical hypotheses, I will employ our neurobiological data to theoretically and empirically support the view that several cognitive faculties are based on sensory-motor simulations, and thus that cognition is embodied. Hopefully, the use of biological data to support neuropsychological and/or neurophilosophical concepts of cognition will contribute to the advancement of the contemporary theories of knowledge.

RECOGNIZING THE ACTIONS OF OTHER SUBJECTS: GRASPING WITH THE MIND'S HAND

In this and the following five sections, I will present some of our experimental findings concerning the cortical areas of the primate brain involved in the execution and observation of the same action and discuss them in relation to (i) the theory of mental simulation, i.e. the internal rehearsal of action, and (ii) the theory of embodied cognition, i.e. the sensory-motor instantiation of motor cognitive operations.

We performed a series of quantitative neuroimaging experiments on awake-behaving monkeys. Some monkeys were trained to reach and grasp a small 3-dimensional (3D) object either in the light or in the dark, and other monkeys were trained to observe the experimenter reaching to grasp the same object. As expected, both the primary motor and somatosensory cortical areas representing the forelimb (arm/hand) were somatotopically activated during reaching-to-grasp movements. Unexpectedly, we found that the forelimb area of the primary motor cortex (MI-forelimb region) was also activated during mere observation of reaching-to-grasp movements, i.e. even though the observer did not execute any movements (Raos et al. 2004). Activation of the MI-forelimb region normally indicates a brain command for movement of the forelimb. Yet, subjects did not execute any forelimb movement during action-observation, nor were any of their forelimb muscles activated. Consequently, we surmised that activation of the MI-forelimb region in the brain of the observer reflects mental simulation of the observed action, i.e. motor mental imagery. When I use the term *mental imagery* I do not wish to imply that a conscious process is necessarily in operation. This is particularly true of non human primates, in which the involvement of mental imagery is speculative as it can not be assessed directly. Instead, I use it to refer to the retrieval of internal representations of an act which were memorized months before the experiment.

Moreover, the forelimb region of the primary somatosensory cortex (SI-forelimb region) was found to be activated in the same observing subjects (Raos et al. 2004). Activation of this cortical region is normally due to the re-afferent feedback signals it receives from activated muscles of the moving forelimb, informing the brain about the somatosensory consequences of the movement. Since no

actual movement was performed by the observers and no forelimb muscle was activated, no actual sensory feedback could have been transmitted from the peripheral muscles to the activated SI-forelimb area. Thus, its activation for action-observation implies that, triggered by action-observation, the mental simulation of the action contains a somatosensory component akin to the feedback that accompanies overt actions. Our results support the notion that we understand others' actions by covertly rehearsing, not only the motor component of the observed action, but also its somatosensory (kinaesthetic and tactile) consequence, i.e. by motor and somatosensory mental imagery. Presumably, the somatosensory consequences of the movement which are generated *bottom-up* (sensory-driven) during action-execution, and which provide information about the overt movement, are also triggered *top-down* (mentally-driven) during action-observation to represent the predicted kinaesthetic and tactile consequences of the movement that is mentally simulated.

We also found that extrastriate visual cortical area V3 is specifically involved in action-observation (Kilintari et al. 2010). Using control monkeys, we distinguished the effects due to arm-motion and object-presentation from those due to the visual information required to guide the movement. In this manner, we revealed the involvement of area V3 (V3d and V3A) in processing visual information specifically related to the requirements of motor control, i.e. in guiding the forelimb to reach accurately and grasp properly. More specifically, the extrastriate area V3, which was primarily affected in all our experimental cases, has a functional role in stereopsis and internal reconstruction of the visual field. On the basis of its cellular properties, functional role, and inter-cortical connections (Felleman and Van Essen 1987; Poggio et al. 1988; Galletti and Battaglini 1989; Adams and Zeki 2001), we suggest that area V3 may relay to the motor system, via the parieto-frontal visuomotor stream, visuospatial information useful for the reaching part of the action, and 3D-object-related information useful for the grasping part (Kilintari et al. 2010). Actually, our demonstration that area V3 is activated for action-execution in the dark as well as for action observation locates the extrastriate occipital region whose involvement in motor imagery was suspected in fMRI studies (de Lange et al. 2005; Milton et al. 2007; Bakker et al. 2008).

Moreover, we found that the monkeys which were reaching-to-grasp in complete darkness displayed activation of the early visual cortical areas V1, V2 and V3 (Kilintari et al. 2010). This activation

could reflect only top-down feedback signals from higher fronto-parietal dorsal stream areas, presumably representing memorized visual information required for motor control in the dark. Apparently, when vision is removed and concurrent visual feedback is not available, subjects rely on an internal representation of the external environment to guide their movements. Based on psychophysics, it has been reported that memory-guided actions are based on perceptual mechanisms and not on visuomotor coordinates, and that stored information about the target is used for off-line control of the action mediated by the ventral visual stream (Goodale et al. 1994; Hu et al. 1999; Westwood et al. 2000; Lemay and Proteau 2002; Heath and Westwood 2003). In contrast to these reports, our finding that the occipito-parietal V3d segment is activated for action in the dark indicates that memory-guided grasping involves the dorsal rather than the ventral visual stream. Indeed, participation of the dorsal visual stream in the execution of memorized delayed movements has been suggested also by TMS (Cohen et al. 2009) and fMRI (Singhal et al. 2006; Fiehler et al. 2008; Himmelbach et al. 2009) studies. All in all, I suggest that the visual-imagery which may take place during action in the dark could rely on top-down efferent signals (from the fronto-parietal system to the early visual cortices) that trigger the retrieval of the visual representation of the action stored in the dorsal visual stream.

Similarly, during action-observation, area V3 could be receiving top-down corollary discharges (efferent copy) from the motor system, forcing the visual system to focus on aspects important for the successful perception/recognition of the action. In general, top-down antidromic activation (backward signals from association to primary sensory cortices) could modify the information in the early sensory cortices that normally is transmitted orthodromically (bottom-up). For example, top-down signals may provide information to early sensory cortices for more robust processing of the perceptual signal, e.g. for reconstruction of a specific somatosensory or visual map corresponding to the observed action (hand-object interaction). This top-down process has been suggested to occur ceaselessly during mental imagery and during perception, allowing the completion of perceptual maps resulting from bottom-up processing as well as the reconstruction of additional maps in early cortices not targeted by bottom-up signals (Meyer and Damasio 2009).

Thus, we found that early visual cortical areas are activated (i) for grasping a 3D-object in the dark, i.e. for the voluntary manipula-

tion of an invisible/memorized object, and (ii) for the observation of object-grasping performed by another subject, which involves mental simulation of the action, i.e. for the imagined manipulation of a visible object (Kilintari et al. 2010). The specific involvement of extrastriate area V3 in action-observation suggests visual imagery of the observed act during its mental simulation. The activation of the early visual cortical areas for action in the dark corroborates the theory that visual mental imagery occurs both during motor control and cognition. Thus, we recently demonstrated that the single neural buffer used *bottom-up* or *top-down* to represent, respectively, the actual or imaginary consequences of physical or mental practice, extends beyond the frontal primary somatosensory-motor circuit, which we had previously described (Raos et al. 2004, 2007; Evangelidou et al. 2009). It also includes early occipital visual cortices which reflect the physical or mental visuospatial representations of the motor act (e.g. arm position, hand shaping, object geometry and location). Consequently, not only motor and somatosensory but also visual imagery contributes to action recognition. The somatotopic activation of the primary somatosensory cortex during action-observation could serve a veridical kinaesthetic and tactile feeling of the simulated movement by the observer in a first person perspective, i.e. the somatosensory imagery. On the other hand, the activation of the early visual cortices during action-generation in complete darkness indicates a veridical visual portrayal of the invisible/memorized object to be reached and grasped by the invisible arm within the unseen spatial surrounding, i.e. visual imagery (Kosslyn and Ochsner 1994; Roland and Gulyas 1994; Kosslyn et al. 1999).

In summary, our results indicate that movements and their sensory feedback are stored as motor, somatosensory and visual interrelated representations during execution of an action, and are recalled during the observation of the same action, serving as its mental simulation or its *grasp with our mind's hand*. Therefore, we are led to conclude that action-recognition may be constrained by the stored sensory-motor repertory of the observer. A consequence of this claim is that it might be possible to activate (and thus train) our execution-system by mere observation. This would explain our ability to acquire skills by observation of the actions of others. It would further explain our ability to build our motor repertory by incorporating not only our sensory-motor experiences but also those of other individuals. The fact that action-execution and

action-observation rely on interrelated motor and sensory representations provides empirical support for the action-perception correspondence or contagion, the parity between perception and action, which has been suggested on theoretical grounds within the frame of the common coding theory (Prinz 1984).

COGNITION IS GROUNDED IN SENSORY-MOTOR CODES

To perceive is to have sensory stimulation one understands. As Kant held, concepts without intuitions are empty, and intuitions without concepts are blind (Smith 1929). Perception is thoughtful activity. Like touch, vision is an active exploration of the world, palpation with the eyes (Merleau-Ponty 1964). We gain content by looking around just as we gain tactile content by moving our hands. Perception (e.g. vision or touch) gains content through our skilful movements. We bring content to experience, by action. The process of perceiving is an activity of skilful exploration (Noe 2004). Perceiving the world presupposes and affords active behavior, such as the use of all sorts of movements of eyes, limbs and body. On the other hand, action control is anticipatory, i.e. it is based on representations of the consequences of the intended action. Actions are represented in terms of their sensory effects (Hommel et al. 2001). Thus based on theoretical grounds, action plans and their perceptual consequences are interrelated and may share combined codes.

In fact, experimental studies on sensory-motor synchronization (participants are asked to tap with a finger in synchrony with a periodical sequence of auditory clicks) demonstrate that action control is not so much concerned with the synchrony between the auditory input and the motor output but with the synchrony between the perceived click and the perceived tap (Aschersleben and Prinz 1995). In brief, actions are controlled by the anticipation of their effects. Even more enlightening was the finding that local anaesthesia applied to the tapping finger (inhibiting the transmission of afferent signals from the skin without affecting the efferent pathways) increased the anticipatory error. Presumably, action effects become integrated with the action they follow, so that the presence of an effect triggers the associated action. Indeed, our neuroimaging findings reveal that early visual cortices along with the forelimb regions of the primary somatosensory and the primary motor cortices are activated not only for grasping-execution but also for grasping-ob-

servation (Raos et al. 2004, 2007; Evangelidou et al. 2009; Kilintari et al. 2010) and they demonstrate that generation and recognition of the same action are functionally entangled. I suggest that goal-directed actions, both generated and perceived, are represented by the sum total of the relevant motor commands (actual or simulated) and their sensory effects (actual or predicted). Both the generation and the perception of a voluntary action presuppose knowledge about the action-effect relationships. This knowledge is necessary in processes such as planning, acting, and perceiving, for actually or mentally controlling the action before, during and after its execution. As Gibson stated, action would run blind without being perceptually informed about its bodily and environmental preconditions, its progress, and its consequences (Gibson 1950). Thus, our working hypothesis, that a voluntary action is cognitively represented by a precise association of the movement and its sensory counterparts (kinaesthetic, tactile and visual) stored in equivalent (motor, somatosensory and visual) cortices, has theoretical background as well as empirical support. In fact, this suggestion of ours explains several biological results in human and non-human primates, which demonstrate that the somatosensory cortex is activated for action, and the motor cortex is activated for perception (Hari et al. 1998; Raos et al. 2004; Costantini et al. 2005; Avenanti et al. 2007; Gazzola and Keysers 2009). Even when the effector is absent (as in patients with peripheral amputation) simply seeing movements reactivates the motor cortex (Giraux and Sirigu 2003), suggesting that visual effects (in addition to the somatosensory ones) are interweaved with motor commands in integrated action codes.

The operation of such shared representations can help understand the behavior of other subjects at multiple levels of abstraction. Each simple sensory-motor representation could implement a functional conceptual system. Complex representations could in turn be produced by integrating combinations of simpler representations. Sophisticated forms of cognition, such as conceptualized thought, would then emerge from the complex interaction of multiple simple conceptual systems. It has been suggested that subsets of perceptual states in sensory-motor systems may function as unimodal representations, and that conceptual representations may be multimodal simulations distributed across modality-specific systems (Barsalou 1999). For example, visual perception of others' behavior may restore from memory the associated somatosensory-motor representations, which correspond to the behavior's partial components. This

process could serve the understanding of each behavioral component separately and in relation with each other (by mental rehearsal, without resulting to any overt behavior) and thus could serve the understanding of the entire observed behavior. The demonstrated activation of the same primary sensory-motor neural network for the generation and the perception of an action indicates that its perception and its generation share the same neural representations. This implies that there is no need for separate sensory-motor and conceptual systems to process goal-directed actions. The fact that only the forelimb regions of the primary motor and somatosensory cortices are activated for observation of reaching-to-grasp indicates that the activated system, indeed, encodes the meaning of the observed action. The somatotopic activation of the somatosensory-motor system during mere observation of an action, cannot be unrelated to the meaning of the action. Consequently, our empirical data (Raos et al. 2004) support the theory of embodied cognition. Thus far, there are no neurobiological data indicating the existence of two separate systems, one representing the ‘intelligence’ of an action and another one representing the action itself. Both can be supported by a common representational system. In fact, the notion that motor cognition is embodied in action supports perceptual rather than amodal theories of knowledge, implying that sensory-motor simulators implement fully functional conceptual systems (Barsalou 1999). Furthermore, other studies have demonstrated that even sensory empathy (Haggard et al. 2003; Blakemore and Frith 2005) and empathy for pain (Avenanti et al. 2005; Bufalari et al. 2007) are based on sensory-motor representations.

In summary, there is empirical support suggesting that conceptual representations are embodied and modal. Our neurobiological data indicate that mental re-enactment (mental simulation of an observed action or motor imagery) provides a powerful interface between perception and cognition. Other neurobiological data indicate that mental experience of senses and emotions provide the basis of empathy. All these experimental data offer a solution to the symbol grounding problem of Searle (Searle 1992) if we consider cognition and knowledge as grounded in sensory-motor codes. Needless to say, this approach cannot explain all types of human cognitive faculties. In addition to our experimental data, there are several neurobiological findings supporting the notion that motor cognition is modal and embodied, and that the sensory consequences of an action are integrated to become part of the action’s cognitive represen-

tation (see following section). An actor, when learning to act, has to acquire the contingency between a particular movement and its perceivable outcome (i.e. to form a movement-effect association), while an observer has to use the code of the perceived outcome to intentionally select the associated action.

COMMON NEURAL SUBSTRATE FOR EXPERIENCES AND THEIR MENTAL IMAGERY

In addition to the effects on the primary somatosensory, primary motor and early visual cortices described above, we also examined the effects of execution and observation of the same action on premotor, supplementary motor and supplementary somatosensory, cingulate, parietal and parieto-occipital cortices. When we examined the frontal lateral and medial cortex involved in generation and perception of the reaching-to-grasp action, we revealed that there was an extensive overlap of the two underlying cortical networks, including medial frontal (areas 8, 9 and 24ab), lateral premotor (areas F2, F4 and F5), cingulate (areas 24c and 24d), supplementary motor (area F6) and supplementary somatosensory (SSA) cortices (Raos et al. 2007). When we examined the parietal association areas involved in generation and perception of the same action, we found that the overlap of the two underlying cortical networks was also very extensive including superior parietal (areas PE-lateral and PEc), inferior parietal (area PF), intraparietal (areas PEip, 5VIP, AIP and 7VIP), medial parietal (areas PGm and retrosplenial 29/30), and parieto-occipital (area V6) cortical areas (Evangelidou et al. 2009). In brief, we found that during action-observation numerous parieto-frontal sensory-motor association cortical regions are recruited, mostly the same ones which are responsible for the execution of the same action.

These findings corroborate our suggestion that during observation of an action performed by another subject an internal motoric experience of the specific action is generated in the observer's mind. Actually, our findings complement the results of other studies reporting activation of a few individual areas of the above mentioned parieto-frontal cortical network, by mere observation of goal-directed hand actions (Grafton et al. 1996; Rizzolatti et al. 1996; Decety et al. 1997; Hari et al. 1998; Buccino et al. 2001; Avikainen et al. 2002; Cisek and Kalaska 2004; Nelissen et al. 2005; Filimon et al.

2007; Tkach et al. 2007; Gazzola and Keysers 2009). Therefore, observation of an action performed by another subject reflects our previous knowledge about the act and its predicted/anticipated sensory consequences and associations. Our finding that observing an action excites virtually the same sensory, motor and association cortical areas supporting execution of that same action implies that observation of an action corresponds to simulation of its overt counterpart. In other words, to recognize the actions of another subject, the observer may be *putting himself in the actor's shoes*, may internally recite or mentally rehearse the observed action along with its sensory and higher cognitive associations. We may decode the actions of others by activating our own action system. We may understand observed actions by performing them mentally. Mental simulation of an action, along with its sensory effects and higher associations, underlies motor cognition. Furthermore, simply waiting to observe an upcoming movement made by another individual triggers the motor system of the observer (Kilner et al. 2004; Urgesi et al. 2010). These results demonstrate the anticipatory simulation of future actions, emphasizing the predictive coding of others' motor behavior, the shared representations by motor control and motor cognition.

The production, perception and mental imagery of a behavior may rely on a common coding, sharing not only motor representations but also sensory and affective ones. The neuroscience literature contains several examples supporting this notion. First, visual mental imagery involves representations analogous to viewing the real images, representations that functionally preserve properties of the external world (visual field) rather than consisting of bundles of propositions (Kosslyn 1994). Secondly, observation of still pictures of lip forms, on-line imitation of them, and execution of similar forms in a self-paced manner induce activation of overlapping temporo-parieto-frontal areas (Nishitani and Hari 2002). Also, reading lips in the absence of any sound activates both primary and association auditory cortices, and the evoked activity pattern overlaps considerably with that elicited upon hearing spoken words (Calvert et al. 1997). The lip movement, its associated sound, and the auditory map of that sound are integrated into a combined neural representation. Moreover, audiovisual speech perception activates cortical motor areas involved in planning and executing speech production (Skipper et al. 2005), including the mouth area of MI (Watkins et al. 2003). Furthermore, viewing speech modulates activity in the

mouth area of human SI (Mottonen et al. 2004), reflecting mental simulation of the other's action-related sensations, enabling the observer to experience what the actor feels while performing the act. Also, the comprehension of action words that are semantically related to different parts of the body (e.g. lick, pick, kick) automatically activates the motor system (somatosensory-motor cortex) in a somatotopic manner, as if understanding language means relating language to one's own actions through a linkage of sensory and motor information (Pulvenmuller 2005), as if understanding speech echoes mental simulation of its bodily content. Also, the impairment of language and symbol perception and comprehension after lesion in the inferior frontal lobe, including Broca's area, indicates that language mechanisms involve functionally interdependent brain systems for expression and comprehension (Pulvermuller and Fadiga 2010). Finally, the participation of the body representation in mental simulation is indicated by the finding that the availability of an efficient body schema is necessary not only for recognizing one's own actions, but also for understanding the actions of others (Ramachandran and Rogers-Ramachandran 1996).

There are also several examples indicating that mental simulation underlies empathy for sensations, pain and emotions: The brain circuits activated for actual-sensation and for empathy of the same sensation overlap (Keysers et al. 2004; Avenanti et al. 2005; Blakemore et al. 2005; Bufalari et al. 2007). Even more so, the activity in the primary somatosensory cortex is correlated with the accuracy with which a person judges how another person feels (Zaki et al. 2009). Improvement of tactile acuity associated with viewing the arm, indicates mental simulation of the somatosensory perception process under the influence of visual input (Kennett et al. 2001). The fact that bodily representation contexts provided by vision occur within the primary somatosensory cortex itself, indicates a top-down driven mental simulation which serves sensory empathy (Haggard et al. 2003). Furthermore, because visual and proprioceptive inputs modify the body schema, which in turn is used to calibrate perception of the external world (de Vignemont et al. 2005), a constantly updated mental simulation process may support the dynamics of this system. In other words, a constantly updated cross-modal mental simulation of (i) the somatosensory perception process under the influence of visual input and (ii) the visual perception process under the influence of somatosensory input may take place, due to the cross-talk between these two mo-

dalities and the fact that they influence each other. Moreover, observing other individuals who display emotional facial expressions activates neural circuits that largely overlap those involved when feeling the same emotions (Carr et al. 2003; Wicker et al. 2003). The notion that a mental simulation mechanism is recruited during empathy for pain is also supported by a single cell recording study in a human subject (Hutchison et al. 1999). The reduction of excitability of hand muscles during the mere observation of painful stimuli delivered to a model, suggests that the model's painful experience is mentally simulated by the observer, serving the empathy for pain (Avenanti et al. 2005). Indeed, recent neurobiological findings provide evidence in support of inter-individual sharing of pain, challenging the widely held notion that the experience of pain is inherently private. Observing (Avenanti et al. 2005) as well as imagining (Singer et al. 2004; Singer et al. 2006) the pain of others induces neural changes in the same set of structures involved in personal experience of pain.

In conclusion, mental simulations may serve not only motor cognition but also sensory and emotional empathy. The performance of an action and its perception, or the physical experience of a sensation and its empathy are represented in common neural domains. Observing the behavior/experience of another subject is not a passive procedure, but an active planning and testing process.

MENTAL SIMULATION OF BEHAVIOR IN THE SERVICE OF BEHAVIOR COGNITION

A comprehensive explanation of behavior requires a combination of (i) the sensory-motor approach that views behavior as responses to stimuli, and (ii) the ideomotor approach that views behavior as the resultant of internal causes. After all, voluntary behavior depends on the interaction between internal goals and external opportunities. As already mentioned, the representation of simple goals (e.g. action intention) may reside in the circuitry of the specific-behavior itself (e.g. the action-execution circuitry). According to motor theories of perception, the motor system of an observer is actively involved in the perception of actions when these are performed by a demonstrator. Indeed, neurobiological data support the notion that the human brain does not passively observe others' behavior, but actively understands it and even predicts the forthcoming state, by mentally simulating the actor's behavior. Thus, the interpersonal

communication is based on the combination of the covert internal sensations of one agent (the observer) with the overt external behavior of another (the actor). In the spectator's brain, these interpersonally shared representations serve the off-line operation of restored sensory-motor associations corresponding to the observed behavior. In other words, they serve the covert mental simulation of the observed behavior. Alternative restored sensory-motor associations reflect alternative scenarios. Accordingly, we use as a *theory of mind*, the *simulation-theory* rather than the *theory-theory*.

Much of human behavior and several cognitive faculties may rely on mental simulation. The common representational domain, shared by actual practice and mental rehearsal of any given behavior/experience, not only serves our understanding of others' actions/sensations, but also supports observational-learning, mental-training and social interactive communication between agents. In fact, if we mentally rehearse an action while we observe another subject performing it, its subsequent execution should be facilitated and thus motor skills could be learned by observation. Such mental rehearsal may be the neuronal basis of observational-learning. Activation of the neural circuitry supporting action-execution during observation of the same action facilitates activation of this circuitry during subsequent performances. Indeed, subjects simply watching an experimenter performing a sequence of movements can learn the sequence as efficiently as when practicing the task themselves (Heyes and Foster 2002). Similarly, if we simulate an action while we imagine it, its subsequent execution should be facilitated, suggesting that motor skills can also be learned by mental training. Observational learning and mental training may turn out to be of great social value because they occur as a consequence of simulating behavior without any actual training.

The idea that mental states correspond to simulation of actions and sensations is not new (Jeannerod 2001; Hesslow 2002). For example, the notion that mental states with action content (e.g. recognition, planning or imagination of an action) correspond to simulated actions was supported by several physiological and psychophysical pieces of evidence, which generated the suggestion that covert actions are neurally simulated actions (Jeannerod 1994; Jeannerod 2001). In effect, imagined actions bear the same temporal regularities and the same responsiveness to physical laws as their overt counterparts (Decety et al. 1989; Sirigu et al. 1995). Vegetative responses (i.e. reactions of the autonomic nervous sys-

tem) increase for covert actions in the same way as for overt actions (Decety et al. 1993; Paccalin and Jeannerod 2000). Interference effects between executed and observed movements occur when kinematic aspects (Edwards et al. 2003; Kilner 2003) and the terminal posture (Sturmer et al. 2000; Craighero et al. 2002) are observed. As regards neural substrate, it was originally suggested that although there is a core circuit of action-execution-related areas that pertains to all imagined actions, each one of them retains its own specific network (Jeannerod 2001). However, this suggestion was based on qualitative neuroimaging results of much lower resolution than that used in our studies (Grafton et al. 1996; Rizzolatti et al. 1996; Decety et al. 1997; Lotze et al. 1999; Gerardin et al. 2000; Buccino et al. 2001). Our studies were the first to systematically investigate quantitatively and at a high spatial resolution (20 micrometers), the entire neocortex of the primate brain during execution and observation of the same action. We revealed that it is virtually the entire action-execution network which supports action-observation, rather than a small core circuit of execution related areas (Jeannerod 2001) or the core circuit of premotor area F5 and parietal area PF/PFG (Gallese et al. 1996; Fogassi and Luppino 2005) that had been suggested earlier.

Arguably, a cognitive process need not be equivalent to the neural activity that accompanies it, and even less so to the neural activity detected with presently available methods. Also, neuroimaging data do not directly correspond to a particular stimulus, a specific movement or a specific mental process. Moreover, cognitive processes can be inferred only to a small extent from observed behavior. Nonetheless, neuroscience research leads to approximate understanding of neural correlates of behavior. To date, we have adequate empirical data to demonstrate that executed and observed actions have virtually the same neural substrate, and to suggest that motor control and motor cognition share the same neural correlates. Actually, it is reasonable to ask why the execution and cognition of an action should have different neural correlates. Besides, why would only the premotor and not the primary motor cortex *know* whether the subject is performing the appropriate action? Why would an *intelligent* action have two neural substrates, one supporting the action and another one supporting its *intelligence*? Why would the intelligent execution of an operation consist of one process for *doing* and a separate process for *theorizing*? Wouldn't that be analogous to the dogma of the *ghost in the machine*, and thus

reflect the remains of Cartesian dualism? Wouldn't that correspond to the replacement of the traditional mind/body dissociation by the thinker/doer disengagement?

Our experimental findings support the notion that mental faculties with motor content, e.g. action planning, action-execution, action-recognition and action-prediction, are the emergent properties of the same interacting occipito-temporo-parieto-frontal sensory-motor circuitry. We have not detected any master area dedicated to motor cognition as opposed to motor control. All areas of the circuitry may be necessary and none of them in isolation need be sufficient for either motor control or motor cognition. This suggestion is in agreement with the mental simulation theory of cognition, which implies the use of the observer's sensory-motor structures in a dual role: on-line for the purposes of overt feeling and acting, and off-line for covertly simulating and imagining experiences and behavior. The *intention of action*, the *action planning*, the *prediction of action*, and the *anticipation of action* are not operations separate from *acting* itself. These operations are part of action. In a similar way, *understanding the feeling* of another subject is not disconnected from the *feeling* itself. This sort of understanding is a form of mind-reading through the process of behavior-simulation. In perceiving the actions and expressions of the other person, we simulate the actions, sensations or emotions to understand their meaning. As a consequence, we interpret the behavior of others as our own alternative possibilities. Forecasting of events, and understanding others' feelings and actions consist of elaborating consistent scenarios, or running off-line previously stored programmes. Consequently, the potential gain from simple observation of other subjects' behavior is (i) learning motor skills by social interaction, (ii) enriching one's own feelings as an inter-subjective accomplishment, and (iii) enhancing one's sense of self as an intra-subjective achievement.

THREE PERTINENT QUESTIONS

Our finding that execution and observation of the same action are supported by much of the same neural network (Raos et al. 2004, 2007; Evangelidou et al. 2009; Kilintari et al. 2010) leads us to three major questions.

First question: Why would premotor, motor, sensory and related association cortices display similar somatotopic activations for action-generation and action-perception? As already explained, the

best available answer to this question is that the observer covertly rehearses (mentally simulates) the action while observing it, and in this manner the action-execution network also supports action-observation. What is to be gained from the mental simulation of action during its observation? Why are the primary motor and somatosensory cortices somatotopically involved? It is conceivable that the involvement of primary sensory-motor cortices in action-observation provides the observed actions with a real executed motor format. Qualities such as force, kinematics and biomechanics of movements are not visible. They are represented in the motor areas, which are involved in action-recognition (via action-simulation) in order to provide sufficient information about how the observed action is executed. The motor-related activations during action-observation may operate as a simulator of the observed action to ensure understanding of its motor component, while the sensory-related activations may serve the perceptual (kinaesthetic, tactile and visual) appreciation of the action's consequences. In particular, the recruitment of primary and secondary somatosensory cortices during action-observation may ensure the vividness with which the observer mentally perceives the physical somatosensory consequence (kinaesthetic and haptic end-result) of the movement. The overall understanding of the observed action may reflect recruitment of learned associations between the motorically coded action and its perceived consequences, stored in the entire occipito-parieto-frontal network which supports the visually and kinaesthetically guided execution of the action. For example, to follow a dancing contest is not only to discriminate the moving couples on stage, but also to simulate relevant stored programs, to recruit relevant sensory-motor representations.

Second question: Why doesn't activation of the motor system result in overt movements during observation of an action? Where in the motor system is the execution blocked during action-observation? As some have proposed, a *dual mechanism* may operate at the spinal level, involving a subthreshold excitatory cortico-spinal input and a parallel inhibitory influence suppressing the overt movement (Blakemore et al. 2001; Jeannerod 2001). In fact, there are two possible explanations for the absence of forelimb-muscle activation during action-observation, even though the forelimb region of the primary motor cortex (MI-forelimb region) is activated. Either activation of the MI-forelimb region is subthreshold and cannot stimulate spinal motoneurons to generate a movement, or an inhibi-

tory input reaches the spinal cord preventing the motoneurons from triggering an action during action-observation. Our finding that the activation of the MI-forelimb area was weaker by 50% for action-observation than for action-execution (Raos et al. 2004) supports the first alternative of a subthreshold MI-cortico-spinal activation. However, our finding that anterior premotor areas F5 and F7 are activated much more for observation than for execution (Raos et al. 2007), and the fact that areas F5 and F7 send inhibitory projections to the spinal cord (Moll and Kuypers 1977; Sawaguchi et al. 1996), support the second alternative that during action-observation a parallel inhibitory influence suppresses the overt action at the spinal level. This alternative is further supported by our recent results demonstrating that the spinal section representing the forelimb (the cervical enlargement) is activated for action-execution but is inhibited for action-observation (Stamos et al. 2010). Apparently, our results support both mechanisms of (i) subthreshold MI-cortico-spinal activation and (ii) premotor-cortico-spinal inhibition, which may function in parallel to prevent the execution of the observed movement by the spectator.

Third question: Does the largely overlapping network, which supports both action-generation and action-perception, mean that the brain represents others' actions in the same way it represents one's own? If the same neuronal circuit is assigned the double-responsibility of execution and observation of an action, why don't we confuse the actions of others with ours? How do we distinguish between the observer and the actor if we recruit the action-execution neural circuit to simulate the action when we observe it? How do we attribute the action to the correct agent, i.e. to the self during action-generation and to the other during action-observation? How do we distinguish self and other, actor and spectator? Indeed, observation of an action implicates its perception (action-recognition) as well as its attribution to the correct agent (agency-attribution). In the following section I will describe how agency-attribution is based on separate neural correlates for the execution and observation of the same action which are responsible for distinguishing the self from the other in action. Based on our findings, I will present the potential neural substrate and biological mechanisms supporting the attribution of an action to the correct agent.

ATTRIBUTION OF ACTION TO THE CORRECT AGENT

As already mentioned, the observer of an action has not only to recognize the action but also to attribute it to the proper agent. The *shared representations* in execution and observation of the same action necessitate a separate *who system* for the attribution of agency (Daprati et al. 1997; Georgieff and Jeannerod 1998). The occipito-parieto-frontal activations, which we found to be common for execution and observation of the same action, are self-relative but agent-neutral (since they are shared by both actor and spectator), and thus can serve action-recognition but not action-attribution. In other words, action-recognition is represented by the common sensory-motor activations for execution and observation of the action, which correspond to the *shared representations* invoked by Jeannerod (2001). Conversely, there must be self-referential representations (that the actor does not share with the spectator), thus agent-specific, serving the agency-attribution network (or the *who system* by Jeannerod). Until recently (Raos et al. 2007; Evangelidou et al. 2009), the process of agency-attribution was assigned to distinct parietal (Sirigu et al. 1999; Ruby and Decety 2001; Farrer and Frith 2002) or prefrontal (McCabe et al. 2001; Vogeley et al. 2001; Platek et al. 2004) cortical areas of the primate brain. Instead, our findings suggest that agent-specific representations are not encoded in one agency-master cortical area apart from the execution/observation network, but are distributed within the entire net, as differences in intensity and lateralization of activations induced in the observer and the actor.

More specifically, we found that the spatial distribution of cortical activations induced by the execution and the observation of the same action were similar, in that the two networks overlapped extensively. This qualitative impression is consistent with the results of several other neuroimaging studies on monkeys and humans, which demonstrated activations induced by observation of action in small parts of the network revealed in our studies (Grafton et al. 1996; Decety et al. 1997; Hari et al. 1998; Buccino et al. 2001; Filimon et al. 2007; Gazzola and Keysers 2009). However, the qualitative similarity of the two networks may be more apparent than real, as it may mask quantitative differences in the intensity of activation of different nodes. The autoradiographic ^{14}C -deoxyglucose method (Sokoloff et al. 1977), which we have been using, is the only avail-

able neuroimaging method allowing (i) absolute quantification of functional activity (in glucose consumption rather than blood flow) in each single cortical area simultaneously, and (ii) much higher spatial resolution than any other contemporary neuroimaging method. Furthermore, this is the only presently available neuroimaging method that provides histological processing of sections neighboring those used for autoradiography, and thus the cytoarchitectonic identification of activated areas. Using this powerful method, we were able to demonstrate quantitative differences between the actors and the spectators, in the intensity and lateralization of effects, which may account for (or contribute to) the attribution of action to the correct agent. The following is a description of these quantitative differences between actors and spectators.

Within the frontal sensory-motor system, the activations induced by observation of action in the anterior premotor areas were stronger than those induced by action-execution (Raos et al. 2007), in contrast to the activations in the primary motor and somatosensory (MI/SI) forelimb areas which were weaker than those induced by action-execution (Raos et al. 2004). Also, the effects induced by action-observation were mainly bilateral, whereas those induced by action-execution were mostly contralateral to the moving forelimb. We have suggested that these differential activations of premotor and primary somatosensory-motor cortices play a role in attributing the action to the correct agent, i.e. to the other agent during action-observation and to the self during action-execution (Raos et al. 2007). For example, the higher level of MI-forelimb cortical activity for action-execution may reflect the intended movement (activity of the premotor cortical terminals in MI) and the actual motor command (MI cellular activity), whereas the 50% lower activity in MI-forelimb region for action-observation may reflect the intended movement only (due to mental simulation of the action during its observation). Moreover, the stronger SI-forelimb activation for action-execution may reflect the anticipated/predicted somatosensory consequence of the movement (based on efferent copy of the motor command from MI) and the actual re-afferent feedback (signal from the muscles), whereas the 50% lower activity in SI-forelimb region for action-observation may reflect only the predicted somatosensory consequence of the movement during its mental simulation. In the case of action-execution, the actual somatosensory re-afferent feedback signal from the muscles matches the predicted signal based on the efferent copy, and this matching may contribute to

the attribution of the action to oneself. In the case of action-observation, the predicted signal does not match any actual somatosensory feedback, and this mismatch contributes to the attribution of the action to another subject (Wolpert et al. 1995; Blakemore et al. 1998). In this manner, the comparison between efferent and re-afferent signals may serve the self identification in action. Moreover, the fact that in the case of action-execution the activations of the forelimb regions in the primary motor and primary somatosensory cortices are localized in the hemisphere contralateral to the moving hand signifies specificity of the effects related to hand-identity. In contrast, the activation of the same regions in both hemispheres for action-observation demonstrates that the information related to hand lateralization is not necessary for the perception of the action. These lateralization differences may also contribute to the attribution of action.

The bilateral and more intense activation of anterior premotor cortical area F5 and F7, and the less intense activation of the cingulate motor areas for action-observation as compared to action-execution in our studies (Raos et al. 2007), may reflect the incongruity between the mentally recalled/simulated action and its predicted/simulated sensory (kinaesthetic, tactile and visual) consequences on one hand, and the lack of its actual re-afferent sensory feedback during its mere observation on the other hand. The incongruity between imagined end-result of the action and its actual feedback may contribute to the attribution of action to the correct agent. This interpretation of our results is in agreement with the previous suggestion that the experience of ourselves or others as the cause of an action may be based on comparison of motor commands with the re-afferent feedback from the moving muscles and the external events caused by these commands (Johnson and Haggard 2005), the temporal attraction between self-produced actions and their sensory consequences binding them together to serve the experience of agency (Haggard et al. 2002). Likewise, the parietal activations induced by action-observation in our studies were in general weaker than those induced by action-execution, and displayed smaller inter-hemispheric differences (indicative of visuo-manual rather than hand-identity specificity) as compared with those induced by action-execution which were mostly contralateral to the moving forelimb preserving hand-identity specificity (Evangelidou et al. 2009). These differential activations of parietal cortical areas, which parallel those in the forelimb regions of the primary motor

and somatosensory areas, may also contribute to the attribution of action to the correct agent. Thus, our findings suggest that the frontal and parietal cortical areas associated with attribution of action to the correct agent may constitute a central component of the execution/perception distributed sensory–motor network, rather than an extra path aside from this network.

Finally, the extrastriate occipital visual cortical area V3 which was activated in all experimental cases of our studies and has been associated with processing visual features of action representations (de Lange et al. 2005; Milton et al. 2007; Bakker et al. 2008) may correspond to the human extrastriate body area (EBA). EBA in humans (Astavief et al. 2004) has been associated with (i) visual perception of body parts, compatible with its activation during action-execution in the light and action-observation, (ii) limb movements to visual targets even when the eyes are shut (compatible with its activation for action-execution in the light and in the dark), and (iii) mental imagination of goal-directed movements (compatible with its activation for action-observation). Interestingly, EBA has been implicated in the ability to distinguish between self and others (Jeannerod 2004; Saxe et al. 2006), a faculty inevitably involved in discriminating between the actor and the spectator. The argument for the involvement of EBA in agency-attribution has been that it integrates external (visually perceived) body signals with internal action signals (Jeannerod 2004). However, what is required for the attribution of an action to the correct agent is the integration of constantly updated information from sensory signals produced during the execution (or observation) of a movement with central signals that contribute to the generation (or mental simulation) of that movement. What is thus required is constantly integrated information about the motor intention and motor command as well as about the somatosensory and visual predicted and actual re-afferent feedbacks. Our experimental data do not indicate that the EBA is involved in any more specific way than the other cortical areas of the activated circuitry that also integrate visual with motor body-related information. There is no experimental evidence thus far that this type of information is integrated in any single area of the brain. Such elaborate integration of multimodal information can only be accomplished by the entire execution/observation sensory-motor circuitry specifically involved in each given behavior/experience.

In conclusion, the frontal component of the execution/observation action system participates in the process attributing an ac-

tion to the correct agent by integrating motor intended with motor command information, and somatosensory predicted (efferent) with re-afferent feedback signals. The parietal and the occipital components of the execution/perception system participate in the process of agency-ascription by integrating effector-related sensory-motor inputs with visual inputs, thus contributing to a coherent representation of the bodily self. The differences between the effects induced by execution and observation of the same action (which are agent-specific) consist in (i) the degree of activation of the various parts of the common circuitry, and (ii) the degree of lateralization of the common activations. These agent-specific differences may contribute to the attribution of the action to the correct agent. Thus, the attribution of an action to the self or to the external agent may be a function distributed within and throughout the action-execution/observation occipito-parieto-frontal network, and not a function assigned to one or two agency-dedicated areas on the side of this network. One does not need to postulate an additional system for monitoring the agency-attribution. No separate master area is needed to verify that it is *you who* is acting or feeling. The sense of agency may reside in the original stream of action and perception. Action-generation, action-perception and action-attribution may all be supported by different states of the same system rather than by different systems. Once in place the action-execution system can function as simulator for motor-cognition (supporting action-planning, action-recognition, action-prediction and motor imagery) and simultaneously can house the agency-attribution mechanism.

MIRROR NEURON SYSTEM THEORY AND MENTAL SIMULATION THEORY

Mirror neurons, which were discovered by Rizzolatti's group in the ventral premotor area F5c of the macaque monkey, were reported to respond selectively to actions both when generated and when observed by the monkey. It is important to note that the encounter frequency of mirror neurons in this area is about 8% (Gallese et al. 1996) and thus much remains to be discovered concerning area F5. Later, the same group reported mirror neurons also in the parietal area PF/PFG (Fogassi et al. 2005). Based on the discharge of a similarly small number of mirror neurons (16) that could distinguish grasping to eat from grasping to place, these authors were led to the conclusion that area PF/PFG encodes a dictionary of *goals* (Fogassi

et al. 2005). Even today it is not clear whether the mirror neurons of areas F5 and PF/PFG encode a *dictionary of actions* or a *dictionary of goals* (Gallese et al. 1996; Fogassi et al. 2005; Bonini et al. 2010; Rizzolatti and Sinigaglia 2010). Also it is not clear which areas are considered part of the so called *mirror neuron system* and the grounds on the basis of which they have been included in this system by Rizzolatti's group. For example, it is not clear why the lateral intraparietal (Shepherd et al. 2009) and the ventral intraparietal (Ishida et al. 2009) areas are considered part of this system, whereas the primary motor (Tkach et al. 2007) and the dorsal premotor cortices (Cisek and Kalaska 2004; Tkach et al. 2007) are not (Rizzolatti and Sinigaglia 2010), despite the fact that both groups of areas contain neurons responding to both the execution and the observation of the same action. More remarkably, it is not clear why area AIP is considered part of the *mirror neuron system* (Rizzolatti and Sinigaglia 2010) in spite of the fact that it has not been shown to contain neurons with *mirror* properties.

In addition to the single cell recording studies on monkeys described above, neuroimaging studies have demonstrated cortical areas of the monkey brain activated for both the execution and the observation of the same action. However, it is not clear why area STS (in the temporal sulcus) was early on considered to be part of the *mirror neuron system* (Rizzolatti et al. 2001), or why it is no longer thought to be part of that system (Rizzolatti and Sinigaglia 2010). Also it is not clear why the ventral premotor areas F5a and F5p, which were found in a fMRI study to be activated for both execution and observation of the same action (Nelissen et al. 2005), are included in the mirror neuron system (Rizzolatti and Sinigaglia 2010), whereas several frontal and parietal areas that were also found to be activated for both conditions in other neuroimaging studies of higher resolution (Raos et al. 2004, 2007; Evangelidou et al. 2009) are not included (Rizzolatti and Sinigaglia 2010). Nor is it clear why areas F5a and F5p are included in the mirror system since mirror neurons were encountered only in area F5c by single cell recording (Gallese et al. 1996). More generally, some of the areas that are activated for both action-execution and action-observation are arbitrarily excluded from Rizzolatti's action-recognition system, while other areas are included (Rizzolatti and Sinigaglia 2010) even if their activation is neither more specific nor better related to the generation and perception of action. For example, while the ventral premotor area F5 and the inferior parietal area PF/PFG are

included in the action recognition system, the primary motor and the dorsal premotor cortices are not. Moreover, the activation of the primary and secondary somatosensory areas is dismissed as due to *additional mechanisms* (for example, internal models) triggered by the mirror mechanism and the activation of the dorsal premotor and the superior parietal cortices is also dismissed as reflecting *motor preparation* (Rizzolatti and Sinigaglia 2010).

The discovery of mirror neurons was a major advance that led to the development of a whole new field. Mirror neurons have been invoked in accounts of empathy, evolution of language, social interaction, autistic spectrum disorder, etc. However, as argued above, these accounts are often divorced from empirical facts (Dinstein et al. 2008; Hickok 2009). There are several reasons for this development. First, there has been no systematic quantitative study of the properties of neurons in the two areas (F5 and PF/PFG) in which mirror neurons were discovered. Second, there has been no systematic search for neurons with the so-called *mirror properties* in all areas involved in action-execution. Third, there have been no lesion studies demonstrating that primates are unable to understand observed actions after inactivation of area F5c. Hickok detailed eight problems which undermine the claim that mirror neurons play a different role than other sensory–motor neurons in F5 in action understanding (Hickok 2009). Fourth, several regions have so far been found activated during both action-execution and action-observation in recording and neuroimaging experiments, but there is no principled method for selecting only those areas selected by Rizzolatti for inclusion in the *mirror neuron system*. Finally, most human studies on the effects of action-observation or action-imitation have been limited to the two *mirror areas* homologous to monkey areas F5 and PF/PFG and thus ignored the rest of the cortex. In general, there is little hard evidence about the so-called monkey and human *mirror neuron system*, since we do not know which brain areas contain mirror neurons and the exact behavioral correlates of their discharge. Theories attempting to capitalize on the mirror neuron system to explain imitation, empathy, verbal communication, theory of mind and autism are highly speculative, to say the least.

As described above, the *mirror neuron system* was originally located in the premotor area F5c. Later, the parietal areas PF/PFG and AIP were added. Recently, mirror neurons were also discovered in areas MI, F2, VIP and lateral parietal. On occasion, areas without motor properties such as STS (Rizzolatti et al. 2001; Iacoboni et al.

2005) and even pure somatosensory areas with neither motor nor visual properties (Avikainen et al. 2002; Keysers et al. 2004) have been considered part of the system. Nowadays, frontal areas BA6, SFG/MFG, preCG, BA44, parietal areas SI, SII, SPL, the supramarginal gyrus of the inferior parietal lobule, and the temporal areas MTG/ITG are suggested to be part of the *mirror neuron system* (Gazzola et al. 2007). Considering all the many cortical areas involved in action-observation, one wonders if action-perception involves the entire occipito-temporo-parieto-frontal cortical circuitry that controls action-execution, and not merely a few specific *mirror* regions. The proliferation of areas thought to comprise the *mirror neuron system* is a symptom of its crisis. However, this theory can be seriously challenged only by an alternative candidate that better explains the available biological data in the neuroscience literature.

Since the *mirror neuron system* is unlikely to be responsible alone for understanding actions, it is reasonable to ask if another system is. An affirmative answer is provided by our systematic and exhaustive search of the entire monkey cortex and the spinal cord (Raos et al. 2004, 2007; Evangeliou et al. 2009; Kilintari et al. 2010; Kilintari et al. (in press), Stamos et al. 2010; and unpublished observations of Raos and Savaki on the prefrontal and temporal lobes) using a high-resolution imaging method employing ^{14}C -deoxyglucose. Our studies demonstrated that most of the cortical networks supporting action-execution are activated during action-observation, while the spinal cervical enlargement is suppressed. To be specific, the frontal network activated for action-observation extends well beyond premotor area F5c (Raos et al. 2007) where mirror neurons were originally discovered (Gallese et al. 1996). Similarly, the relevant parietal network extends well beyond area PF/PFG (Evangeliou et al. 2009) where mirror neurons have also been reported (Fogassi et al. 2005). We revealed an extended overlap between the cortical areas activated for action-execution and those activated for action-observation in the frontal (Raos et al. 2004, 2007), parietal (Evangeliou et al. 2009), occipital (Kilintari et al. 2010), prefrontal and temporal (unpublished observations of Raos and Savaki) lobes. Our findings thus support the suggestion that *a process broader than mirroring is responsible for action-recognition* (Goldman and Sebanz 2005). Indeed, the specific activation of the forelimb region of the primary motor and primary somatosensory cortices, for observation of a goal-directed forelimb movement, indicates that the observer mentally simulates the observed movement. In other words, the neural

networks that normally support the generation of actions operate off-line (without leading to movement) in order to understand the actions of other subjects. In brief, our findings contradict the widely held, albeit unsubstantiated belief that the mirror neurons of areas F5c and PFG are necessary and sufficient for encoding the meaning of observed actions; instead, our findings support the theory that we understand the actions of others by activating our own action system, by mentally simulating observed acts.

CONCLUSION

Our high-resolution quantitative brain-imaging studies revealed that the neural substrate employed by monkeys in the generation of an action is largely re-employed during observation of the same action performed by another subject. The finding that the same cortical network underlies action-generation by the actor and action-perception by the observer, demonstrates that primates are able to use the resources of their own neural motor controller to perceive the motor behavior of other subjects. Sharing substantial portions of the underlying neural architecture for execution and observation of the same action indicates that action-perception relies on simulation of the observed action. It is as if the observer mentally rehearses the action of another subject in order to understand the nature of the act, its purpose and its justification from the actor's point of view. Of course this interpretation assumes that observer and actor have a standard policy, and that certain situations are linked to certain actions (Gordon 1995). In any case, neural overlap of first-person and third-person grasp of voluntary actions implies that the same mental program is implicated in both motor action and motor simulation. Analogies between mentally-simulated and actual states have been recognized in the domain of visual imagery, and now are well documented in the domain of motor imagery. Indeed, our finding that actual and mentally simulated actions share virtually the same neural network is analogous to earlier findings that vision and visual imagery share substantial portions of the underlying neural substrate.

Motor imagery or mental simulation of an action may enable us not only to understand the behavior of others, but also to distinguish among action options available to the acting agent, i.e. to predict the intentions and actions of others. In such prediction one behavior control system is used to model others, by a process-driven simula-

tion rather than by a theory-driven prediction. Mind-reading is thus an attempt to replicate the mental life of the acting agent, in which third person mental processes are simulated by first person processes. Mental simulation may also help us choose among our own action options, by running off-line alternative scenarios based on memorized experiences, using stored brain programs. Accordingly, intention, prediction, anticipation, recollection, planning, execution and recognition of an action may be supported by different states of one system (the motor controller), rather than by several different systems in the brain. Motor cognition is thus encoded in the motor system. By extrapolation, the character of our consciousness at any given moment may be determined by the state that our sensory and motor systems are in at that moment. Our findings thus support a globalist rather than a localizationist approach to awareness. They support the notion that the different aspects of motor awareness are represented by the different states of a distributed network underlying action-execution, rather than by a specific *awareness dedicated* area the function of which is both necessary and sufficient to produce motor awareness.

In general, our experimental findings discussed above support the notion that motor cognition relies on running the same motor apparatus which evolved to generate voluntary actions, upon simulation of memorized actions. And if *action-recognition is but restoration of the act*, and *understanding is but recalling*, then Plato's proposal that *knowledge is but remembrance* is more broadly true than he would have realized.

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REFERENCES

- Adams DL, Zeki S (2001) Functional organization of macaque V3 for stereoscopic depth. *J Neurophysiol* 86:2195-2203
- Aschersleben G, Prinz W (1995) Synchronizing actions with events: the role of sensory information. *Percept Psychophys* 57:305-317
- Astavief S, Stanley CM, Shulman GL, Corbetta M (2004) Extrastriate body area in human occipital cortex responds to the performance of motor actions. *Nat Neurosci* 7:542-548
- Avenanti A, Buetti D, Galati G, Glimcher SM (2005) Transcranial magnetic stimulation highlights the sensorimotor side of empathy for pain. *Nat Neurosci* 8:955-960
- Avenanti A, Bolognini N, Maravita A, Glimcher SM (2007) Somatic and motor components of action simulation. *Curr Biol* 17:2129-2135
- Avikainen S, Forss N, Hari R (2002) Modulated activation of the human SI and SII cortices during observation of hand actions. *NeuroImage* 15:640-646
- Bakker M, De Lange FP, Helmich RC, Scheeringa R, Bloem BR, Toni I (2008) Cerebral correlates of motor imagery of normal and precision gait. *Neuroimage* 41:998-1010
- Barsalou LW (1999) Perceptual symbol systems. *Behav Brain Sci* 22:577-609
- Blakemore SJ, Wolpert DM, Frith C (1998) Central cancellation of self-produced tickle sensation. *Nat Neurosci* 1:635-640
- Blakemore SJ, Frith CD, Wolpert DW (2001) The cerebellum is involved in predicting the sensory consequences of action. *NeuroReport* 12:1879-1885
- Blakemore SJ, Frith C (2005) The role of motor contagion in the prediction of action. *Neuropsychologia* 43:260-267
- Blakemore SJ, Bristow D, Bird G, Frith C, Ward J (2005) Somatosensory activations during the observation of touch and a case of vision-touch synaesthesia. *Brain* 128:1571-1583

- Bonini L, Rozzi S, Serventi FU, Simone L, Ferrari PF, Fogassi L (2010) Ventral premotor and inferior parietal cortices make distinct contribution to action organization and intention understanding. *Cereb Cortex* 20:1372-1385
- Buccino G, Binkofski F, Fink GR, Fadiga L, Fogassi L, Gallese V, Seitz RJ, Zilles K, Rizzolatti G, Freund HJ (2001) Action observation activates premotor and parietal areas in a somatotopic manner: an fMRI study. *Eur J Neurosci* 13:400-404
- Bufalari I, Aprile T, Avenanti A, Di Russo F, Aglioti SM (2007) Empathy for pain and touch in the human somatosensory cortex. *Cereb Cortex* 17:2553-2561
- Byrne RW, Whiten A (1988) *Machiavellian intelligence: social expertise and the evolution of intellect in monkeys, apes, and humans*. Clarendon Press, Oxford, UK
- Calvert GA, Bullmore ET, Brammer MJ, Campbell R, Williams SC, McGuire PK, Woodruff PW, Iversen SD, David AS (1997) Activation of auditory cortex during silent lip reading. *Science* 276:593-596
- Carr L, Iacoboni M, Dubeau MC, Mazziotta JC, Lenzi GL (2003) Neural mechanisms of empathy in humans: a relay from neural systems for imitation to limbic areas. *Proc Natl Acad Sci USA* 100:5497-5502
- Carruthers P, Smith PK (1996) *Theories of theories of mind*. Cambridge University Press, Cambridge, UK
- Cisek P, Kalaska JF (2004) Neural correlates of mental rehearsal in dorsal premotor cortex. *Nature* 431:993-996
- Cohen NR, Cross ES, Tunik E, Grafton ST, Culham JC (2009) Ventral and dorsal stream contributions to the online control of immediate and delayed grasping: a TMS approach. *Neuropsychologia* 47:1553-1562
- Costantini M, Galati G, Ferretti A, Caulo M, Tartaro A, Romani GL, Aglioti SM (2005) Neural systems underlying observation of humanly impossible movements: an fMRI study. *Cereb Cortex* 15:1761-1767
- Craighero L, Bello A, Fadiga L, Rizzolatti G (2002) Hand action preparation influences the responses to hand pictures. *Neuropsychologia* 40:492-502

- Daprati E, Franck N, Georgieff N, Proust J, Pacherie E, Dalery J, Jeannerod M (1997) Looking for the agent: an investigation into consciousness of action and self-consciousness in schizophrenic patients. *Cognition* 65:71-86
- de Lange FP, Hagoort P, Toni I (2005) Neural topography and content of movement representations. *J Cogn Neurosci* 17:97-112
- de Vignemont F, Ehrsson HH, Haggard P (2005) Bodily illusions modulate tactile perception. *Curr Biol* 15:1286-1290
- Decety J, Jeannerod M, Prablanc C (1989) The timing of mentally represented actions. *Behav Brain Res* 34:35-42
- Decety J, Jeannerod M, Durozard D, Baverel G (1993) Central activation of autonomic effectors during mental simulation of motor actions in man. *J Physiol* 461:549-563
- Decety J, Grezes J, Costes N, Perani D, Jeannerod M, Procyk E, Grassi F, Fazio F (1997) Brain activity during observation of actions. Influence of action content and subject's strategy. *Brain* 120:1763-1777
- Dinstein I, Thomas C, Behrmann M, Heeger DJ (2008) A mirror up to nature. *Curr Biol* 18:R13-18
- Edwards MG, Humphreys GW, Castiello U (2003) Motor facilitation following action observation: a behavioural study in prehensile action. *Brain Cogn* 53:495-502
- Evangelidou MN, Raos V, Galletti C, Savaki HE (2009) Functional imaging of the parietal cortex during action execution and observation. *Cereb Cortex* 19:624-639
- Farrer C, Frith CD (2002) Experiencing oneself vs another person as being the cause of an action: the neural correlates of the experience of agency. *NeuroImage* 15:596-603
- Felleman DJ, Van Essen DC (1987) Receptive fields properties of neurons in area V3 of macaque monkey extrastriate cortex. *J Neurophysiol* 57:889-920
- Fiehler K, Burke M, Engel A, Bien S, Rosler F (2008) Kinesthetic working memory and action control within the dorsal stream. *Cereb Cortex* 18:243-253

- Filimon F, Nelson JD, Hagler DJ, Sereno MI (2007) Human cortical representations for reaching: mirror neurons for execution, observation, and imagery. *Neuroimage* 37:1315-1328
- Fodor JA (1983) *Modularity of mind: an essay on faculty psychology*. MIT Press, Cambridge, MA
- Fogassi L, Luppino G (2005) Motor functions of the parietal lobe. *Curr Opin Neurobiol* 15:626-631
- Fogassi L, Ferrari PF, Gesierich B, Rozzi S, Chersi F, Rizzolatti G (2005) Parietal lobe: from action organization to intention understanding. *Science* 308:662-667
- Gallese V, Fadiga L, Fogassi L, Rizzolatti G (1996) Action recognition in the premotor cortex. *Brain* 119:593-609
- Galletti C, Battaglini PP (1989) Gaze-dependent visual neurons in area V3A of monkey prestriate cortex. *J Neurosci* 9:1112-1125
- Gazzola V, Keysers C (2009) The observation and execution of actions share motor and somatosensory voxels in all tested subjects: single-subject analyses of unsmoothed fMRI data. *Cereb Cortex* 19:1239-1255
- Gazzola V, van der Worp H, Mulder T, Wicker B, Rizzolatti G, Keysers C (2007) Aphasics born without hands mirror the goal of hand actions with their feet. *Curr Biol* 17:1235-1240
- Georgieff N, Jeannerod M (1998) Beyond consciousness of external reality: a *who* system for consciousness of action and self-consciousness. *Conscious Cogn* 7:465-477
- Gerardin E, Sirigu A, Lehericy S, Poline J-B, Gaymard B, Marsault C, Agid Y, and Le Bihan D (2000) Partially overlapping neural networks for real and imagined hand movements. *Cereb Cortex* 10:1093-1104
- Gibson JJ (1950) *The perception of the visual world*. Houghton Mifflin, Boston, MA
- Giraux P, Sirigu A (2003) Illusory movements of the paralyzed limb restore motor cortex activity. *Neuroimage* 20 Suppl 1:S107-111
- Goldman AI, Sebanz N (2005) Simulation, mirroring, and a different argument from error. *Trends Cogn Sci* 9:320; author reply 321
- Goodale MA, Jakobson LS, Keillor JM (1994) Differences in the visual control of pantomimed and natural grasping movements. *Neuropsychologia* 32:1159-1178

- Gordon RM (1986) Folk psychology as simulation. *Mind Lang* 1:158-171
- Gordon R (1995) *Folk psychology as simulation*. Blackwell Publishers, Oxford, UK
- Grafton ST, Arbib MA, Fadiga L, Rizzolatti G (1996) Localization of grasp representations in humans by positron emission tomography. 2. Observation compared with imagination. *Exp Brain Res* 112:103-111
- Haggard P, Clark S, Kalogeras J (2002) Voluntary action and conscious awareness. *Nat Neurosci* 5:382-385
- Haggard P, Taylor-Clarke M, Kennett S (2003) Tactile perception, cortical representation and the bodily self. *Curr Biol* 13:R170-173
- Hari R, Forss N, Avikainen S, Kirveskari E, Salenius S, Rizzolatti G (1998) Activation of human primary motor cortex during action observation: a neuromagnetic study. *Proc Natl Acad Sci* 95:15061-15065
- Heal J (1986) *Replication and functionalism*. Cambridge University Press, Cambridge
- Heath M, Westwood DA (2003) Can a visual representation support the online control of memory-dependent reaching? Evidence from a variable spatial mapping paradigm. *Motor Control* 7:346-361
- Hesslow G (2002) Conscious thought as simulation of behaviour and perception. *Trends Cogn Sci* 6:242-247
- Heyes CM, Foster CL (2002) Motor learning by observation: evidence from a serial reaction time task. *J Exp Psychol* 55:593-607
- Hickok G (2009) Eight problems for the mirror neuron theory of action understanding in monkeys and humans. *J Cogn Neurosci* 21:1229-1243
- Himmelbach M, Nau M, Zundorf I, Erb M, Perenin MT, Karnath HO (2009) Brain activation during immediate and delayed reaching in optic ataxia. *Neuropsychologia* 47:1508-1517
- Hommel B, Musseler J, Aschersleben G, Prinz W (2001) The theory of event coding (TEC): a framework for perception and action planning. *Behav Brain Sci* 24:849-878

- Hu Y, Eagleson R, Goodale MA (1999) The effects of delay on the kinematics of grasping. *Exp Brain Res* 126:109-116
- Hutchison WD, Davis KD, Lozano AM, Tasker RR, Dostrovsky JO (1999) Pain-related neurons in the human cingulate cortex. *Nat Neurosci* 2:403-405
- Iacoboni M, Molnar-Szakacs I, Gallese V, Buccino G, Mazziotta JC, Rizzolatti G (2005) Grasping the intentions of others with one's own mirror neuron system. *PLoS Biol* 3:1-7
- Ishida H, Nakajima K, Inase M, Murata A (2009) Shared mapping of own and others' bodies in visuotactile bimodal area of monkey parietal cortex. *J Cogn Neurosci* 22:83-96
- Jeannerod M (1994) The representing brain: neural correlates of motor intention and imagery. *Behav Brain Sci* 17:187-245
- Jeannerod M (2001) Neural simulation of action: a unifying mechanism for motor cognition. *Neuroimage* 14:S103-109
- Jeannerod M (2004) Visual and action cues contribute to the self-other distinction. *Nat Neurosci* 7:422-423
- Johnson H, Haggard P (2005) Motor awareness without perceptual awareness. *Neuropsychologia* 43:227-237
- Kennett S, Taylor-Clarke M, Haggard P (2001) Noninformative vision improves the spatial resolution of touch in humans. *Curr Biol* 11:1188-1191
- Keysers C, Wicker B, Gazzola V, Anton JL, Fogassi L, Gallese V (2004) A touching sight: SII/PV activation during the observation and experience of touch. *Neuron* 42:335-346
- Kilintari M, Raos V, Savaki HE (2010) Mental imagery serving action cognition includes visual in addition to the motor and kinesthetic components. *Soc Neurosci Abstract Viewer/Itinerary Planner Program No. 485.X. 2010*
- Kilintari M, Raos V, Savaki HE (in press) Grasping in the dark activates early visual cortices. *Cereb Cortex*
- Kilner JM (2003) An interference effect of observed biological movement on action. *Curr Biol* 13:522-525
- Kilner JM, Vargas C, Duval S, Blakemore SJ, Sirigu A (2004) Motor activation prior to observation of a predicted movement. *Nat Neurosci* 7:1299-1301

- Kosslyn SM (1994) Image and brain: the resolution of the imagery debate. MIT Press, Cambridge, MA
- Kosslyn SM, Ochsner KN (1994) In search of occipital activation during visual mental imagery. *Trends Neurosci* 17:290-292
- Kosslyn SM, Pascual-Leone A, Felician O, Camposano S, Keenan JP, Thompson WL, Ganis G, Sukel KE, Alpert NM (1999) The role of area 17 in visual imagery: convergent evidence from PET and rTMS. *Science* 284:167-170
- Lemay M, Proteau L (2002) Effects of target presentation time, recall delay, and aging on the accuracy of manual pointing to remembered targets. *J Motor Beh* 34:11-23
- Lotze M, Montoya P, Erb M, Hulsmann E, Flor H, Klose U, Birbaumer N, Grodd W (1999) Activation of cortical and cerebellar motor areas during executed and imagined hand movements: an fMRI study. *J Cogn Neurosci* 11: 491-501
- McCabe K, Houser D, Ryan L, Smith V, Trouard T (2001) A functional imaging study of cooperation in two person reciprocal exchange. *Proc Natl Acad Sci USA* 98:11832-11835
- Merleau-Ponty (1964) *Merleau-Ponty a la Sorbonne, resume de cours 1949-1952*. Gallimard, Paris, FR
- Meyer K, Damasio A (2009) Convergence and divergence in a neural architecture for recognition and memory. *Trends Neurosci* 32:376-382
- Milton J, Solodkin A, Hlustik P, Small SL (2007) The mind of expert motor performance is cool and focused. *Neuroimage* 35:804-813
- Moll L, Kuypers HGJM (1977) Premotor cortical ablations in monkeys: contralateral changes in visually guided reaching behavior. *Science* 198:317-319
- Mottonen R, Jarvelainen J, Sams M, Hari R (2004) Viewing speech modulates activity in the left SI mouth cortex. *NeuroImage* 24:731-737
- Nelissen K, Luppino G, Vanduffel W, Rizzolatti G, Orban GA (2005) Observing others: multiple action representation in the frontal lobe. *Science* 310:332-336
- Nishitani N, Hari R (2002) Viewing lip forms: cortical dynamics. *Neuron* 36:1211-1220

- Noe A (2004) *Action in perception*. MIT Press, Cambridge, MA
- Paccalin C, Jeannerod M (2000) Changes in breathing during observation of effortful actions. *Brain Res* 862:194-200
- Platek SM, Keenan JP, Gallup GG Jr., Mohamed FB (2004) Where am I? The neurological correlates of self and other. *Cogn Brain Res* 19:114-122
- Poggio GF, Gonzalez F, Krause F (1988) Stereoscopic mechanisms in monkey visual cortex: binocular correlation and disparity selectivity. *J Neurosci* 8:4531-4550
- Premack D, Woodruff G (1978) Does the chimpanzee have a theory of mind? *Behav Brain Sci* 4:515-526
- Prinz W (1984) *Modes of linkage between perception and action*. Springer, Berlin, DE
- Pulvenmuller F (2005) Brain mechanisms linking language and action. *Nat Rev Neurosci* 6:576-582
- Pulvermuller F, Fadiga L (2010) Active perception: sensorimotor circuits as a cortical basis for language. *Nat Rev Neurosci* 11:351-360
- Ramachandran VS, Rogers-Ramachandran D (1996) Denial of disabilities in anosognosia. *Nature* 382:501
- Raos V, Evangelidou MN, Savaki HE (2004) Observation of action: grasping with the mind's hand. *NeuroImage* 23:193-201
- Raos V, Evangelidou MN, Savaki HE (2007) Mental simulation of action in the service of action perception. *J Neurosci* 27:12675-12683
- Rizzolatti G, Sinigaglia C (2010) The functional role of the parieto-frontal mirror circuit: interpretations and misinterpretations. *Nat Rev Neurosci* 11:264-274
- Rizzolatti G, Fadiga L, Matelli M, Bettinardi V, Paulesu E, Perani D, Fazio F (1996) Localization of grasp representations in humans by PET: 1. Observation versus execution. *Exp Brain Res* 111:246-252
- Rizzolatti G, Fogassi L, Gallese V (2001) Neurophysiological mechanisms underlying the understanding and imitation of action. *Nat Rev Neurosci* 2:661-670

- Roland PE, Gulyas B (1994) Visual imagery and visual representation. *Trends Neurosci* 17:281-287; discussion 294-287
- Ruby P, Decety J (2001) Effect of subjective perspective taking during simulation of action: a PET investigation of agency. *Nat Neurosci* 4:546-550
- Sawaguchi T, Yamane I, Kubota K (1996) Application of the GABA antagonist bicuculline to the premotor cortex reduces the ability to withhold reaching movements by well-trained monkeys in visually guided reaching task. *J Neurophysiol* 75:2150-2156
- Saxe R, Jamal N, Powell L (2006) My body or yours? The effect of visual perspective on cortical body representations. *Cereb Cortex* 16:178-182
- Searle J (1992) *The rediscovery of the mind*. MIT Press, Boston, MA
- Shepherd SV, Klein JT, Deaner RO, Platt ML (2009) Mirroring of attention by neurons in macaque parietal cortex. *Proc Natl Acad Sci USA* 106:9489-9494
- Singer T, Seymour B, O'Doherty J, Kaube H, Dolan RJ, Frith CD (2004) Empathy for pain involves the affective but not sensory components of pain. *Science* 303:1157-1162
- Singer T, Seymour B, O'Doherty JP, Stephan KE, Dolan RJ, Frith CD (2006) Empathic neural responses are modulated by the perceived fairness of others. *Nature* 439:466-469
- Singhal A, Kaufman L, Valyear K, Culham JC (2006) fMRI reactivation of the human lateral occipital complex during delayed actions to remembered objects. *Vis Cogn* 14:122-125
- Sirigu A, Cohen L, Duhamel JR, Pillon B, Dubois B, Agid Y, Pierrot-Deseilligny C (1995) Congruent unilateral impairments for real and imagined hand movements. *NeuroReport* 6:997-1001
- Sirigu A, Daprati E, Pradat-Diehl P, Franck N, Jeannerod M (1999) Perception of self-generated movement following left parietal lesion. *Brain* 122:1867-1874.
- Skipper JI, Nusbaum HC, Small SL (2005) Listening to talking faces: motor cortical activation during speech perception. *NeuroImage* 25:76-89
- Smith NK (1929) *A commentary to Kant's critique of pure reason*. Macmillan, London, UK

- Sokoloff L, Reivich M, Kennedy C, Des Rosiers MH, Patlak CS, Pettigrew KS, Sakurada O, Shinohara M (1977) The [14C]-deoxyglucose method for the measurement of local cerebral glucose utilization: theory, procedure, and normal values in the conscious and anesthetized albino rat. *J Neurochem* 28:879-916
- Stamos AV, Savaki HE, Raos V (in press) The spinal substrate of the suppression of action during action observation. *J Neurosci*
- Sturmer B, Aschersleben G, Prinz W (2000) Correspondence effects with manual gestures and postures: a study of imitation. *J Exp Psychol Hum Percept Perform* 26:1746-1759
- Tkach D, Reimer J, Hatsopoulos NG (2007) Congruent activity during action and action observation in motor cortex. *J Neurosci* 27:13241-13250
- Urgesi C, Maieron M, Avenanti A, Tidoni E, Fabbro F, Aglioti SM (2010) Simulating the future of actions in the human corticospinal system. *Cereb Cortex* doi:10.1093/cercor/bhp292
- Vogeley K, Bussfeld P, Newen A, Herrmann S, Happe F, Falkai P, Maier W, Shah NJ, Fink GR, Zilles K (2001) Mind reading: neural mechanisms of theory of mind and self-perspective. *Neuroimage* 14:170-181
- Watkins KE, Strafella AP, Paus T (2003) Seeing and hearing speech excites the motor system involved in speech production. *Neuropsychologia* 41:989-994
- Westwood DA, Heath M, Roy EA (2000) The effect of a pictorial illusion on closed-loop and open-loop prehension. *Exp Brain Res* 134:456-463
- Wicker B, Keysers C, Plailly J, Royet JP, Gallese V, Rizzolatti G (2003) Both of us disgusted in my insula: the common neural basis of seeing and feeling disgust. *Neuron* 40:655-664
- Wilson M (2002) Six views of embodied cognition. *Psychon Bull Rev* 9:625-636
- Wolpert DM, Ghahramani Z, Jordan MI (1995) An internal model for sensorimotor integration. *Science* 269:1880-1882
- Zaki J, Weber J, Bolger N, Ochsner K (2009) The neural bases of empathic accuracy. *Proc Natl Acad Sci USA* 106:11382-11387

