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'Mirror Neuron Theory' versus 'Simulation Theory' for Action Understanding.

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Introduction.

Simulation, contrary to the popular conception of the term, refers to processes not only representing the same phenomenon, but also exhibiting important similarities in the means of its representation. The simulated and simulating functions generate similar results, when fed similar input. Mental simulation came to rise as an alternative to the cognitivistic consensus in the cognitive science of mentalizing, i.e. the mental mechanism underlying the recognition and attribution of intentional states to other putative agents, but also to oneself. The cognitivistic approach supports the notion that the use of implicit or explicit theories is central to mentalizing. These theories are generally ceteris paribus folk psychological laws that concern behavioral prediction. These laws generally take the following form: ‘‘Whenever an agent has a certain preferred desire (over competing desires) and believes that a certain behavioral scheme is the best means to fulfill said desire, the agent makes the decision to implement that behavioral scheme.’’ Knowledge of other minds is thus ideally the product of rational inference of some sort.

Theorists of the cognitivist persuasion have not been of a uniform view on such matters, with disputes arising with respect to the very epistemic nature of thinking about minds, but also about the way these abilities emerge and develop. Schools of thought such as the “rationality theory” (Davidson, 1984; Dennett, 1987), and the “theory-theory” (Botterill and Carruthers, 1999; Stich and Nichols, 2003) came to answer the first set of questions. Rationality theorists posit that beliefs consist of all the truths relevant to the agent's interests (or desires) that the agent's experience to date has made available (Dennet, 1987). Theory-theorists reject the normative aspect of mentalizing and substitute it with a truth-value neutral set of theories (Stich and Nichols, 2003). In essence, according to the theory-theory school of thought, mentalizing consists of the implementation of explicit or tacit theories of how an agent's mind works. Empiricism (Wimmer and Perner, 1983) and modularity-nativism (Baron-Cohen et al., 1985) were the main rival accounts of the development of mind reading. According to modularity/nativism, theories about minds are implemented by modules, i.e. informationally encapsulated functions (Fodor, 1983) that are usually innate and independent of a subject's experiences. Empiricists, on the other hand, disagree with the notion that mentalizing faculties are innate. For empiricists, the environment plays a crucial role in the development of mindreading faculties.

The debate about mentalizing in the 1970's and 1980's was partly philosophical and a priori, informed by the then vigorous defense of computationalism by Jerry Fodor (Fodor, 1975), and partly based on the findings of developmental psychologists, who developed novel experimental paradigms, involving false belief attribution (Leslie, 1987; Frith and Frith, 1999). The contribution of neuroscience was minimal, and restricted to the discourse about modularity, perhaps due to the dominance of functionalism in both cognitive psychology and the philosophy of mind.

Gordon (Gordon, 1986), Heal (Heal, 1986), and Goldman (Goldman, 1989), formulated and defended the mental simulation theory in the late eighties, attempting to establish the role of non-rational, causal and experiential processes in mentalizing. Mental simulation, according to these theorists, is the noetic function of temporary and perhaps confined adoption of the mental states of other mentally similar agents by the subject. This function generates results about intentional states of other agents, such as desires, beliefs and goals. Heal's arguments for simulation theory were mainly a priori, whereas Gordon and Goldman provided integrative and empirically informed arguments.

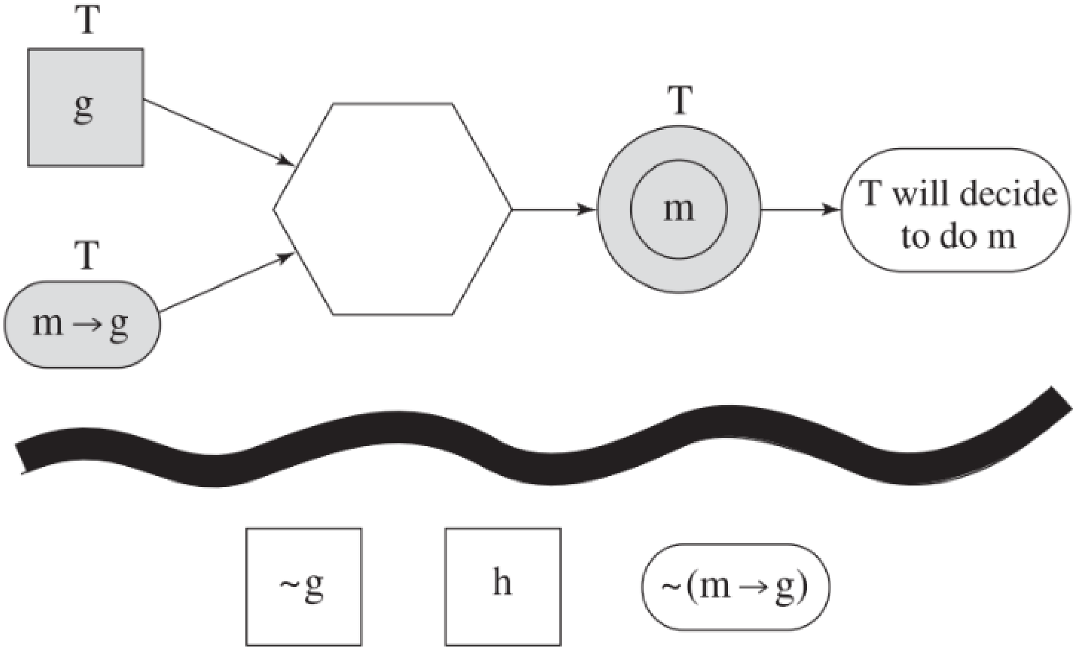

Figure 1.
A schematic representation of Goldman's theory. Rounded rectangles: Beliefs. Squares: Desires. Double circle: Decision. Hexagon: Decision-making mechanism. Black line: Quarantine of the subject's own beliefs and desires. The simulated desire is represented by “g”. The simulated belief is “m->g” (behavior m will fulfill desire g). “m” thus is the course of action that the simulated agent will have to take to fulfill desire “g”. Simultaneously, the subject will have to quarantine her desire “h”, her lack of desire “g”, and her belief that behavior “m” will not fulfill desire “g”. Reproduced from Goldman, 2009.

Figure 1 represents a schema of the mental simulation theory. The mentalizing process involves the input of pretend desires, beliefs and/or goals in a reasoning mechanism, that results in the prediction of the target agent's behavior. This process is taken offline, in the sense that the mental states of the subject, specifically her beliefs or desires, are isolated from the reasoning process in order to prevent self-centered biasing. The process of removing the subject's own perspective from the mentalizing function is called quarantine by Goldman (Goldman, 2009).

Goldman attempted to provide a link between premotor mirror-neurons and the mental simulation theory (Gallese & Goldman, 1998). As we will see in detail in the following paragraphs, mirror neurons are neurons that respond when a specific action is observed by a subject and when the subject itself executes that specific action. Mirror neurons were thought to be complementary to the simulation theory for the following reason. The presence of shared visual and motor representations of the action can putatively account for a simulation mechanism in a subject's brain. Specifically observation of a particular action induces a corresponding action state on the observing agent, mirroring the action state of the observed agent. This mirroring effect, hypothetically mediated by mirror neurons, would provide the subject with sufficient information to understand the observed action by experiencing it. Since 1998, mirror neurons were also recorded in the inferior parietal lobule (IPL). Other studies using action observation/execution paradigms, were also used to support the putative existence of a wide cortical mirror neuron “system” in the primate brain, underlying action understanding faculties. These studies have been integrated into the “mirror-neuron theory” of action understanding. This theory was later expanded to include accounts of diverse aspects of mental life such as language acquisition, imitation and empathy.

However, the mirror neuron theory has certain flaws that preclude it from providing a satisfying neural account of mentalization. The focus of the present report will be whether the mirror neuron theory can explain the mental faculty of action understanding. We will demonstrate that mirror neuron theory fails to explain the understanding of the actions of others at multiple levels. Even though the existence of mirror neurons is an important discovery, their function as a part of a supposedly mirror neuron system is not supported by neuroscientific data. An alternative to mirror neuron theory will be discussed, that is both more robust empirically and more supportive of the simulation theory.

Mirror Neurons.

Mirror neurons in non-human primates

Mirror neurons are neurons that significantly increase their firing rate compared to its baseline activity both when a specific action is performed by the subject and when the same or a similar action is observed by the subject (Rizzolatti and Craighero, 2004).

Neurons displaying mirror neuron properties were first reported by di Pellegrino et al. in 1992. The researchers recorded neuronal activity in the monkey cortical area caudal to the arcuate sulcus, namely the caudal part of area F5, while using an experimental paradigm in which the subject performed a specific hand action or observed the experimenter performing the same, similar or different actions. They differentiated the recorded neurons, based on their activity, into 4 categories. The first category consisted of neurons (12/128) in which the effective observed action and the effective executed action corresponded to each other. The coded action could be grasping with the mouth, grasping with the hands, object rotation, or object manipulation. The second category was formed by neurons (6/128) displaying increased firing rate when the subject executed specific hand actions and observed these same actions when executed by the experimenter, but also when the subject observed similar actions being executed. The third category comprised neurons (11/128) which did not respond to the observation and execution of the same actions but to actions that belonged to the same causal chain. For example a neuron of this type was responsive when the subject observed an object being placed on a table and also when the subject grasped the same object. The fourth category comprised neurons (10/128) which only had visual properties. These neurons responded to the observation but not the execution of specific actions.

In a following study the same group reported that there were three types of mirror neurons in the F5c area of the macaque monkey (Gallese et al., 1996). The first type, were strictly congruent mirror neurons (29/92). The observed actions that triggered responses in those neurons presumably shared goals and types of movements with the executed actions, for which those neurons were tuned. The second type involved broadly congruent mirror neurons (56/92). Broadly congruent mirror neurons were divided into three subcategories. One subcategory consisted of neurons (7/56) that were sensitive to the execution of specific actions, but responded to a broader repertoire of observed actions. The observed actions differed in one of their properties such as the specific grip used by the experimenter. Another subcategory consisted of mirror neurons with specific motor activity but nonspecific visual activity (46/56). The final subcategory involved neurons (3/56) with motor and visual selectivities presumably sharing the same goal. The third type of neurons (7/92) displayed no congruence of motor and visual activity whatsoever.

The interpretation of the motor activity of mirror neurons in terms of goal-coding is based on two representative studies (Rizzolatti et al., 1988, Umilta et al., 2008). F5c single neuron activity was recorded during the execution of various reaching to grasp paradigms (Rizzolatti et al., 1988). It was reported that F5c neuronal activity corresponding to specific prehension movements, such as tearing (n=11), holding (n=20), and grasping with the hand and the mouth (n=142). They divided recorded neurons into distal, which displayed activity correlated with the hand actions (n=173), and proximal, with activity correlated with the arm movements (n=22). The distal F5c neurons, with activity related to grasping, were further subdivided into precision grip (56/142), finger prehension (42/142), whole hand prehension neurons (6/142), and neurons with nonspecific grasping activity (38/142). In a later electrophysiological study the hypothesis that monkey F5c neurons encode a motor vocabulary of actions was suggested (Umilta et al., 2008). By studying the use of a pair of normal and reverse pliers for object prehension tasks, the researchers observed that a large part of the recorded neuronal population (n=113) coded the same epoch or epochs of the task regardless of the type of pliers used. This observation led them to conclude that motor neurons do not code specific motor action components, but a higher order representation that is related to the intention of the motor act. Interestingly, they obtained similar results from F1 neurons.

Knowledge about the localization and properties of mirror-neurons was somewhat enriched in later studies. In one such study the concluding segment of the observed action was obscured from the subject (Umilta et al., 2001). Mirror neurons, recorded from the monkey F5c, responded as they normally would, regardless if the target object was visible or not. This response was attenuated during the observation of mimed, intransitive movements. More importantly, the same pattern of neuronal responses was observed when the targeted object was removed and the final segment of the mimed intransitive action was obscured. Thus the behavior of the studied neuronal population was interpreted as reflecting the knowledge that the object/target of the movement was removed.

In a different study auditory properties were reported for motor neurons in the macaque F5c (Kohler et al., 2002). Thirteen percent of the recorded motor neurons were reported as being responsive to the sound produced by the execution of the movement to which they were sensitive. Many of these neurons (63/497) were sensitive to the mere sound produced by the observed/executed action that elicited an increase in firing rate. The preferred movements to those neurons were breaking and tearing, i.e. movements that produce distinct sounds. A more intriguing finding was that a part of the examined neuronal population (22/497) also exhibited visual activity, and more specifically sensitivity to action observation. Additionally a correspondence was reported between the executed, observed and heard actions to which the aforementioned tri-modal neurons were responsive.

In another study, out of the 105 mirror neurons recorded, 26% showed sensitivity to observed actions taking place in the monkey's extrapersonal space (Caggiano et al., 2009). The firing rates of those neurons exhibited a monotonic increase as a function of the distance of the observed action. Another 27% displayed sensitivity to observed actions that were executed in the monkey's peripersonal space, with the firing rates of the population decreasing as a function of the distance between the subject and the observed action. The rest exhibited no distance sensitivity. Another reported property was the plasticity of the receptive fields of some of the recorded neurons. Receptive fields seemed to represent what the authors defined as operational space, namely the space that the subject had motor access to. Operational space was constrained by the subject's freedom of movement. Consequently operational space had a small volume when the monkey was restrained, and extended when the monkey was free to execute arm movements. Only part of the population exhibited such functional plasticity, while other mirror neurons kept their receptive fields intact.

In addition to the macaque F5, the existence of mirror neurons was reported in the posterior parietal cortex and more specifically the inferior parietal lobule (IPL) (Fogassi et al., 2005). The activity of single neurons in the areas PF and PFG at the convexity of the IPL was recorded. The activity of all the studied neurons (n=165) was associated with hand grasping movements. Interestingly 60% of these neurons were reported to fire preferentially when these grasping movements were part of a larger goal directed sequence of movements. Specifically the firing rate of those neurons was significantly influenced by the movement following the movement to which they were sensitive. A subset of the latter neurons displayed typical mirror neuron activity (n=42). The majority of these neurons (16/42) were categorized as congruent mirror neurons.

A study that is interpreted as demonstrating the existence of mirror neurons in the ventral intraparietal area (VIP) of the monkey cortex was performed by Ishida et al. (Ishida et al., 2009). The VIP has been known to contain bimodal neurons with visual and somatosensory properties (Duhamel et al., 1998). In addition to the existing data, Ishida et al. reported novel response properties for some bimodal VIP neurons (n=23). A part of the VIP population could be divided into 3 categories. Mirror image matching neurons (10/23) were sensitive to tactile and visual stimuli on the left part of the subject's face or body, but also to the observation of similar stimulation of the right part of the experimenter's face or body. Central matching neurons (10/23) responded preferentially to visual and tactile stimulation of central areas of the subject's body. Also central matching neurons increased their firing rates during the observation of stimulation of the experimenter's central body areas that corresponded to the aforementioned central areas in the subject's body. Anatomical matching neurons (3/23) were similar to mirror image matching neurons, but exhibited an important difference. Similarly to mirror image matching neurons, anatomical matching neurons preferentially responded to the visual and tactile stimulation of specific parts of the subject's body. Whereas mirror image matching neurons were sensitive to the stimulation of the experimenter's contralateral side, anatomical matching neurons responded to stimulation of the experimenter's ipsilateral side. Even though Ishida et al. did not investigate whether those neurons exhibited motor properties, Rizzolatti and Sinigaglia interpreted the neurons' visual activity as a motor representation of the movement that induced the activity (Rizzolatti and Sinigaglia, 2010).

Along with the IPL and the VIP, another posterior parietal area that is considered by some authors to contain mirror neurons is the lateral intraparietal area (LIP). It is well known by earlier studies (e.g. Colby et al., 1996) that part of the LIP neuronal population consists of neurons with occulomotor, but also visual properties. In a recent electrophysiological study on monkeys, Shepherd et al. observed visuomotor responses in a subset of LIP neurons that were interpreted as reflecting mirror neuron activity (Shepherd et al., 2009). Specifically a subset of the recorded population increased its firing rate both when the subject executed saccades towards a preferred direction and when it observed another monkey executing saccades in the same direction. Another subset of the population exhibited suppression of its responses under the aforementioned condition.

Finally, investigation of single neuron activity in the dorsal premotor cortex revealed that part of the studied population exhibited an increase in neuronal responses during both the execution and the observation of the same action (Cisek and Kalaska, 2004; Tkach et al., 2007). Increased single neuron firing rate elicited by both action observation and action execution has also been reported for the primary motor cortex (Tkach et al., 2007).

In conclusion, mirror neurons were found not only in areas F5 and PF/PFG, but also in areas MI and dorsal premotor which for an obscure reason are not included in the so called ‘mirror neuron system’ Equally unsubstantiated is the inclusion of areas VIP and LIP in this system, as we will see below.

The Mirror-Neuron System in Humans

Some initial observations leading Rizzolatti's group to posit the existence of the mirror system in humans were reported in Fadiga et al., 1995. In this study motor evoked potentials (MEPs) were recorded from hand and arm muscles related to grasping during the observation of grasping actions. MEPs were elicited by transcranial magnetic stimulation (TMS) of the motor cortex. The detection of an increase in MEP size compared to control conditions indicated sub-threshold activity in the motor cortex during the observation task. A later TMS study reproduced the previous results and furthermore provided evidence for a motor cortical modulation correlated with the degree of correspondence between the orientation of the observer and the orientation of the observed action (Maeda et al., 2002). Furthermore Gangitano et al. observed that MEP modulation during the observation of actions reflected specific phases of said actions (Gangitano et al., 2001).

The results of several recent studies in humans have been used to further support the notion that a homologous and functionally similar system to the monkey mirror neuron system exists in humans. However, several additional areas are reported to be activated for both execution and observation of the same action in humans, additionally to the ones comprising the mirror neuron system in monkeys. The methods used range from functional imaging (PET, fMRI) to the use of EEG, MEG and TMS. In a PET study activation in the caudal part of the left inferior frontal gyrus (corresponding to Broca's area) was reported (Rizzolatti et al., 1996b). This finding was reproduced by later studies, which added the anterior component of the inferior parietal lobule and the ventral part of the precentral gyrus, as well as the primary motor and somatosensory cortices, to the network of motor areas activated by action observation (e.g., Grafton et al., 1996; Grezes et al., 1998, 2001, 2003; Iacoboni et al., 1999, 2001; Nishitani & Hari 2000, 2002; Buccino et al., 2001; Decety et al., 2002; Perani et al., 2001; Koski et al., 2002, 2003; Manthey et al., 2003; Gazzola et al., 2007; Chong et al., 2008). For instance, Chong et al. in an fMRI study using an adaptation paradigm, interpreted their results as revealing selective activity in the right IPL during both action observation and action execution (Chong et al., 2008). Since adaptation after exposure to repetitive stimulation is considered to reflect specificity (Grill-Spector, 2001), these results were thought to reflect mirror neuron activity in the IPL (Rizzolatti and Sinigaglia, 2010). Another group investigated the dependence of the aforementioned frontal activation on the dynamicity of the observed action or the presence of an explicit goal (Johnson-Frey et al., 2003). The stimuli used in the study were static pictures of hands engaging objects in a prehensile manner. The researchers suggested that frontal activation was independent of the action dynamic, as long as the picture represented a goal-directed action. Buccino et al. observed a pattern of lateralization during the observation of mouth actions performed either by con-specifics or non-con-specifics (Buccino et al., 2004). Human subjects displayed specific right hemisphere activations in these areas for the observation of human mouth actions, whereas increased activity was reported in the left hemisphere, regardless of species of the agent under observation. Later neuroimaging studies added MI (Gazzola et al., 2007), SI, SII and SPL (Gazzola et al., 2007; Gazzola and Keysers, 2009) to the set of areas specifically activated during the observation and executions of transitive actions.

The Mirror-Neuron Theory of Motor Cognition and Action Understanding.

It has been suggested that mirror neurons may be involved in diverse cognitive functions such as motor cognition, action understanding, imitation (Rizzolatti et al., 2001), empathy (Gallese et al., 2004), the acquisition of language skills (Rizzolatti and Craighero, 2004), and mindreading (Gallese et al., 2004). Moreover dysfunction of the mirror neuron system (MNS) has been hypothesized to account for Autism Spectrum Disorders (Rizzolatti and Craighero, 2004). The present report will focus on the claim of MNS theorists that this system is responsible for motor cognition and action understanding.

It is far from documented that mirror neurons can provide an exhaustive account of the biological machinery supporting action understanding, in contrast to what is often claimed in contemporary neuroscientific and cognitive scientific literature. An initial problem is the scarcity of mirror neurons. Mirror neurons were encountered at a frequency of 8% in F5c (Gallese et al., 1996), whereas only 16 mirror neurons were reported in PF/PFG (Fogassi et al, 2005). It would be excessive to qualify these two clusters as a system. On the other hand the choice of cortical structures that are included in the mirror system is arbitrary. Mirror-neuron theorists, for instance, include area AIP in the mirror system (Rizzolatti and Sinigaglia, 2010). This area however does not contain neurons with mirror-neuron properties. Also arbitrary was the inclusion of VIP in the system (Rizzolatti and Sinigaglia, 2010), given that motor properties have not been recorded in VIP neurons. In an earlier review, Rizzolatti and his co-authors included area STS in the mirror neuron system (Rizzolatti et al., 2001). Even though STS was later removed from the mirror system (Rizzolatti and Sinigaglia, 2010), its initial inclusion is rather puzzling, as it is an area with no documented motor activity. The findings of Shepherd et al. are open to alternative interpretations to those of Rizzolatti and Sinigaglia. The changes in firing rates that were reported in the latter study, during action observation, may for instance be seen as reflecting effects of a covert shift of attention to socially relevant stimuli (Shepherd et al., 2008). Saccadic movements cannot be easily seen as being part of a specific motor vocabulary. It would therefore be far-fetched to describe LIP neurons as mirror neurons.

The notion that mirror neurons encode not only a dictionary of actions but also a dictionary of goals is also not substantiated. For example the results obtained by Fogassi et al., with regard to IPL mirror neuron activity during action observation, can be seen as supporting not the encoding of goals but rather the effect of an anticipatory feed forward motor command. Similar reasoning can be applied to F5c mirror neuron behavior (Hickok, 2009).

In a monkey fMRI study, Nelissen and colleagues reported the involvement of the anterior component of area F5, that lies in the depth of the arcuate sulcus, in action observation/execution tasks (Nelissen et al., 2005). That area was additionally activated during the observation of isolated arm actions, mimicked actions, and grasping movements performed by a non-biological effector, none of which elicited activity in F5c. The authors interpreted their results as reflecting a functional segregation in the frontal mirror-neuron system. According to them, whereas the sulcal F5 component codes the action as such, the caudal component represents the action in its intentional context. The absence of evidence for the presence of mirror neurons in the sulcal component of F5 (Gallese et al., 1996) makes its later inclusion in the mirror system problematic. The latter problem is generally apparent in mirror neuron theorists' interpretations of imaging results. For instance there haven't been convincing reports of single unit mirror neuron activity in AIP or VIP, even though they were later included in the mirror neuron system (Rizzolatti and Sinigaglia, 2010). Other researchers simply assumed that the activation of areas SI, SII and SPL, in both action execution and action observation, reflects mirror neuron activity (Gazzola et al., 2007; Gazzola and Keysers, 2009), even though there is neither electrophysiological evidence of mirror neurons nor documented motor activity in these areas. It is then a large leap to interpret imaging activations in these areas, during action observation/execution paradigms, as reflecting mirror neuron activity. The claim that the area of Broca contains mirror neurons (Rizzolatti et al., 1996b) is equally unsubstantiated. The locus of activation in Broca's area that was reported in that study during action observation tasks didn't overlap with the locus of activation during action execution tasks. It is therefore impossible that the same neurons were directly responsible for the reported activation patterns. Mirror neurons were therefore not at work in that case.

Of course these reported activations can be integrated into an alternative view about the neurobiological foundations of action understanding. As we will see in a later section, there is strong evidence of the involvement of a wide fronto-parieto-occipital network in action observation/execution. Whereas some of the areas that exhibit activity in imaging studies using the action observation/execution paradigm are arbitrarily included in the mirror system, others are equally arbitrarily excluded from it. For instance, frontal areas such as Brodmann's areas 6 and 44, the superior and middle frontal gyri, parietal areas SI, SII, the superior parietal lobule, the supramarginal gyrus, and the middle and inferior temporal gyri are considered part of the mirror system (Gazzola et al., 2007), whereas area MI and the dorsal premotor cortex are not, in spite of strong evidence that neurons in these areas have mirror properties (Kisek and Calaska, 2004; Tkach et al., 2007).

In addition to the lack of coherence of the theory underlying the term, there are further problems with the notion that the mirror-neuron system is central in action understanding. A particular objection that can be raised to the theory of Rizzolatti and colleagues, regarding the role of the mirror neuron system in action understanding, is that there is no positive evidence supporting its necessity in such a function. For instance a decrement in action perception has never been reported from monkey F5 lesion studies. On the contrary areas in the mirror-system can be trained to be decoupled from a specific observed action and coupled to another, with no change in action specific recognition (Catmur et al., 2007; 2008).

If mirror neuron theory is to be rejected, how can one interpret the numerous findings reported above? An alternative that is both more parsimonious and consistent with empirical findings will be described below.

Mental Simulation and the Fronto-Parieto-Occipital Network.

As we saw several studies have established that observation and execution of the same action involve overlapping cortical areas. These areas span across a large part of both the frontal and parietal lobes. Moreover, these areas activated for both observation and execution of the same action only partly overlap with the areas claimed to constitute the mirror-neuron system. Additionally, since the data presented below mainly come from neuroimaging studies, it is not certain that the reported overlaps involve the same populations of neurons.

Numerous imaging studies indicate that one of the frontal areas involved in both the execution and observation of grasping movements is the caudal dorsal premotor cortex (PMcd; alternatively area F2 in monkeys) (Grafton et al., 1996; Decety et al., 1997; Buccino et al., 2001; Raos et al., 2004; Filimon et al., 2007; Raos et al., 2007). Additionally the convexity of the rostral ventral premotor cortex (PMrv; or F5c in monkeys) has repeatedly been reported to display increased activity in grasping execution/observation paradigms (Grafton et al., 1996; Rizzolatti et al., 1996b; Decety et al., 1997; Nelissen et al., 2005; Raos et al., 2007). The supplementary motor area-proper is reported to be involved only in action execution tasks (Raos et al., 2007). Numerous studies have reported increased medial frontal activity in grasping execution and observation (Stephan et al., 1995; Grafton et al., 1996; Gerardin et al., 2000; Nishitani and Hari, 2000; Costantini et al., 2005; Filimon et al., 2007). A ^{14}C-deoxyglucose study reported that these medial frontal activations corresponded to the pre-supplementary motor area (pre-SMA; or F6 in monkeys), the medial components of Brodmann areas 8 and 9 (corresponding to the dorsomedial prefrontal cortex), and the anterior part of Brodmann area 24 (corresponding to the caudal part of the anterior cingulate gyrus) (Raos et al., 2007). The medial cortical area 9 and the anterior part of area 24 are thought to control movement selection based on the current behavioral goals of the subject (Matsumoto et al., 2003). Activation of the caudalmost region of the cingulate gyrus has been observed during action observation and action execution (Raos et al., 2007). This cortical area corresponds to the supplementary somatosensory area (Morecraft et al., 2004). An equally important finding is that the anterior premotor areas F5 and F7 are activated much more for observation than for execution (Raos et al. 2007). The importance of this finding will be discussed later.

A similar picture emerges from the study of the parietal lobe. Parts of the lateral superior and inferior parietal lobe, are activated in imaging studies both for execution and observation of actions involving the arm and hand (Bonda et al., 1996; Grafton et al., 1996; Decety et al., 1997; Grezes et al., 1998; Buccino et al., 2001). A ^{14}C-deoxyglucose study, offering higher spatial resolution, reported that the areas activated in the lateral superior and inferior parietal cortex, were areas PE and PEc, and area PF, respectively (Evangeliou et al., 2009). Areas PE and PEc receive somatosensory afferents from the primary somatosensory cortex and share connections with the primary motor cortex (Jones et al., 1978), the lateral premotor cortex (Marconi et al., 2001) and the supplementary motor area (Pandya and Seltzer 1982). Their activation may reflect processing of information about hand and target position for reaching, and/or movement kinematic information (Ashe and Georgopoulos 1994). Area PF is connected with the primary somatosensory cortex, areas PG, PFG, and the premotor arm-representations (Pandya and Seltzer 1982). Intraparietal areas exhibiting increased activity for both action observation and execution are the intraparietal component of PE (PEip), the medial intraparietal area (MIP), the ventral intraparietal (VIP) area and the anterior intraparietal area (AIP) (Evangeliou et al., 2009). Area MIP is known to respond to somatosensory and visual signals (Colby and Duhamel, 1991). There is also evidence that VIP encodes visual information about the spatial location of targets for motor acts (Gregoriou and Savaki, 2001). AIP neurons encode information about hand configurations during grasping (Murata et al., 2000). In addition to lateral parietal areas, medial parietal areas, namely the retrosplenial cortex and area PGm, and the parietoccipital area V6 are recruited for both observation and execution of the same action (Evangeliou et al., 2009). Area V6 contains motion sensitive neurons (Galletti et al. 1996). PGm exhibits sensitivity to visual, arm control and occulomotor information (Ferraina, Johnson, et al. 1997), presumably processing signals related to target localization and reaching.

Predominantly visual areas also participate in the observation/execution network. Kilintari et al. demonstrated that extrastriate areas V3d and V3a are activated during tasks involving the observation of grasping, but also during the execution of grasping movements by the subject in the light, i.e. under visual guidance (Kilintari et al., 2010). V3 is connected to many of the parietal areas mentioned above (Felleman et al., 1997) providing visual input for visuomotor transformation, especially during reaching and grasping movements with the forelimb (Nakamura et al., 2001; Galletti et al., 1997). The occipitoparietal segment of V3d may be involved in mental imagery (Sathian and Zangalandze, 2002; Darling et al., 2007). It may also correspond to the extrastriate body area (Astavief et al., 2004). Actually, during the execution of grasping in complete darkness, in addition to V3, V1 and V2 were activated (Kilintari et al., 2010). The latter activations may reflect the mobilization of stored visual representations necessary to guide the forelimb in the dark, i.e. in the absence of any visual input.

Strong evidence for mental simulation also comes from the detection of increased activity in the primary motor and somatosensory cortices (MI/SI). Hari et al. performed a MEG study on human subjects during the observation and execution of transitive movements (Hari et al., 1998). Five hundred (500) ms after stimulation of the median nerve, one can observe increased power in 20Hz oscillations in the precentral area. This change in activity, referred to as rebound, is associated with an increase of MI inhibition. Hari et al. observed a decrease in 20Hz oscillation power during action observation, and suggested an increase in MI activity. Suppression of the rebound is also observed during action execution. In this condition the suppression is double of the suppression reported during action observation. Similar findings have been reported when the auditory result of the action is heard by the subject (Caetano et al., 2007). Furthermore SI MEG signals are enhanced during object manipulation and execution (Avikainen et al., 2002). Raos et al. reported a specific increase in activity of the forelimb representation in both MI and SI cortices for both grasping observation and grasping execution, with significantly greater activation for execution. The latter results complement previous TMS findings in humans (Fadiga et al., 1995; Gangitano et al., 2001; Maeda et al., 2002). The presence of MEPs in muscles during action observation is compatible with the MI-forelimb activation for observation of forelimb movements reported by Raos et al., 2004.

Since Rizzolatti and colleagues deny that MI contains mirror neurons, all the above results contradict fundamental assumptions of the mirror neuron theory.

The SI activation for action observation may be indicative of the presence of sensory-motor representations in the subject's brain, which are recruited during action observation. There is evidence that somatosensory signals are tightly interwoven with movement execution. For example predictive grip force, during object manipulation, is known to be modulated by sensory feedback, e.g. by the expected 3-D properties of the object to be manipulated (Blakemore et al., 1998a). Furthermore, Weiskrantz et al. studied the psychophysical characteristics of tickling oneself and being tickled, and concluded that self-administered tickles are less effective than externally produced ones. They also observed that passive arm movements of a subject reduce the strength of tickle sensation (Weiskrantz et al., 1971). The tickliness of a tactile stimulus, was found to be proportional to the error produced by the comparison between the predicted sensory consequences of a motor command and the actual sensory feedback from the movement (Blakemore et al., 1999). These results are further complimented by the finding that haptic deafferentiation, i.e. the loss of proprioceptive afferents, severely impairs the ability of a subject to accurately predict the consequences of a motor command (Farrer et al., 2003). Consequently, the finding of MI and SI co-activation for action observation is highly suggestive of (conscious or unconscious) action rehearsal during action observation.

Finally, of importance is that in the studies of Savaki and colleagues (Raos et al., 2004; Raos et al., 2007; Evangeliou et al., 2009) the reported activations for the observation and the execution of reaching-to-grasp were confined to the forelimb representations of motor and somatosensory cortices, demonstrating that the effects were highly specific. These studies used the ^{14}C-deoxyglucose method (Sokoloff et al., 1977), which offers a higher spatial resolution than the PET and fMRI imaging methods. Moreover, this method is more directly indicative of neural activity, because it measures glucose consumption rather than blood flow and also permits the cytoarchitectonic identification of cortical domains activated during performance of the behavior under investigation.. The enhanced activity in SI-forelimb representation for grasping- observation was interpreted as the mentally predicted/anticipated somatosensory feedback from the involved forelimb muscles. In other words, it was suggested that during action observation the observer mentally simulates the observed movement along with its somatosensory consequences (Savaki, 2010).

Imagery: A possible means of Simulation.

Bearing in mind the role that imagery and internal rehearsal play in human imagination, one is warranted to assume that mental simulation is often implemented in primates. Motor imagery is considered to be a way to access motor intentions or plans, in which the representation of a given action is internally performed without any overt motor output (Jeannerod, 2001). There are several lines of evidence supporting that motor imagery strongly depends on the implementation of motor representations.

Motor imagery is characterized by psychophysical features that underlie overt action execution (Decety et al., 1989). Imagined actions retain the same temporal characteristics as the corresponding overt actions (Jeannerod, 2001). Response times in mental and manual rotation of the same kinetic characteristics are indistinguishable, while discordance in the used axes between the two conditions disfacilitates mental rotation (Wohlschlager & Wohlschlager, 1998). Mental object rotation is slower if hand movements are planned in a direction opposite to the presumed mental rotation direction, but only if the axes of hand rotation and mental object rotation are parallel in space, regardless of putative preparatory movements (Wohlschlager, 2001). Fitts' law suggests that the total duration of a movement is inversely related to the logarithm of target width (Fitts, 1992). Fitts' law has been shown to account equally well for actual and imagined movements in healthy subjects (Decety and Jeannerod, 1996), while it fails to describe imagined finger movements in patients with unilateral parietal lesions (Sirigu et al., 1996).

Several studies have shown that the neural correlates of motor imagery exhibit a significant overlap with the neural correlates of motor execution. These studies involve tasks that probe motor imagery functions. For example the subject can imagine executing a set of movements. Motor imagery studies have shown that during motor imagery tasks activation can be seen in MI (Decety et al., 1994), the ventral (Parsons et al., 1995; Stephan et al., 1995; Gerardin et al., 2000) and dorsal premotor cortex (Parsons et al., 1995; Stephan et al., 1995; Grafton et al., 1996; Gerardin et al., 2000; Johnson et al., 2002; Naito et al., 2002; Filimon et al., 2007), parts of the anterior cingulate gyrus (Decety et al., 1994), the superior parietal lobule (Stephan et al., 1995; Johnson et al., 2002), the inferior parietal lobule (Decety et al., 1994; Johnson et al., 2002) and parts of the intraparietal sulcus (Stephan et al., 1995; Johnson et al., 2002). This overlap clearly demonstrates that largely the same cortical areas participate in action execution and motor imagery.

A biological account of Mental Simulation.

If the mirror neuron theory is in fact unfit to account for the biological basis of action understanding, can one formulate a suitable alternative? The data presented above suggest a plausible candidate. As indicated by the involvement of similar cortical areas in observation, imagery and execution of an action, movements and their sensory feedback are processed as corresponding motor, somatosensory and visual representations during the execution of an action, and are recruited during observation and imagery of the same action. It is worth repeating that these activations are highly specific, corresponding to the involved effector. In other words, when a grasping action is performed, the forelimb representations of the primary somatosensory and motor areas are recruited. During action observation or imagery of the same action, the same sensory-motor representations are re-implemented. This suggests that these representations are stored and available to the agent in a multitude of action scenarios. Whenever a different agent performs a particular motor task, corresponding mental states are induced in the observer. The observer experiences the sensory-motor contingencies that the actor experiences. The subject can additionally mobilize these experiences at will in mental rehearsal. Thus, a large part of the necessary information to evaluate the context of a certain action is stored in our brain during its prior execution. This knowledge is needed for planning and actively controlling an action. The existence of sensorimotor representations of action goals makes abstract concepts of behavioral prediction redundant, contrary to what cognitivists may suggest. Furthermore the fact 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 action simulation. As already mentioned in the introduction, similarity of the means of a representation is central to simulation. Thus, it becomes clear that the data presented above support the simulation theory of action understanding.

Quarantine.

Two questions remain. The first one concerns the fate of the motor facilitation that is observed during action observation. Specifically, the issue of why action observation does not cause action execution must be resolved. The second question regards the cortical mechanism underlying the attribution of action to the correct agent. If the network underlying action execution and observation is common, how does the subject differentiate between one's own and others' actions?

The answer to the first question involves corticospinal interactions. Specific patterns of EMG activity were demonstrated during reaching to grasp movements (Lemon et al, 1995). Extrinsic hand muscles, which act to orientate the hand and finger tips, and muscles that contribute to transportation of the forelimb receive strong excitatory input during the reach phase of the action, whereas intrinsic hand muscles receive strong cortical input during grasping. The inverse pattern was also reported during the induction of the H-Reflex in a finger flexor muscle of a subject who observed hand actions (Baldissera et al., 2001). This effect may reflect spinal or motor cortical activity that counteracts the efferent excitatory signals produced by the fronto-parieto-occipital observation/execution network.

Recent evidence supports the second interpretation, according to which cortical efferents inhibit spinal cord activity during action observation. The existence of corticospinal neurons in the monkey F5 area that modulate their firing rate during action observation has been reported (Kraskov et al., 2009). These neurons may be inhibitory since it is well known that areas F5 and F7 influence the spinal cord through inhibitory projections (Sawaguchi et al., 1996). This observation complements the findings of Raos et al., 2007. Specifically the fact that premotor areas F5 and F7 exhibit larger activations for observation than for execution of the same action, supports the hypothesis that during action-observation a parallel inhibitory influence suppresses the action signal sent to the spinal cord from the primary motor cortex (Raos et al. 2007). Indeed the effect of action observation on the spinal forelimb representation was recently investigated in monkeys, and bilateral suppression of its activity was reported for action observation, whereas action execution significantly increased local activity as expected (Stamos et al., 2010).

In the parietal cortex, cortical activations for action execution are generally stronger compared to the activations observed during action observation (Evangeliou et al., 2009). This holds true for areas MI and SI as well (Raos et al., 2004). In contrast to the above, the premotor areas F5 and F7 tend to display increased activation for action observation as compared to action execution (Raos et al., 2007). Moreover, the effects observed across the frontoparietal network during action observation are mainly bilateral, whereas those induced by action execution are generally contralateral to the effector (Raos et al., 2004; 2007; Evangeliou et al., 2009). These differential activations (with regard to intensity and lateralization) for action observation and action execution may underlie the ability of the subject to attribute the action to the correct agent. Specifically, the awareness of oneself as the source of a particular action may depend on the comparison between a motor command and re-afferent proprioceptive signals from the muscles used in the execution of such an action (Wolpert et al., 1995; Johnson and Haggard, 2005). The manipulation of this motor command by transcranial magnetic stimulation affects the timing of the phenomenology of agency (Haggard et al., 2002). This general hypothesis has also been tested by Blakemore et al., who reported increase in SI activity during self-produced tactile stimulation, and decreased activity when the stimulation was induced by another subject (Blakemore et al., 1998b). Furthermore, the felt somatosensory effects of muscle twitches induced by TMS to the M1 were less intense when the stimulation was caused by a voluntary action of the subject, compared to effects of involuntary actions (Tsakiris and Haggard, 2003). Thus, there is evidence that the fronto-parietal network participates in the comparison between feed forward action commands and the sensory feedback generated from the resulting movements.

Conclusion.

The specific role of mirror neurons and their contribution to action generation, observation and understanding is still unclear. More research is needed in order to elucidate their involvement. The present evidence does not support the claim that they form a mirror system in primates. Some of the areas claimed to belong to this system don't display motor activity, a property necessary for mirror neurons. Other areas that would fit that description have been disregarded. The rest of the findings that have been used to support the existence of such a system can be integrated into a more plausible neural account of action understanding. Action understanding is made possible by mental simulation. Mental simulation, indeed, is indicated by the common activation of a large set of frontal parietal and occipital areas that constitute the neural correlates of action execution, action observation and motor imagery. The specific pattern of activations in this network, including lateralization effects and the differential activation of some the involved areas across conditions, can account for the attribution of an action to the correct agent. The suppression of cortical motor output at the level of the spinal cord for action observation elucidates why the motor representations that are generated during action observation and imagery don't induce overt movements. All in all, here I presented the biological basis of action observation/recognition, which supports the mental simulation theory rather than the mirror neuron theory.

References.

Ashe, J., Georgopoulos, A. Movement parameters and neural activity in motor cortex and area 5. Cerebral Cortex 4, 590-600 (1994).

Astavief, S., Stanley, C., Shulman, G., Corbetta, M. Extrastriate body area in human occipital cortex responds to the performance of motor actions. Nature Neuroscience 7, 542-548 (2004).

Avikainen, S., Forss, N., Hari, R. Modulated activation of the human SI and SII cortices during observation of hand actions. NeuroImage 15, 640-646 (2002).

Baldissera, F., Cavallari, P., Craighero, L., Fadiga, L. Modulation of spinal excitability during observation of hand actions in humans. European Journal of Neuroscience 13, 190-194 (2001).

Baron-Cohen, S., Leslie, A., Frith, U. Does the autistic child have a ‘‘theory of mind’’? Cognition 21, 37-46 (1985).

Blakemore, S., Goodbody, S., Wolpert, D. Predicting the Consequences of Our Own Actions: The Role of Sensorimotor Context Estimation. The Journal of Neuroscience 18 (18), 7511-7518 (1998a).

Blakemore, S., Wolpert, D., Frith, C. Central cancellation of self-produced tickle sensation. Nature Neuroscience 1 (7), 635-640 (1998b).

Blakemore, S., Frith, C., Wolpert, D. Spatio-Temporal Prediction Modulates the Perception of Self-Produced Stimuli. Journal of Cognitive Neuroscience 11 (5), 551-559 (1999).

Bonda, E., Petrides, M., Ostry, D., Evans, A. Specific involvement of human parietal systems and the amygdala in the perception of biological motion. The Journal Neuroscience 16, 3737-3744 (1996).

Botterill, G., Carruthers, P. The Philosophy of Psychology. Cambridge University Press (1999).

Buccino, G., Binkofski, F., Fink, G., Fadiga, L., Fogassi, L., Gallese, V., Seitz, R., Zilles, K., Rizzolatti, G., Freund, H. Action observation activates premotor and parietal areas in a somatotopic manner: an fMRI study. European Journal of Neuroscience 13, 400-404 (2001).

Buccino, G., Lui, F., Canessa, N., Patteri, I., Lagravinese, G., Benuzzi, F., Porro, C., Rizzolatti, G. Neural circuits involved in the recognition of actions performed by non-conspecifics: an fMRI study. Journal of Cognitive Neuroscience 16, 1-14 (2004).

Caetano, G., Jousmaki, V., Hari, R. Actor’s and observer’s primary motor cortices stabilize similarly after seen or heard motor actions. Proceedings of the National Academy of Sciences of the U.S.A. 104 (21), 9058-9062 (2007).

Caggiano, V., Fogassi, L., Rizzolatti, G., Thier, P., Casile, A. Mirror Neurons Differentially Encode the Peripersonal and Extrapersonal Space of Monkeys. Science 324, 403-406 (2009).

Catmur, C., Walsh, V., Heyes, C. Sensorimotor Learning Configures the Human Mirror System. Current Biology 17, 1527-1531 (2007).

Catmur, C., Gillmeister, H., Bird, G., Liepelt, R., Brass, M., Heyes, C. Through the looking glass: counter-mirror activation following incompatible sensorimotor learning. European Journal of Neuroscience 28, 1208-1215 (2008).

Chong, T., Cunnington, R., Williams, M., Kanwisher, N., Mattingley, J. fMRI Adaptation Reveals Mirror Neurons in Human Inferior Parietal Cortex. Current Biology 18, 1576-1580 (2008).

Cisek, P., Kalaska, J. Neural correlates of mental rehearsal in dorsal premotor cortex. Nature 431, 993-996 (2004).

Colby, C., Duhamel, J. 1991. Heterogeneity of extrastriate visual areas and multiple parietal areas in the macaque monkey. Neuropsychologia 23, 517-537 (1991).

Colby, C., Duhamel, J.R., Goldberg, M. Visual, Presaccadic, and Cognitive Activation of Single Neurons in Monkey Lateral Intraparietal Area. Journal of Neurophysiology 76 (5), 2841-2852 (1996).

Costantini, M., Galati, G., Ferretti, A., Caulo, M., Tartaro, A., Romani, G., Aglioti, S. Neural systems underlying observation of humanly impossible movements: an FMRI study. Cerebral Cortex 15, 1761-1767 (2005).

Darling, W., Seitz, R., Peltier, S., Tellmann, L., Butler, A. Visual cortex activation in kinesthetic guidance of reaching. Experimental Brain Research 179, 607-619 (2007).

Davidson, D. Inquiries into Truth and Interpretation. Oxford University Press (1984).

Decety, J., Jeannerod, M., Prablanc, C. The timing of mentally represented actions. Behavioral Brain Research 34: 35-42 (1989).

Decety, J., Perani, D., Jeannerod, M., Bettinardi, V., Tadary, B., Woods, R., Mazziotta, J., Fazio, F. Mapping Motor Representations with PET. Nature 371, 600-602 (1994).

Decety, J., Jeannerod, M. Mentally simulated movements in virtual reality: does Fitts's law hold in motor imagery? Behavioural Brain Research 72, 127-134 (1996).

Decety, J., Grezes, J., Costes, N., Perani, D., Jeannerod, M., Procyk, E., Grassi, F., Fazio, F. Brain activity during observation of actions; Influence of action content and subject's strategy. Brain 120, 1763-1777 (1997).

Decety, J., Chaminade, T., Grezes, J., Meltzoff, A. A PET exploration of the neural mechanisms involved in reciprocal imitation. Neuroimage 15, 265-272 (2002).

Dennett, D. The Intentional Stance. MIT Press (1987).

Duhamel, J.R., Colby, C., Goldberg, M. Ventral Intraparietal Area of the Macaque: Congruent Visual and Somatic Response Properties. Journal of Neurophysiology 79 (1), 126-136 (1998).

Evangeliou, M., Vassilis Raos, V., Galletti, C., Savaki, H. Functional Imaging of the Parietal Cortex during Action Execution and Observation. Cerebral Cortex 19 (3), 624-639 (2009).

Fadiga, L., Fogassi, L., Pavesi, G., Rizzolatti, G. Motor facilitation during action observation: a magnetic stimulation study. Journal of Neurophysiology 73, 2608-2611 (1995).

Farrer, C., Franck, N., Paillard, J., Jeannerod, M. The role of proprioception in action recognition. Consciousness and Cognition 12, 609-619 (2003).

Felleman, D., Burkhalter, A., Van Essen, D. Cortical connections of areas V3 and VP of macaque monkey extrastriate visual cortex. The Journal of Comparative Neurology 379, 21-47 (1997).

Ferraina, S., Johnson, P., Garasto, M., Battaglia-Mayer, A., Ercolani, L., Bianchi, L., Lacquaniti, F., Caminiti, R. Combination of hand and gaze signals during reaching: activity in parietal area 7m of the monkey. Journal of Neurophysiology 77, 1034-1038 (1997).

Filimon, F., Nelson, J.D., Hagler, D.J., Sereno, M.I. Human cortical representations for reaching: mirror neurons for execution, observation, and imagery. NeuroImage 37 (4), 1315-1328 (2007).

Fitts, P. The Information Capacity of the Human Motor System in Controlling the Amplitude of Movement. Journal of Experimental Psychology 121 (3), 262-269 (1992).

Fodor, J. The Language of Thought. Harvard University Press (1975).

Fodor, J. The Modularity of Mind: An Essay on Faculty Psychology. M.I.T. Press (1983).

Fogassi, L., Ferrari, P.F., Gesierich, B., Rozzi, S., Chersi, F., Rizzolatti, G. Parietal Lobe: From Action Organization to Intention Understanding. Science 308, 662-667 (2005).

Frith, C., Frith, U. Interacting Minds – A biological Basis. Science 286, 1692-1695 (1999).

Gallese, V., Fadiga, L., Fogassi, L., Rizzolatti, G. Action Recognition in the Premotor Cortex. Brain 119, 593-609 (1996).

Gallese, V., Goldman, A. Mirror neurons and the simulation theory of mind-reading. Trends in Cognitive Sciences 2 (12), 493-501 (1998).

Gallese, V., Keysers, C., Rizzolatti, G. A unifying view of the basis of social cognition. Trends in Cognitive Sciences 8 (9), 396-403 (2004).

Galletti, C., Fattori, P., Battaglini, P., Shipp, S., Zeki, S. Functional demarcation of a border between areas V6 and V6A in the superior parietal gyrus of the macaque monkey. European Journal of Neuroscience 8, 30-52 (1996).

Gangitano, M., Mottaghy, F., Pascual-Leone, A. Phase specific modulation of cortical motor output during movement observation. NeuroReport 12, 1489-1492 (2001).

Gazzola, V., Rizzolatti, G., Wicker, B., Keysers, C. The anthropomorphic brain: The mirror neuron system responds to human and robotic actions. NeuroImage 35, 1674-1684 (2007).

Gazzola, V., Keysers, C. The observation and execution of actions share motor and somatosensory voxels in all tested subjects: single-subject analyses of unsmoothed fMRI data. Cerebral Cortex 19, 1239-1255 (2009).

Gerardin, E., Sirigu, A., Lehericy, S., Poline, J.B., Gaymard, B., Marsault, C., Agid, Y., LeBihan, D. Partially Overlapping Neural Networks for Real and Imagined Hand Movements. Cerebral Cortex 10, 1093-1104 (2000).

Goldman, A. Interpretation psychologized. Mind and Language 4, 161-185 (1989).

Goldman, A. Simulating Minds: The Philosophy, Psychology and Neuroscience of Mindreading. Oxford University Press (2009).

Gordon, R. Folk psychology as simulation. Mind and Language 1, 158-171 (1986).

Grafton, S., Arbib, M., Fadiga, L., Rizzolatti, G. Localization of grasp representations in humans by positron emission tomography 2. Observation compared with imagination. Experimental Brain Research 112, 103-111 (1996).

Gregoriou, G., Savaki, H. The intraparietal cortex: subregions involved in fixation, saccades, and in the visual and somatosensory guidance of reaching. Journal of Cerebral Blood Flow and Metabolism 21, 671-682 (2001).

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

Grezes J, Decety J. Functional anatomy of execution, mental simulation, observation, and verb generation of actions: a meta-analysis. Human Brain Mapping 12, 1-19 (2001).

Grezes J., Armony J., Rowe J., Passingham R. Activations related to “mirror” and “canonical” neurones in the human brain: an fMRI study. Neuroimage 18, 928-937 (2003).

Grill-Spector, K. Selectivity of adaptation in single units: implications for fMRI experiments. Neuron 49, 170-171 (2001).

Haggard, P., Clark, S., Kalogeras, J. Voluntary action and conscious awareness. Nature Neuroscience 5, 382-385 (2002).

Hari, R., Forss, N., Avikainen, S., Kirveskari, E., Salenius, S., Rizzolatti, G. Activation of human primary motor cortex during action observation: A neuromagnetic study. Proceedings of the National Academy of Sciences of the U.S.A. 95, 15061-15065 (1998).

Heal, J. Replication and functionalism. In J. Butterfield, ed., Language, Mind, and Logic. Cambridge University Press (1986).

Hickok, J. Eight Problems for the Mirror Neuron Theory of Action Understanding in Monkeys and Humans. Journal of Cognitive Neuroscience 21:7, 1-15 (2009).

Iacoboni, M., Koski, L., Brass, M., Bekkering, H., Woods, R., Brass, M., Bekkering, H., Woods, R., Dubeau, M.C., Mazziotta, J., Rizzolatti, G. Reafferent copies of imitated actions in the right superior temporal cortex. Proceedings of the National Academy of Sciences of the U.S.A. 98: 13995-13999 (2001).

Iacoboni, M., Woods, R., Brass, M., Bekkering, H., Mazziotta, J., Rizzolatti, G. Cortical mechanisms of human imitation. Science 286, 2526-2528 (1999).

Ishida H, Nakajima K, Inase M, Murata A. Shared mapping of own and others' bodies in visuotactile bimodal area of monkey parietal cortex. Journal of Cognitive Neuroscience 22 (1), 83-96 (2009).

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

Jeannerod, M. Neural Simulation of Action: A Unifying Mechanism for Motor Cognition. NeuroImage 14, S103-S109 (2001).

Johnson, H., Haggard, P. Motor awareness without perceptual awareness. Neuropsychologia 43, 227-237 (2005).

Johnson, S., Rotte, M., Grafton, S., Hinrichs, H., Gazzaniga, M., Heinze, H. Selective Activation of a Parietofrontal Circuit during Implicitly Imagined Prehension. NeuroImage 17, 1693-1704 (2002).

Jones, E., Coulter, J., Hendry, H. Intracortical connectivity of architectonic fields in the somatic sensory, motor and parietal cortex of monkeys. The Journal of Comparative Neurology 181, 291-348 (1978).

Kilintari, M., Raos, V., Savaki, H. Grasping in the Dark activates Early Visual Cortices. Cerebral Cortex 21, 949-963 (2011).

Kohler, E., Keysers, C., Umilta, A., Fogassi, L., Gallese, V., Rizzolatti, G. Hearing Sounds, Understanding Actions: Action Representation in Mirror Neurons. Science 297, 846-848 (2002).

Koski, L., Iacoboni, M., Dubeau, M., Woods, R., Mazziotta, J. Modulation of cortical activity during different imitative behaviors. Journal of Neurophysiology 89, 460-471 (2003).

Koski, L., Wohlschlager, A., Bekkering, H., Woods, R., Dubeau, M. Modulation of motor and premotor activity during imitation of target-directed actions. Cerebral Cortex 12, 847-855 (2002).

Kraskov, A., Dancause, N., Quallo, M., Shepherd, S., Lemon, R. Corticospinal Neurons in Macaque Ventral Premotor Cortex with Mirror Properties: A Potential Mechanism for Action Suppression? Neuron 64, 922-930 (2009).

Lemon, R., Johansson, R., Westling, G. Corticospinal control during reach, grasp, and precision lift in man. The Journal of Neuroscience 15, 6145-6156 (1995).

Leslie, A. Pretence and representation: The origins of ‘‘theory of mind.’’ Psychological Review 94, 412-426 (1987).

Maeda, F., Kleiner-Fisman, G., Pascual-Leone A. Motor facilitation while observing hand actions: specificity of the effect and role of observer's orientation. Journal of Neurophysiology 87, 1329-1335 (2002).

Marconi, B., Genovesio, A., Bataglia-Mayer, A., Ferraina, S., Squatrito, S., Molinari, M., Laquaniti, F., Caminiti, R. Eye-hand coordination during reaching. I. Anatomical relationships between parietal and frontal cortex. Cerebral Cortex. 11, 513-527 (2001).

Matsumoto, K., Suzuki, W., Tanaka, K. Neuronal correlates of goal-based motor selection in the prefrontal cortex. Science 301, 229-232 (2003).

Morecraft, R., Cipolloni, P., Stilwell-Morecraft, K., Gedney, M., Pandya, D. Cytoarchitecture and Cortical Connections of the Posterior Cingulate and Adjacent Somatosensory Fields in the Rhesus Monkey. The Journal of Comparative Neurology 469, 37-69 (2004).

Murata, A., Gallese, V., Luppino, G., Kaseda, M., Sakata, H. Selectivity for the shape, size, and orientation of objects for grasping in neurons of monkey parietal area AIP. Journal of Neurophysiology 83, 2580-2601 (2000).

Nakamura, H., Kuroba, T., Wakita, M., Kusunoki, M., Kato, A., Mikami, A., Sakata, H., Itoh, K. 2001. From three-dimensional space vision to prehensile hand movements: the lateral intraparietal area the area V3A and the anterior intraparietal area macaques. The Journal of Neuroscience 21, 8174-8187 (2001).

Naito, E., Kochiyama, T., Kitada, R., Nakamura, S., Matsumura, M., Yonekura, Y., Sadato, N. Internally Simulated Movement Sensations during Motor Imagery Activate Cortical Motor Areas and the Cerebellum. The Journal of Neuroscience 22(9), 3683-3691 (2002).

Nelissen, K., Luppino, G., Vanduffel, W., Rizzolatti, G., Orban, G. Observing Others: Multiple Action Representation in the Frontal Lobe. Science 310, 332-336 (2005).

Nishitani, N., Hari, R. Temporal dynamics of cortical representation for action. Proceedings of the National Academy of Sciences of the U.S.A. 97, 913-918 (2000).

Pandya, D., Seltzer, B. Intrinsic connections and architectonics of posterior parietal cortex in the rhesus monkey. The Journal of Comparative Neurology 204, 196-210 (1982).

Parsons, L., Fox, P., Downs, H., Glass, T., Hirsch, T., Martin, C., Jerabek, P., Lancaster, J. Use of Implicit Motor Imagery for Visual Shape Discrimination as revealed by PET. Nature 375, 54-58 (1995).

Di Pellegrino, G., Fadiga, L., Fogassi, L., Gallese, V., Rizzolatti, G. Understanding motor events: a neurophysiological study. Experimental Brain Research 91, 176-180 (1992).

Perani, D., Fazio, F., Borghese, N., Tettamanti, M., Ferrari, S., Decety, J., Gilardi, M. Different brain correlates for watching real and virtual hand actions. Neuroimage 14, 749-758 (2001).

Raos, V., Evangeliou, M., Savaki, H. Observation of action: grasping with the mind's hand. NeuroImage 23, 193-201 (2004).

Raos, V., Evangeliou, M., Savaki, H. Mental Simulation of Action in the Service of Action Perception. The Journal of Neuroscience 27 (46), 12675-12683 (2007).

Rizzolatti, G., Camarda, R., Fogassi, L., Gentilucci, M., Luppino, G., Matelli, M. Functional organization of inferior area 6 in the macaque monkey. II. Area F5 and the control of distal movements. Experimental Brain Research 71, 491-507 (1988).

Rizzolatti, G., Craighero, L. The Mirror-Neuron System. Annual Review of Neuroscience 27, 169-192 (2004).

Rizzolatti, G., Fadiga, L., Gallese, V., Fogassi, L. Premotor cortex and the recognition of motor actions. Cognitive Brain Research 3, 131-141 (1996a).

Rizzolatti, G., Fadiga, L., Matelli, M., Bettinardi, V., Paulesu, E., Perani, D., Fazio, F. Localization of grasp representations in humans by PET: 1. Observation versus execution. Experimental Brain Research 111, 246-252 (1996b).

Rizzolatti, G., Fogassi, L., Gallese, V. Neurophysiological mechanisms underlying the understanding and imitation of action. Nature Reviews Neuroscience 2, 661-670 (2001).

Rizzolatti, G., Sinigaglia, C. The functional role of the parieto-frontal mirror circuit: interpretations and misinterpretations. Nature Reviews Neuroscience 11, 264-274 (2010).

Sathian, K., Zangaladze, A. Feeling with the mind’s eye: contribution of visual cortex to tactile perception. Behavioral Brain Research 135, 127-132 (2002).

Savaki, H. How do we understand the actions of others? By mental simulation, not mirroring. Cognitive Critique 2, 99-140 (2010).

Sawaguchi, T., Yamane, I., Kubota, K. 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. Journal of Neurophysiology 75, 2150-2156 (1996).

Shepherd, S., Klein, J., Deaner, R., Platt, M. Mirroring of attention by neurons in macaque parietal cortex. Proceedings of the National Academy of Sciences of the U.S.A. 106 (23), 9489-9494 (2008).

Sirigu, A., Duhamel, J.R., Cohen, L., Pillon, B., Dubois, B., Agid, Y. The Mental Representation of Hand Movements After Parietal Cortex Damage. Science 273, 1564-1568 (1996).

Sokoloff, L., Reivich, M., Kennedy, C., Des Rosiers M., Patlak, C., Pettigrew K., Sakurada, O., Shinohara, M. The [14C]-deoxyglucose method for the measurement of local cerebral glugose utilization: theory, procedure, and normal values in the conscious and anesthetized albino rat. The Journal of Neurochemistry 28, 879-916 (1977).

Stamos, A., Savaki, H., Raos, V. The spinal substrate of the suppression of action during action observation. The Journal of Neuroscience 30 (35), 11605-11611 (2010).

Stephan, K., Fink, G., Passingham, R., Silbersweig, D., Ceballos-Baumann, A., Frith, C., Frackowiak, R. Functional Anatomy of the Mental Representation of Upper Extremity Movements in Healthy Subjects. Journal of Neurophysiology 73 (1), 373-386 (1995).

Stich, S., Nichols, S. Mindreading. An Integrated Account of Pretence, Self-Awareness, and Understanding Other Minds. Oxford University Press (2003).

Tkach, D., Reimer, J., Hatsopoulos, N. Congruent Activity during Action and Action Observation in Motor Cortex. The Journal of Neuroscience 27 (48), 13241-13250 (2007).

Tsakiris, M., Haggard, P. Awareness of somatic events following a voluntary action. Experimental Brain Research 149, 439-446 (2003).

Umilta, M., Kohler, E., Gallese, V., Fogassi, L., Fadiga, L., Keysers, G., Rizzolatti, G. I Know What You Are Doing: A Neurophysiological Study. Neuron 31, 155-165 (2001).

Umilta, M., Escola, L., Intskirveli, I., Grammont, F., Rochat, M., Caruana, F., Jezzini, A., Gallese, V., Rizzolatti, G. When pliers become fingers in the monkey motor system. Proceedings of the National Academy of Sciences of the U.S.A. 105 (6), 2209-2213 (2008).

de Vignemont, F., Ehrsson, H., Haggard, P. Bodily Illusions Modulate Tactile Perception. Current Biology 15, 1286-1290 (2005).

Weiskrantz, L., Elliott, J., Darling, C. Preliminary Observations of Tickling Oneself. Nature 230, 598-599 (1971).

Wimmer, H., Perner, J. Beliefs about beliefs: Representation and constraining function of wrong beliefs in young children’s understanding of deception. Cognition 13, 103-128 (1983).

Wohlschlager, A., Wohlschlager, A. Mental and Manual Rotation. Journal of Experimental Psychology 24 (2), 397-412 (1998).

Wohlschlager, A. Mental object rotation and the planning of hand movements. Perception and Psychophysics 63 (4), 709-718 (2001).

Wolpert, D., Ghahramani, Z., Jordan, M. An Internal Model for Sensorimotor Integration. Science 269, 1880-1882 (1995).

'Mirror Neuron Theory' versus 'Simulation Theory' for Action Understanding.

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Abstract

Since their discovery in the monkey ventral premotor cortex (Di Pellegrino et al., 1992), mirror neurons have been the subject of heated debate in cognitive neuroscience. Mirror neurons allegedly constitute a so-called “mirror-neuron system” in human and non-human primates (Rizzolatti and Craighero, 2004). It has been suggested that this system is responsible for a diverse repertoire of cognitive functions, one of which is action understanding. This has led some neuroscientists to claim that a “mirror neuron theory” can successfully account for the neurobiological foundations of social cognition (Rizzolatti and Fabbri-Destro, 2008). “Mirror neuron theory” is however empirically ill-founded, at least with regard to action understanding. Both action execution and observation evidently involve a wide Fronto-Parieto-Occipital network (Savaki, 2010). This network consists of cortical areas arbitrarily excluded from the so-called “mirror-neuron system”. This pattern of cortical activation during both action observation and execution likely reflects the implementation of a mental simulation mechanism in action understanding. Furthermore differential neural activity between action execution and action observation can plausibly explain how actions are attributed to the right agent.

Περίληψη

Από την ανακάλυψη τους στον κοιλιακό προκινητικό φλοιό των Μακάκα (Di Pellegrino et al., 1992) και έκτοτε, οι κατοπτρικοί νευρώνες βρίσκονται στο επίκεντρο της γνωστικής νευροεπιστήμης. Οι κατοπτρικοί νευρώνες, σύμφωνα με ορισμένους ερευνητές ορίζουν το αποκαλούμενο σύστημα κατοπτρικών νευρώνων στα πρωτεύοντα (Rizzolatti and Craighero, 2004). Στο σύστημα αυτό έχει αποδωθεί πληθώρα γνωστικών λειτουργιών, μια εκ των οποίων είναι η κατανόηση πράξεων. Αυτή η εξέλιξη οδήγησε στη διατύπωση της αποκαλούμενης θεωρίας των κατοπτρικών νευρώνων, η οποία θεωρείται ότι παρέχει μια πλήρη εικόνα των νευροβιολογικών θεμελίων των κοινωνιο-γνωστικών λειτουργιών των πρωτευόντων (Rizzolatti and Fabbri-Destro, 2008). Τα εμπειρικά δεδομένα που έχουν προκύψει τα τελευταία χρόνια στο χώρο της γνωστικής νευροεπιστήμης μειώνουν την εγκυρότητα της θεωρίας των κατοπτρικών νευρώνων παρ’ολ’αυτά, τουλάχιστον σε ό,τι αφορά την κατανόηση πράξεων. Ένα κοινό μέτωπο-βρεγματο-ινιακό δίκτυο υπόκειται της εκτέλεσης και παρατήρησης πράξεων (Savaki, 2010). Το δίκτυο αυτό περιλαμβάνει εγκεφαλικές περιοχές οι οποίες αυθαίρετα αποκλείονται από το αποκαλούμενο σύστημα των κατοπτρικών νευρώνων. Το ίδιο δίκτυο είναι πολύ πιθανά υπεύθυνο για την εφαρμογή ενός μηχανισμού νοητικής προσομοίωσης όταν το υποκείμενο καλείται να κατανοήσει μια πράξη. Παράλληλα η διαφορική δραστηριότητα αυτού του συστήματος κατά την διάρκεια της εκτέλεσης πράξεων και κατά τη διάρκεια παρατήρησης πράξεων εξηγεί το πως αποδίδεται η πράξη στο υποκείμενο που την εκτέλεσε.