CHAPTER THIRTEEN

IF THE MOTOR SYSTEM IS NO MIRROR

MARIA BRINCKER

COLUMBIA UNIVERSITY &
UNIVERSITY OF MASSACHUSETTS, BOSTON

Largely aided by the neurological discovery of so-called "mirror neurons," the attention to motor activity during action observation has exploded over the last two decades. The idea that we internally "mirror" the actions of others has led to a new strand of implicit simulation theories of action understanding[1] (Gallese 2003, 2004, 2007; Gallese & Goldman 1998; Goldman 2009; Hurley 2008). The basic idea of this sort of simulation theory is that we, via an automatic covert activation of our own action representations, can understand the action and possibly the goal and/or intentions of the observed agent. In this way motor "simulation" is seen as the basis for low-level "mind-reading"; i.e. for the ascription of goals and intentional mental states to others. The thought is that one, through mirroring simulations, can get beyond the observable behaviour to the hidden minds of others.

I am questioning the idea of an exclusively "mirroring" role of the motor system in social perception, which is tacitly assumed in this sort of simulation theories. Is motor activity during action observation really primarily a simulation, a detailed "echo" of the others action? My point is not that we never simulate what we observe, but rather to question whether such processes are representative of the overall motor contribution to social cognition. More and more studies on the functional properties of mirror neurons and motor facilitation during perception points to a more complex role of the motor system in action perception. Recently, several proposals have been made attempting to reinterpret and critique the

---

[1] The present focus is implicit simulation theories in regards to action observation, and emotion and explicit simulation theories will not be discussed.

function of motor activity in social situations. I shall here briefly touch on a few of these and sketch parts of my own alternative "social affordance" hypothesis of the sensorimotor contribution to social perception. By way of these analyses I highlight how traditional discussions are marred by problematic theoretical assumptions. It seems to me that we need a thorough reinterpretation not just of mirror neurons and mirroring, but also of what we take motor and social cognition to be. In my view the details of the sensorimotor findings underline the need to move beyond the simplistic idea of the motor system as a unitary output system. In terms of social cognition I question the traditional focus on hidden mental states. I suggest that the motor contribution might have more to do with understanding the process of how others choose their actions, navigate the world and relate to others than with simulating specific actual actions or mental states.

I conclude that (1) low-level simulation theories, which see the motor role in social perception as passive "mirroring," are faced with serious empirical challenges, and that (2) the motor system serve a much more proactive and complex cognitive role in social perception and interaction than previously thought. But my claim is also that many empirical tensions have slipped out of focus due to entrenched theoretical assumptions. Narrow theoretical expectations have marked not only the interpretations but the research itself and I propose that we are in dire need of more studies of actual contextual and interactive social perception.

1. Linking "As If" Simulation, Mirror Neurons and Motor Cognition

Explicit simulation theories of "mind-reading" and intention understanding have been around for a long time in philosophy.[2] The basic idea being that we explicitly pretend to be in another's shoes and by way of this simulative perspective taking get some insight into another's mental life and reasoning process. However, the idea of implicit motor simulation re-emerged as an influential theory a couple of decades ago when a University of Parma group led by Giacomo Rizzolatti and Vittorio Gallese reported the discovery of so-called mirror neurons in the premotor cortex

---

[2] Traditional high-level simulation theories propose that one, by explicit imagination, sets up a pretence scenario of the other point of view and thought processes. Goldman for example supports such an explicit theory for "high-level mind-reading" (2009). But simulation theories of other minds has roots further back, for example in Mill's argument from analogy.

of macaque monkeys (di Pellegrino et al. 1992).[3] The wonder of these sensorimotor neurons is that they are modulated both by the execution and observation of certain kinds of goal-directed actions. It was quickly suggested that such neurons could form an automatic and low-level embodied link between self and other and thus maybe also provide an answer to the social cognitive riddle of how we, based on third person action observation, can understand another's hidden mental life.

The theory was further broadened by evidence of areas with "mirror qualities," not only in pre-motor areas but also in the parietal lope (Fogassi et al. 2005; Gallese et al. 2002).[4] But these and other single cell findings are based on monkey studies. Thus, a crucial development has been the indirect evidence of analogous mirror neurons systems in humans. An important source here is neuroimaging studies showing that the same regions are modulated by both observation and execution of particular actions (Hari et al. 1998; Fadiga et al. 2005).[5] Human mirroring processes have also been assessed in behavioural studies of motor resonance and facilitation during action observation. An often replicated finding in this area is that there is a consistent reaction time advantage of observing and executing the same (congruent) as opposed to different (incongruent) actions (Fadiga, Craighero & Olivier 2005). Further, a rather strict somatotopic and temporal analogy between the observed movement and recorded motor facilitation has been found (Buccino et al. 2001, Buccino, Bikofski & Riggio. 2004; Fadiga, Craighero & Olivier 2005). These results all point towards an automatic and rather detailed covert kinetic imitation process. This motor "mirroring" process has been implied both in observation of simple motor acts like finger movements and in the case of experts observing complex movements, where a person's exact motor repertoire seems crucial to the understanding of the observed action.[6]

---

[3] The discovery of mirror neurons was pivotal in extending the idea of motor simulation to the field of social cognition. But, earlier empirically inspired motor theories of cognitive processes include, for example, Liberman's motor theory of speech perception.

[4] Whether or not one counts the inferior parietal lope (IPL) as part of the motor system proper, this area supports multi-modal sensory and motor integration, and hence is key to an understanding the role of motor cognition in perception.

[5] Mirroring responses has also been documented for emotional and somatosensory stimuli (Keysers & Gazzola 2009)

[6] See Calvo-Merino et al. 2006 and the evidence of expert dancers using their own motor repertoire to understand observed dance moves. Similar studies has been performed with pianists: see Haueisen & Knosche (2001).

Lastly, evidence for mirroring and its social function might be inferred from clinical data.[7]

In short, the theory of premotor areas as underlying a neural mechanism, which automatically "mirror" observed behaviour by engaging in covert re-enactment of the action, seems to be richly supported by both the mirror neuron findings and the broader behavioural evidence. Gallese, Rizzolatti and their colleagues have, over the last decades in dozens of articles, developed ideas about how such mirror mechanisms could underlie various simulative processes and cognitive functions. In a 2004 article, Gallese et al. summarize the simulation idea as follows:

> The core of the proposal is that the observation of an action leads to the activation of parts of the same cortical neural network that is active during its execution. The observer understands the action because he knows its outcomes when he does it. (Gallese et al. 2004)

They suggest that mirror neuron systems provide unique neurological evidence for this sort of automatic simulation in action perception, because: "Although we do not overtly reproduce the observed action, part of our motor system becomes active 'as if' we were executing that very same action that we were observing." Furthermore: "When only the cortical centers, decoupled from their peripheral effects, are active, the observed action or emotions are 'simulated' and thereby understood" (Gallese et al. 2004). Thus, given descriptions like these, the proposal seems to be that mirror neurons contribute to the understanding of the action intention by way of a simulative "as if" process, where the action plan of the other is mirrored in the observer.[8]

---

[7] For clinical evidence, see for example Lhermitte's studies of "imitation behaviour" (Lhermitte et al. 1986) and Gallese & Goldman's (1998) reference to autism as possibly involving a defect of the mirror neuron system. Mirroring responses also appear within the normal behavioural spectrum, such as portrayed by the so-called "Chameleon effect," i.e. that we in social interaction have a strong tendency to socially mimic or assimilate our behaviour to each other (Wilson & Knoblich 2005).

[8] With the idea of action observation as automatically triggering a covert imitation, there is a natural bridge from low-level simulation theories to the presence of the rare ability to imitate exact action sequences. There is a great deal of controversy regarding the extent of "true imitation" in non-human primates and little evidence of such abilities in macaque monkeys where mirror neurons were first found. Some suggest that the issues of imitation should already raise some suspicion regarding a low-level simulative interpretation of mirror neuron activity (see Csibra 2007).

In terms of the idea of motor simulation as activation of covert action representations, Marc Jeannerod presents us with a similar but more generalized story of "as if" action in his recent book on motor cognition (Jeannerod 2001, 2006).[9] Given his own empirical work, I find it surprising that Jeannerod would make the theoretical proposal that motor simulation is not just a feature of "some," but rather a "unifying mechanism" for <u>all</u> motor cognition.[10] But it should be noted that it is precisely by way of this notion of detailed motor simulation that he opposes the mirror theory for social cognition. While we might simulate the actions of others, he does not think that this motor mirroring process can give us much in terms of understanding the intentions of others. Jeannerod (2006) and Jacob & Jeannerod (2005) use Seale's distinction between "motor intentions" and "prior intentions"[11] to make the point that even if we can infer the "motor intentions" of people we observe via action simulation, we should not expect to infer the more abstract prior intentions from this of automatic motor simulation. According to them, the inference of prior intentions relies on various other contextual factors like the physical surroundings in which the movements take place, and prior knowledge of the scenario, etc. It seems reasonable to say that simple non-contextual copies of the observed motor activity do not give us much in terms of abstract intentions or distal goals. However, as Jacob & Jeannerod point out themselves, most simulation theorists might actually have a different sort of mirroring in mind for intention ascription than this kinematic and context-independent kind. Their argument thus alerts us to a possible tension between their interpretation of motor cognition as a low-level simulation process and the view underlying many of the arguments of, for example, Gallese & Rizzolatti. Jacob & Jeannerod write that most

---

[9] Instead of the terminology of trying to take another's perspective, Jeannerod and many other simulation theorists focus on the idea of an agent neutral representation of the action, and most proponents sees this neutrality as an advantage and readily admits that one needs an additional "who" system to attribute the action, goal or intention to oneself or someone else. See Jeannerod 2006, Hurley 2008 & Gallese et al. 2004. For a criticism of the "who system" see Gallagher 2007; Brincker 2011; and for empirical evidence against common self-other representation see Schutz-Bosbach et al. 2006.

[10] A 2001 article of his is entitled "Neural simulation of action: A unifying mechanism for motor cognition." In 2006 he writes "we will develop the concept of simulation as a potential explanation for unifying the various aspects of motor cognition" (Jeannerod 2006, 129).

[11] Seale (1983) uses "motor intentions" and "prior intentions" to distinguish between simple intentional motor acts like turning the knob of the water fountain and the more global intention of getting something to drink.

motor theorists "tinker with the concept of motor simulation" and continue: "We disapprove of this strategy because it relaxes the fundamental link between simulation and the requirements of the motor system, which we take very seriously" (Jacob & Jeannerod 2005, 21). Thus, it looks like Jacob & Jeannerod begin with the assumption that ALL motor activity during perception is a low-level and highly load-constrained simulative process and then go on to conclude that it is ill-fitted for both mind-reading and also interactive instances of social perception. They write:

> The motor properties of the mirror system are well designed for representing an agent's motor intention involved in an object-oriented action, not for representing an agent's social intention, let alone communicative intention. The mirror system does not seem well designed for promoting fast responses to the perception of social actions directed towards conspecifics. For example, in response to threat, it might be adaptive to flee, not to simulate the threatening agent's observed movements. (Jacob & Jeannerod 2005, 24)

The underlying assumptions are here 1) that our motor system can only produce or simulate actions, and 2) that this can only be done one action at the time. Given this restricted view motor processes, they do seem rather useless for understanding "prior intentions" and for reacting and interacting with others, as the latter would depend on simulating multiple agents at once. In other words, it is the idea of motor processes as always simulative that leads to their conclusion that these processes are largely impotent not only for social cognition but for higher cognitive processes more broadly. The question is of course whether this narrow notion of motor cognition is empirically plausible, and thus whether one should accept the conclusion that most action understanding might be "purely perceptual" as Jacob & Jeannerod hypothesize.

Curiously the Parma group—and also Jeannerod himself[12]—well before the discovery of mirror neurons, made significant strides to move beyond Penfield's traditional picture of the cortical motor system as relatively unified, uniquely frontal and topologically organized, and functionally mainly limited to specifying the kinetic properties of actions.[13] The traditional view was challenged by functional and

---

[12] See here for example his early work on sensorimotor processes in neglect (Jeannerod 1988) and motor organization (Jeannerod 1987).

[13] In accordance with the famous findings from Penfield's 1930s stimulation studies, the cortical motor system was anatomically located just in front of the central sulcus and generally thought to consist of two areas: primary motor cortex

anatomical findings of multiple parallel sensori-motor circuits between relatively separate pre-motor and parietal areas (e.g. Rizzolatti & Gentilucci 1988). Thus, motor areas are engaged by perceptual input in "parallel" and further there are as many connections "feeding back" into parietal areas as there are leading to premotor areas. Further, it was shown that pre-motor neurons often are modulated not by particular body parts or movements but rather by relatively "abstract goals." In brief, it is clear that neither the anatomical nor the functional division between motor, perceptual and higher cognitive functions are as clear as hitherto thought. Unfortunately, the theoretical debate over what motor cognition is has largely been a non-event in the simulation and mirror neuron literature and has mostly played out between the lines, if at all. My view is that describing motor activity during action perception as a covert "as if" action simulation has misguided a lot of theoretical discussions, and further that it is empirically problematic both in relation to the mirror neuron findings and to the broader sensorimotor findings.

2. Idealized Mirroring and the Unreported Heterogeneity of the Findings

As mentioned, the recent explosion of theories of the motor system as an off-line simulation tool for social cognition was in large part due to empirical findings not only of mirror neurons but also of overlapping regional activation, action facilitation etc. Given all the single-cell, imaging and behavioural findings that I alerted to in the previous section, one might say that covert simulative mirroring processes during action perception are undeniable. However, the problem is that from the first findings of mirror neurons in monkeys the data have been much more heterogeneous than the typical idealized summaries suggest (Gallese et al. 1996). From the very first reports, it was clear that most of these sensorimotor neurons were not responsive to exactly the same types of actions during perception and during execution. Visuomotor neurons found to have symmetrical action modulation were labelled "strictly congruent" mirror neurons. But most were reported to be "broadly congruent" or as having a "logical connection" between perceptual and

---

and pre-motor cortex each equipped with a full somatotopical homunculi representation of the moving body parts. The underlying logic of the motor system theory was that via these body representations it could orchestrate the movements of the body, a story that fits neatly with the traditional cognitivist idea of the motor system as a peripheral output system. See Penfield & Rasmussen (1952) and for a typical representation of the Penfield inspired motor homunculi.

motor modulation or in certain cases as "non-congruent" when no such relation were found at all (di Pellegrino, G. et al. 1992; Gallese et al. 1996)[14]. However, due to the focus on "congruency," asymmetric properties of each of these subgroups were left largely unexplored.

It should be noted that in spite of use of the mirror metaphor, the report stated from the beginning that these premotor neurons do not just mirror any old movement but are particularly tuned towards object-directed actions. They are typically modulated by the meaning or goal of such actions, rather than the exact movements by which the goal was obtained. This "goal rather than movement" preoccupation of mirror neurons has been abundantly replicated since.[15] Thus, numerous studies imply that most of these action sensitive neurons might not exactly mirror the observed motor action. Further, neural modulation is never all or none, and more and more studies suggest that the activity is not all that symmetric between observation and execution. Early reports suggested that most mirror neurons showed no significant quantitative modulation differences between execution and observation. Further, it was claimed that these neurons as opposed to other sensorimotor neurons did not habituate to repeated stimulation (Gallese et al. 1996). Both of these claims seem essential to the idea of a ubiquitous, agent neutral and context-independent mirror mechanism. However, it is now generally accepted by the Parma researchers that the neurons are not all that agent-neutral (Gallese, personal communication) and show a more complex pattern of habituation.[16]

My goal with this discussion is not to cover all the details about the empirical reports and interpretations. Rather my aim is to alert to the fact that a theoretical decision was made early on that mirror neurons and areas were symmetric enough to warrant the enigmatic idea of a mirroring mechanism and function. The question is whether this choice, to idealize the observation-execution matching in a certain subgroup of premotor

---

[14] Note that these are neurons *with* mirror qualities, and do not include other neurons in the same functional area such as "canonical" neurons responding to objects with certain affordances and the execution of such afforded actions. See Grèzes et al. 2003.

[15] Findings of mirror neuron activity depending on intention and goal abstraction rather than simply motor act simulation or covert imitation is widespread, but here are a few interesting examples: (a) Audiovisual mirror neurons tuned to goals (Kohler et al. 2002; Keysers et al. 2003); (b) More pre-motor activity in goal-directed that non-goal directed imitation (Koski et al. 2002); (c) Similar mirror neuron responses to human and robot actions (Gazzola et al. 2007).

[16] The habituation question is given an interesting spin by recent imaging studies finding habituation when an observed action is followed by execution but not the other way around (see Lingnau et al. 2009; Schütz-Bosbach et al. 2006).

neurons, rendered the general function of the fronto-parietal sensorimotor circuits more obscure. Rizzolatti proposed in the 1980s a general theory of F5 premotor neurons as contributing to a "motor vocabulary" of action types (Rizzolatti & Gentilucci 1988). This theory might have further contributed to problematic experimental simplifications, as single-cells were typically classified independently of the task and context simply according to their sensitivity to particular action-types (such as, for example, grasping, reaching, manipulating etc.) during, respectively, observation and execution. In the later years it has been shown that the premotor neurons often seem to be modulated in much more complex, dynamic and context sensitive ways than earlier assumed. It has now been documented that the activity of single action sensitive "mirror" neurons often vary dynamically with the pragmatic "context" of the observer for example by tracking of occluded objects (Umilta et al. 2001). Further, a very recent study showed that most mirror neurons selectively carry information about the pragmatic and spatial relation between self, other and intentional object (Caggiano et al. 2009).

Findings like these are difficult to account for within a traditional theory of action mirroring, as they show that single sensorimotor neurons do not just represent visually presented actions "as if" they were executed. Rather, I suggest with my alternative social affordance view that a sophisticated dynamic sensorimotor tracking is taking place in the fronto-parietal circuits. The idea is that "present" actions and objects are tracked in parallel according to their teleological properties. Importantly these "trackings" are schematic and not full kinematic simulations. Further, not only actual but also "anticipated" and "potential" reactions and relations of self and other to the present affordances (i.e. action invitations) of the particular context are continuously monitored. Thus, functionally these sensorimotor circuits are proposed to support our relational and teleological understanding of the shared physical and social affordance space, and thereby our process of action choice and coordination.

The affordance model will be discussed more below. The point for now is that the complexity in the motor response, which serves as the empirical foundation of my alternative view, generally has been thoroughly ignored by both proponents and critics of the social role of mirroring simulation. The theoretical focus on symmetric and context-independent simulative mirroring might even generally intensify as researchers make the theoretical move from single-cell findings in monkeys to behavioural and imaging evidence in humans. When interpreting motor facilitation or regional neuroimaging results one might ask why one should take an imitative motor response as evidence for a

"ubiquitous" mirror mechanism or rather simply the appropriate global action given the "specific present context"? Or to pose the question the other way around: How do we know that the function of single mirror neurons is a "full simulation" of the indicated action? I suggest that there is little if any evidence supporting the idea that mirror neuron activity alone can be equated with fully specified actions or covert simulations thereof. To the contrary, detailed mental imagery of actions and temporally specified simulations seems to involve much more than premotor areas, not to mention single or small populations of mirror neurons.[17] I suspect that the focus on motor cognition as simulation, i.e. as either overt or covert output production of the type Jeannerod suggests, represents a step back in our understanding of motor cognition, as it obscures the more abstract and parallel functional aspects of motor and sensorimotor areas. These empirical problems with typical simulative stories hopefully will become clearer as we look more at the debate that has surrounded the traditional interpretations of mirror neurons and their function.

3. The Debate Over the Social Function of Mirroring Simulation

The findings of kinematic abstraction in the cortical sensorimotor circuits have, as mentioned, often been neatly left out of the story by those who think of the motor response as low-level simulative action mirroring. Based on some of the above-mentioned basic descriptions of the functional properties of single mirror neurons in monkeys, Gergely Csibra poignantly criticizes the theory of strict mirroring action simulation. He writes:

> The generally weak congruence between motor and perceptual properties of MNs [mirror neurons] suggests that while the same neural structure is recruited for representing executed and observed actions of the same effectors (e.g., hands), the actual representations do not necessarily match across domains. Rizzolatti et al. (2001) realized this problem and asserted that the broad congruence found in MNs indicated that they "generalize the goal of the observed action across many instances of it" (p. 662). They were probably right. However, one cannot have one's cake and eat it too. MNs either simulate observed actions in order to understand them, or generalize already interpreted actions into abstract action-concepts. The

---

[17] Implied regions for motor imagery are SMA, premotor, somatosensory, and various cerabellar areas and possibly also primary motor cortex (for example, see Lotze et al. 1999).

> broad congruence found in MNs is more compatible with the latter idea. (Csibra 2005).

Thus, Csibra moves from the empirical evidence of a lack of low-level congruence in most mirror neurons to an argument about process and function. He argues, similarly to Jeannerod, that one must choose between whether mirror neurons mirror low-level movements or abstract action goals. But this leads him to question not just the function but also the order and directness of the low-level process. His argument goes something like this: The simulation was supposed to start by mirroring the observed action and from this covert action simulation the intentions or goals could be inferred. But the mirror neurons often seem to be activated by the recognition of the goal rather than the motor action. He concludes, "If simulation is involved at all in the functioning of MNs, the monkey 'simulates' because he has understood an action rather than he understands the action because he simulates" (Csibra 2005). Notably, Csibra's argument is here based on a somewhat questionable assumption: Namely, that the motor system must either <u>exclusively</u> move from "action-to-goal" or "goal-to-action." However, given that fronto-parietal areas have been shown to have massively parallel and recurrent sensorimotor circuits, this mutually exclusive dichotomy of process directions seems to be empirically wanting. However, given his dichotomy, Csibra argues for the latter and suggests that mirror neuron activity correlates to a post-hoc or late stage of action understanding, which specifies kinematic details of already understood goals. He sees the function of mirror neurons as pertaining primarily to action prediction rather than social cognition per se:

> In fact, a plausible counter-hypothesis for the role of MNs would be that they are involved in the prediction or anticipation of subsequent—rather than in the simulation of concurrent—actions of the observed individual. MNs seem to be primarily sensitive to instrumental actions that are performed in order to enable further actions, and the "logically" related actions that have been described as examples of broad congruence between executed and observed actions may indeed reflect this kind of sequential relation. (Csibra 2005)

The idea of mirror neurons as being involved in action prediction is interesting because accumulating evidence points to mirror neurons and motor areas more broadly as having various predictive functional properties. Kilner et al. (2004), for example, found that knowledge of an

upcoming action can activate motor areas <u>prior</u> to observing the action.[18] Findings of motor involvement in action prediction make sense given the general motor planning and temporal sequencing functions of motor areas. Kilner et al. (2004) conclude that whereas the mirror system has been seen as:

> … a passive, automatically triggered motor 'echo' used for action recognition. Our results suggest a more active role for this system in setting up an anticipatory model of another person's action, endowing our brain with the ability to predict his or her intentions ahead of their realization. (Kilner et al. 2004, 1300).

We saw earlier how Jacob & Jeannerod with their "passive" "echo" understanding of action simulation agued against this motor process as essential to prior intention understanding or interactive social perception. Csibra, Kilner and co-authors suggest that mirror neurons are involved with specifying actions given already set goals and in actively predicting and anticipating kinetic details of upcoming actions. But they are overall in agreement with Jacob and Jeannerods conclusion that motor processes are largely irrelevant for the goal understanding as such. Csibra's reasoning is based on findings showing that the motor system does not by default provide such a low-level mirroring simulation, but rather a mirroring of goals and inferred or anticipated actions. He argues that therefore goals "must be" understood prior to the engagement of the motor system. But this reasoning is based on a problematic one-way serial notion of motor processes as always going from "goal-to-action," with one specific locus of sensorimotor translation for each simulative process. The question is whether with a more complex notion of motor cognition one could agree that mirror neurons often respond to predicted goals rather than actual kinetic movements, and yet still take sensorimotor processes as supporting the understanding of intentions or distal goals.

Gallese's aim in one of his recent articles might be such a more complex position (Gallese 2007). Armored with the newly "tinkered" notion of "embodied simulation," he presents us with an idea of mirror neurons as being both action recognizers <u>and</u> action predictors and thereby low-level intention readers:

> Single motor acts are dependent on each other, as they participate in the overarching distal goal of an action thus forming pre-wired intentional

---

[18] See also Fogassi et al. 2005 for anticipatory modulation of parietal mirror neuons. Umilta et al. 2001 for prediction of action goal and Schubotz 2007 for the motor system role in prediction of inanimate external events.

chains, in which each subsequent motor act is facilitated by the previously executed one. This suggests that in addition to recognizing the goal of the observed motor act, mirror neurons allow the observing monkey to predict the agent's next act, henceforth the overall intention. (Gallese 2007, 662)

Gallese thus imagines a mirroring simulation not of low-level movement kinematics but of motor acts defined by their low-level or motor goals.[19] Because of their participation in more distal goals, upcoming motor acts can be anticipated. But Csibra's objection would here be this overarching distal goal—and the intention—would have to be known already in order to predict what motor act to anticipate in the present situation. Hence, his point is that we do not infer intentions by a simulation, but rather that such higher-level understanding must be in place before any simulation can begin. However, this would make simulation irrelevant to intention understanding and that is not what Gallese wants. He instead tries to solve the seeming "chicken versus egg" conundrum by suggesting a "pre-wiring" of motor action strings by prior experience:

> The statistical frequency of act sequences, that are habitually performed or observed in the social environment, could constrain preferential paths of act inference predictions. This could be accomplished by stringing together motor schemata. At a neuronal level, this would be equivalent to the chaining together of different populations of mirror neurons coding not only the observed act, but also those that would normally follow in a given context. (Gallese 2007, 662).

Thus, Gallese tries to argue for a new version of "action sequence" simulation that should allow to him to have his cake and eat it too. Unfortunately, as it stands, this account looks somewhat implausible. The automaticity of the simulation is bought by giving up flexibility, and it is not at all clear how actions can be "pre-wired" and still be sensitive to the contexts. It seems that this sort of process would either lead to wrong predictions in new contexts or have to rely on an already recognized distal goal/prior intention, and therefore have a different function than inferring this very goal/intention. In other words, this account does not seem to capture the contextual sensitivity often found in mirror neurons (Umilta et al. 2001) nor the experienced precision of social perception and action understanding.

In a recent article Shaun Gallagher like Csibra makes the claim that we do not need a simulation process for intention understanding. But his

---

[19] "If mirror neurons really underpin the action understanding, their activity should reflect the meaning of the action rather than its visual features" (Gallesse 2007, 660).

phenomenological reasoning is very different from Csibra's cognitivist line of thought. In Gallagher's view we "directly perceive" the intentions of others.

> "Direct" perception here means perception without some further cognitive or inferential step that goes beyond what is perceived, for example in an attempt to grasp hidden mental states. Thus, in a non-mentalizing way, I am able to see meaning, intention, and emotion in the actions of others, and in their gestures and facial expressions. (Gallagher 2007, 2)

It could look like Gallagher, like Jacob and Jeannerod, is saying that most social perception might be a "purely perceptual process" and that the motor system might be inessential to social perception. But the key to Gallagher's proposal is not that he wants to exclude the relevance of motor cognition, but rather that social cognition is not, as typically assumed, primarily about inferences or simulations of hidden mental states. Hence, his point regards both the goal and the process of social cognition. In regards to the perceptual process he considers it in a broader, less sequential perspective, which very well could include sensorimotor integration. Instead of assuming an independent simulation process, the motor resonance could on this account be seen as an integral part of the perception (Gallagher 2007, 8). What he wants to deny is that we should engage in an inferential simulation process separate from an already acquired "intentionless" perception. Thus, his point is two-pronged. First, it is the claim that there is no meaningful social perception prior to some understanding of the intentional aspects. Secondly, it is a claim about what intentions are; that they are not hidden mental objects that we have to guess or infer. This view of intentions also points to an alternative view of the general aim of social cognitive processes. He writes, "we do not try to get into other peoples minds; we try to get into their world, or more precisely, into a world we already share with them" (Gallagher 2007, 2). I agree. The idea is not that intentions and beliefs are always apparent, or that we never engage in some high-level "mind-reading" involving reasoning and inferences. Rather, the point is that this is not our default process of social understanding. When we look at regular social interactions and also developmental and primate studies, it does appear to be the case that we understand others' actions via a shared world. Gallagher thus gives a critique of both the simulation process and of third-person mindreading as the primary goal of social cognition. However, the question is how his phenomenological analyses relate to the mirror neuron data and the broader sensorimotor findings.

4. A Social and Proactive Affordance Role
of the Motor System

It might be that mirror neurons assist in representing goal-directed actions, and predict and anticipate upcoming actions. To use Csibra's terminology, we, and primates in general and premotor mirror neurons in particular, seem to be "obsessed with goals" (Csibra 2007). By way of some ideo-motor process it is plausible that simply entertaining or understanding an immediate action goal or motor act primes the respective parts of motor cortex and thereby facilitates action.[20] This would fit with many of the behavioural findings of imitative motor resonance during action observation. Csibra suggests that mirror neurons might functionally be involved in an action prediction process, starting with the goal and then predicting the specific actions that should be produced to achieve it (Csibra 2005). But the question that I am raising is why one would assume such serial goal-to-action simulation as the only or even the core function of the motor system in action observation? Why the *a priori* conclusion that predictive motor processes exclude motor areas as irrelevant for goal understanding? Csibra's conclusion seems unwarranted in that it is based on a narrow, one-way serial model of motor cognition and sensorimotor integration. I propose that the heterogeneous sensorimotor findings precisely reveal significantly parallel, abstract and dynamic processes. Thus, these findings are inconsistent with the traditional cognitivist idea of motor cognition as simulative output specification, which we have seen infiltrate the debate about mirror neurons from all fronts. A revision of the notion of motor cognition, which Jacob and Jeannerod claim to "take very seriously," would have broad implications for the mirror mechanism debate and possible sensorimotor groundings of higher cognitive processes more generally. Challenging the notion of what motor cognition is would also reopen the question of what a possible motor contribution to social cognition could even look like. Given recent sensorimotor findings I hypothesize a much more complex and proactive role for motor cognition in social perception than what has hitherto been conceived off. To explain my alternative interpretation of motor cognition during action perception, let me take a step back and also try to gather the treads of the prior sections.

Pre-motor areas are generally thought to be responsible for our own processes of action planning and coordination. Mirroring motor activity

---

[20] The central ideo-motor suggestion is that "human actions are initiated by nothing other than the idea of the sensorimotor consequences that typically arise from them" (Stock & Stock 2004, 176).

during action perception is hypothesized as serving an extra and relatively independent function pertaining to allocentric action understanding. One could label this the sort of view "motor system moonlighting for perception" to highlight how, under this interpretation, the primary perceptual and motor functions and circuits are still neatly divided. The motor system simply takes on an extra job serving social perception. Alternatively, I hypothesize that the motor response to the perception of action serves functions simultaneously more integral to processes of action choice and basic perception: i.e. more integral to coordination of own action choice and to the actual parsing of what is perceived. In other words, the perception of another's actions play an important role in structuring and navigation of one's own pragmatic situation, and further these motor processes are again likely to inform the perceptual dynamics of what is consciously seen.

Further, I propose that the motor contribution to social cognition has to do more with the understanding of the process of action selection than the narrow simulation or prediction of individual actions. Prediction of particular movements is a neat tool, and in some cases it might be all we want. However, in most social situations we might not aim at a detailed kinematic understanding of others actions per se. Rather, our focus is here is typically, as it is in our general perception of inanimate objects, how the observed scenario relates to ones position, motivations and abilities. The motor system might help us understand what an object, situation or social situation invites or "affords" oneself or others to do.

The affordance notion is theoretically interesting in multiple ways as this relational concept effectively collapses several traditional cognitive dichotomies. The perception of an affordance is the perception of a potential action. What would count as a potential or worthwhile action depends on one's past, i.e. action repertoire, one's position and motivation in the present situation. Thus, perceived affordances depend on the history of the organism. But, the affordance notion is of course also deeply future-directed in that it via past experience alerts to a possible outcome, and poses a question of whether or not to actually perform the afforded action. Affordances are deeply relational in that they simultaneously portray the world and our normative evaluative stance and potential reactions towards it. Hence, affordance perception seems to resist a neat perception-action division.

In the case of object perception we know that the motor system plays a role in what one might call "affordance" understanding and tracking. As a matter of fact, the very areas with "mirror" qualities have been implied in the process of integrating pragmatic and perceptual aspects of objects and

tools (Grèzes et al. 2003; Ferrari et al. 2005). Even prior to the discovery of mirror neurons, so-called "canonical neurons" were found in premotor areas. These sensorimotor neurons were modulated by both visual presentations of objects and the appropriate motor actions invited or afforded by such objects, and thus thought of as representing object affordances. To choose appropriate actions we need to somehow track more than one action possibility at the time, and it seems counter-intuitive to assume that canonical neuron activity represents full simulations of the invited action. In fact, each action choice is turning down certain action affordances and opening up others. To use Erik Rietveld's Merleau-Ponty inspired expression, we navigate the world by being situated in a "field of affordances" (Rietveld 2008). This sort of dynamic and parallel affordance tracking fits with the empirical evidence of parallel and recurrent sensorimotor integrations.

Thus, I suggest we should think of the activity of sensorimotor neurons more like schematic and kinetically abstract versions of afforded actions rather than a covert simulation of the full motor response. This is extremely important, because as we saw earlier Jacob & Jeannerod as well as Csibra to a certain extent all rely on a notion of motor cognition where such schematic and parallel motor response seems to be logically ruled out. Now we might fruitfully turn the constraint argument on its head and suggest that due to the temporal constraints of real time interactions and the load constraints of covert simulations our early parallel sensorimotor processes might be more like schematic goal or affordance representations. In other words, there might be a more abstract and non-simulative role of motor cognition, which does not have the same constraints as overt action and motor imagery, for example. All of a sudden a motor role in goal understanding seems far from logically precluded by the nature of motor processes.

Further, in the actual sensorimotor findings, the question is what the justification is for hypothesizing a symmetric "mirror mechanism" independently of these "affordance" neurons? I think that not only the idea of motor cognition as simulative but also the idea of social cognition as third person "mind-reading" of hidden mental states has contributed to an exaggerated focus on action mirroring. Whether or not these theoretical assumptions are to blame, the fact is that affordances and the broader non-mirroring motor responses have been largely ignored as potentially contributing both to action perception and social cognition. My claim is that the empirical findings of, for example, occluded objects modulating single mirror neuron responses (Umilta et al. 2001) clearly suggest a common and interrelated function of the "canonical" object affordance

neurons and action sensitive "mirror" neuron sub-groups. Further, I propose that the function of these integrated sensorimotor circuits is to track the overall affordance space for the purpose of ones own action coordination, but integrally to that also social understanding of others in our shared space. With a dynamic tracking and integration of both the actions and action possibilities of others we seem to have the key ingredients for understanding not only the goals of their actual actions, but more importantly for their potential actions. This means further that I have important clues as to the process of their action choices. This is crucial as there is a lot of social information in seeing what you did not do but could have done. The focus of most philosophical theories of social cognition has been on how we, from a third person perspective, can understand the hidden mental states of others, such as the intention behind the action already chosen by more central cognitive processes. The focus is on minds as perceptually opaque, and mental states as atomistic and stable. Hence, the traditional social cognition debate often leaves out the questions that interest me the most. Namely, how our thoughts flow and decisions proceed, and of course how we relate and change each other's minds already before we are aware of it.

This later point leads me to the issue of "social affordances." Motor processes have been documented to play an important role in understanding the affordances of inanimate objects and tools. My hypothesis is further that they play an equally important role in assessing the present affordances of actions and cultural and social scenarios. I think that the dualistic dichotomizing of "object affordances" and "action mirroring" is problematically simplistic and we have seen that this categorization systematically covers up a series of more complex asymmetric motor responses to third personal action perception. Further, there has been very little experimental work done on motor responses under "second person" conditions, i.e. in actually interactive social scenarios. The lack of experimental data can be attributed in part to the technological difficulty of neurological studies of social interaction. However, I suggest that it is also due to theoretical blind spots, and I would hypothesize that social affordance modulation can be found on both single cell and population levels.

To return to the overall question of the motor role in social cognition, my proposal is that fronto-parietal areas dynamically integrate observed intentional actions and affordances of potential actions and depend on motivational and pragmatic circumstances of the observer. The idea is that such a broader affordance tracking would support not only our own on-going action choices, but integrally to this process support our

understanding of the action choices and possibilities of others. One should note that such a social affordance view proposes a very different role for the motor system in social perception than what is assumed by a "mirroring" simulation theory. Instead of passively "echoing" perceived movements, it is suggested that our motor system is tracking intentional actions and objects in parallel and preparing appropriate reactions. This account is also rather different from the more narrow predictive function Csibra suggests. On the affordance account we can anticipate others' actions in so far as we can understand the relevant parts of their affordance structure. But it is not so much the detailed anticipation of actual actions that is important. Rather, the key motor contribution to social cognition is the understanding of the other's potential actions and how they navigate their world and evaluations leading to their action choice. This view of the motor contribution to social cognition can in many ways be seen as congenial to Gallagher's phenomenological proposal as the locus of the debate becomes inter-subjective world relations and affordances, rather than inferences or simulations of hidden mental states.

Further, an implication of the affordance view is that it is not typically the goals or affordance structures of others that control the specification of our overall overt or covert motor response, but our own goals. This means that we need to look at behavioural motor resonance studies with renewed scrutiny, because most of these are studies of detached third personal action observation and therefore "affords" mirroring imitation rather than complimentary interaction. It is therefore highly problematic to use such studies to suggest a ubiquitous simulative mirroring process. In interactive situations of tight temporal demands for immediate reaction, these differences should show, and several recent studies seem compatible with the idea of motor activity as proactive and non-mirroring during action observation. First, Newman-Norlund and colleges recently found that mirror neuron areas were more active during complimentary rather than imitative actions (Newman-Norlund et al. 2007). Similarly it has been reported that the otherwise so robust reaction time advantage of imitation actions disappears if the action is cued by the object rather than the observed hand (van Schie et al. forthcoming).[21] Another intriguing finding is that motivational factors have been found to modulate human parietal mirror neuron areas (Cheng et al. 2007) suggesting that neuronal process are not acting as a passive or objective "mirror."[22] Also, pre-motor mirror

---

[21] See also Catmur et al. (2007).

[22] Curious implications of motivation modulation of mirror neurons can also be found in the importance of food rewards for ongoing MN response in monkeys.

neurons in monkeys have been found to respond to live action but not video clips of similar actions (Keysers & Perrett 2004, 502). Differences due to "mode of presentation" are expectable on an affordance account, since the video versus live scenario, though similar in action-related facts, present the spectator with very different affordances. This also raises a serious question about traditional experimental paradigms of one-way and non-interactive "social" perception. Often a single spectator observes action sequences or video clips of such, and is required to react either by imitation or pre-specified movements. What kind of reactions do such scenarios afford? My point is that there might often be an "imitation bias" in this sort of experimental set-up, because the object of attention is the observed action. Under such experimental circumstances and incentives there is no action invitation for the detached spectator beyond narrowly following the motor action itself. Thus, given the context, it is expectable that we find covert imitation and congruent action facilitation. However, such experiments lend little support to the idea of a "ubiquitous" simulative mirroring response.

5. Conclusion

Recent studies of social perception seem to suggest a more complex role of motor activity than the symmetric "mirroring" function that has been assumed by implicit simulation theories. Surely we might engage in a covert imitation process of others' actions in some special cases where we take a spectator role and hold the action itself as our "object" of attention. However, my point is that this does not seem to be the default mode of motor activity during actual social and interactive situations. If this is the case then the broader implication is that motor cognition in general should not be limited to an off-line "as if" action rehearsal process, but might have much more complex integrative and cognitive functions. I underlined the insufficiency of simulation theories of motor cognition by discussing some of the experimental mirror neuron findings that initially were taken to support these. The broader sensorimotor findings seem to undermine the traditional mirroring story and call for less symmetric and less simulative reinterpretations. Alternative theories of predictive and affordance related functions of motor activity in social perception were discussed, and I hope with these alternative proposals also to open the door for a broader

---

Csibra (2005) refers to studies were monkey mirror neurons seem to stop firing at the sight of previously effective actions if no food reward is given as a distal goal.

functional domain of motor cognition and for what it means to understand other agents.

I argued that the empirical findings of sensorimotor affordance tracking pose a serious challenge to the idea of motor cognition as highly load-constrained covert action. Multiple potential actions seem to be tracked in parallel in the process of choosing and coordinating our more fully specified response. Given the evidence for schematic parallel affordance tracking in response to object perception, why shouldn't one expect equal sophistication and abstraction in regards to action perception? The basic hypothesis of the social affordance model is that fronto-parietal circuits help us to dynamically track the surrounding teleological agent-environment relations. These relational sensorimotor processes are essential to our choice of action response, but similarly for our understanding of others' choices given the scenario. This proposed multifaceted motor role in action choice is noteworthy, as questions of how we can flexibly choose actions was one of the main motivations for the rise of cognitivism and critique of the rigid reflex arch of classical behaviorism. Thus, I see the discussion of what motor cognition can and cannot do as having important theoretical implications for the possibility of a theory of sensorimotor grounding of higher cognitive processes, which avoids the pitfalls of reflex or simulative motor theories.

Thus the evidence for parallel and schematic motor resonance during both object and social perception might open the door for a motor role in higher cognitive processes. More specifically, the sensorimotor circuits seem to underlie our ability to select appropriate actions and the understanding of social triangulation between agents and shared and separate affordance structures. Functional roles like these are rarely touched on in the "mirroring" and simulation literature. But, I argue that if the motor system is no mirror and if social cognition is not just about getting into others heads, then most of the assumptions of the mirror neuron debate need to change. But the article is not just meant as a theoretical corrective. A theoretical move away from a primarily "mirroring" and sequential "output" function of the motor system in social perception implies that much data needs to be reinterpreted. It also indicates a dire need for new research. One might thus suggest that typical "social" cognitive experimental paradigms with single subjects engaged in one-way observation often carry a bias towards simulation. However, if the motor system is no mirror, then there is no justification for a narrow focus on activity in "areas with mirror qualities," but rather an urgent need for new interactive—and inherently more social—experimental paradigms.

References

Brincker, M. Moving beyond mirroring – A social affordance model of sensorimotor integration during action perception. Doctoral dissertation, Department of Philosophy, Graduate Center, City University of New York. ProQuest, 2011.
http://gradworks.umi.com/34/26/3426710.html (accessed 2012-03-28).

Buccino, G., F. Bikofski, G. R. Fink, L. Fadiga, L. Fogassi, V. Gallese, R. J. Seitz, K. Zilles, G. Rizzolatti & H. J. Freund. Action Observation Activates Premotor and Parietal Areas in Somatotopic Manner: An Fmri Study. *European Journal of Neuroscience* 13 (2001) 400–404.

Buccino, G., F. Bikofski & L. Riggio. "The Mirror Neuron System and Action Recogntion." *Brain and Language* 89 (2004): 370–376.

Caggiano, V., L. Fogassi, G. Rizzolatti, P. & A. Casile. "Mirror Neurons Differentially Encode Peripersonal and Extrapersonal Space of Monkeys." *Science* 324 (2009): 403–406.

Calvo-Merino, B., J. Grèzes, D. E. Glaser, R. E. Passingham & P. Haggard. "Seeing or Doing? Influence of Visual and Motor Familiarity in Action Observation." *Current Biology* 16 (2006): 1905–1910.

Catmur, C., V. Walsh & C. Heyes. "Sensorimotor Learning Configures the Human Mirror System." *Current Biology* 17 (2007): 1527–1531.

Cheng, Y., A. N. Meltzoff & J. Decety. "Motivation Modulates Activity of the Human Mirror Neuron System." *Cerebral Cortex* 17 (2007): 1979–1986.

Csibra, G. "Mirror Neurons and Action Observation. Is Simulation Involved?" 2005.
http://www.cbcd.bbk.ac.uk/people/scientificstaff/gergo/pub/index.html/pub/mirror.pdf (accessed 2012-03-28).

Csibra, G. "'Obsessed with Goals': Functions and Mechanisms of Teleological Interpretation of Actions in Humans." *Acta Psychologica* 124 (2007): 60–78.

di Pellegrino, G., L. Fadiga, L. Fogassi, V. Gallese & G. Rizzolatti. "Understanding Motor Events: a Neurophysiological Study." *Experimental Brain Research* 91 (1992): 176–180.

Fadiga, L., L. Craighero & E. Olivier. "Human Motor Cortex Excitability During the Perception Of Others' Action." *Current Opinion in Neurobiology* 15 (2005): 213–218.

Ferrari, P. F., S. Rozzi & L. Fogassi. "Mirror Neurons Responding to Observation of Actions Made by Tools in Monkey Ventral Premotor Cortex." *Journal of Cognitive Neuroscience* 17 (2) (2005): 212–226.

Fogassi, L. & V. Gallese. "The Neural Correlates of Action Understanding in Non-Human Primates." In *Mirror Neurons and the Evolution of Brain and Language*, edited by M. I. Stamenov & V. Gallese, 13–35. Amsterdam: John Benjamins Publ, 2002.

Fogassi, L., P. F. Ferrari, B. Gesierich, S. Rozzi, F. Chersi & G. Rizzolatti. "Parietal Lobe: From Action Organization to Action Understanding." *Science* 38 (2005): 662–667.

Gallagher, S. "Simulation Trouble." *Social Neuroscience* 2 (3 & 4) (2007): 353–365.

Gallese, V. "The Manifold Nature of Interpersonal Relations: The Quest for a Common Mechanism." *Philosophical Transactions of the Royal Society* LondonB 358 (2003): 517–528.

—. "Intentional Attunement. The Mirror Neuron System and its Role in Interpersonal Relations." 2004. http://www.summer10.isc.uqam.ca/page/docs/readings/BOUCHARD_Denis/interdisciplines%20_%20What%20Do%20Mirror%20Neurons%20Mean.pdf (accessed 2012-03-28).

—. "Before and Below 'Theory of Mind': Embodied Simulation and the Neural Correlates of Social Cogntion." *Philosophical Transactions of the Royal Society B* 362 (2007): 659–669.

Gallese, V., L. Fadiga, L. Fogassi & G. Rizzolatti. "Action Recognition in The Premotor Cortex." *Brain* 119 (1996): 593–609.

—. "Action Representation and the Inferior Parietal Lobule." In *Attention and Performance XIX: Common Mechanisms in Perception and Action*, edited by W. Prinz & B. Hommel, 334–355. New York: Oxford University Press, 2002.

Gallese, V. & A. Goldman. "Mirror Neurons and the Simulation Theory of Mind Reading." *Trends in Cognitive Sciences* 12 (1998): 493–501.

Gallese, V., C. Keysers & G. Rizzolatti. "A Unifying View of the Basis of Social Cognition." *Trends in Cognitive Sciences* 8 (9) (2004): 396–403.

Gazzola, V., G. Rizzolatti, B. Wicker & C. Keysers. "The Anthropomorphic Brain: The Mirror Neuron System Responds to Human and Robotic Actions." *Neuroimage* 35 (2007): 1674–1684.

Goldman, A. I. "Mirroring, Mind-Reading and Simulation." In *Mirror Neuron Systems: The Role of Mirroring Processes in Social Cogntion*, edited by J. Pinedã. Humana Press, 2009.

Grèzes, J., J. L. Armony, J. Rowe, R. E. Passingham. "Activations Related to 'Mirror' and 'Canonical' Neurones in the Human Brain: A fMRI Study." *Neuroimage* 18 (2003): 928–937.

Hari, R., N. Forss, S. Avikainen, E. Kirveskari, S. Salenius & G. Rizzolatti. "Activation of Human Primary Motor Cortex During Action Observation: A Neuromagnetic Study." *PNAS* 95 (1998): 15061–15065.

Haueisen, J. & T. R. Knosche. "Involuntary Motor Activity in Pianists Evoked by Music Perception." *Journal of Cognitive Neuroscience* 13 (2001): 786–792.

Hurley, S. L. *Consciousness in Action*, Harvard University Press. London, England, 1998.

—. "The Shared Circuits Model. How Control, Mirroring, and Simulation Can Enable Imitation and Mind Reading." *Behavioral and Brain Sciences* 31 (2008): 1–22.

Jacob, P. & M. Jeannerod. "The Motor Theory of Social Cogntion: A Critique." *Trends in Cognitive Sciences* 9 (1) (2005): 21–25.

Jeannerod, M. *The Neural and Behavioural Organization of Goal-Directed Movements*. Oxford University Press, 1988.

—.*Neurophysiological & Neuropsychological Aspects of Spatial Neglect.* Elsevier BV, 1987.

—. "Neural Simulation of Action: A Unifying Mechanism For Motor Cognition." *NeuroImage,* 14 (2001): 103–109.

—.Visual and Action Cues Contribute to Self-Other Distinction. *Nature Neuroscience* 7 (2004): 422–423.

—.*Motor Cognition—What Actions Tells the Self.* Oxford: Oxford University Press, 2006.

Keysers, C., E. Kohler, M. A. Umilta, L. Nanetti, L. Fogassi & V. Gallese. *Experimental Brain Research* 153 (2003): 628–636.

Keysers, C. & V. Gazzola. "Expanding the Mirror: Vicarious Activity For Actions, Emotions, and Sensations." *Current Opinion in Neurobiology* 19 (2009): 1–6.

Keysers, C. & D. I. Perrett. "Demystifying Social Cognition: A Hebbian Perspective." *Trends in Cognitive Sciences* 8 (2004): 501–507.

Kilner, J.M., C. Vargas, S. Duval, S. J. Blakemore & A. Sirigu. "Motor Activation Prior to Observation of Predicted Movement." *Nature Neuroscience* 7 (12) (2004): 422–423.

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

Koski, L., A. Wohlschläger, H. Bekkering, R. Woods, M. C. Dubeau, J. C. Mazziotta & M. Iacoboni. *Cerebral Cortex* 12 (2002): 847–855.

Lhermitte, F., B. Pillon & M. Serdaru. "Human Autonomy and the Frontal Lopes Part I: Imitation and Utilization Behavior: A Neurological Study Of 75 Patients." *Annals of Nerology* 19 (1986): 326–334.

Lingnau, A., B. Gesierich & A. Caramazza. "Asymmetric fMRI Adaptation Reveals No Evidence For Mirror Neurons in Humans." *Proceedings of the National Academy of Sciences* 106 (2009): 9925–9930.

Lotze, M., P. Montoya, M. Erb, E. Hulsmann, H. Flor, U. Klose, N. Birbaumer & W. Grodd. "Activation of Cortical and Cerebellar Motor Areas During Executed and Imagined Hand Movements: An fMRI Study." *Journal of Cognitive Neuroscience* 11 (1999): 491–501.

Newman-Norlund, R.D, H. T. van Schie, A. M. J. van Zuijlen & H. Bekkering. "The Mirror Neuron System is More Active During Complementary Compared With Imitative Actions." *Nature Neuroscience* 10 (7) (2007): 817–818.

Rietveld, E. "Unreflective Action: A Philosophical contribution to Integrative Neuroscience." PhD Thesis University of Amsterdam, Department of Philosophy/ILLC. 2008.

Rizzolatti, G., L. Fadiga, L. Fogassi & V. Gallese. "Premotor Cortex and the Recognition of Motor Actions." *Cognitive Brain Research* 3 (1996): 131–141.

Rizzolatti, G. & M. Gentilucci. "Motor and Visual-Motor Functions of the Premotor Cortex." In *Neurobiology of Neocortex*, edited by P. Rakic & W. Singer, 269–284. Chichester: Wiley, 1988.

Schubotz, R. "Prediction of External Events with Our Motor System: Towards A New Framework." *Trends in Cognitive Sciences* 11 (5) (2007): 211–218.

Schütz-Bosbach et al. "Self and Other in the Human Motor System." *Current Biology* 16 (2006): 1830–1834.

Searle, J. *Intentionality: An Essay in the Philosophy of Mind.* Cambridge University Press, New York, 1983.

Stock, A. & C. Stock. "A Short History of Ideo-Motor Action." *Psychological Reseach* 68 (2004): 176–188.

Umiltà, M. A., E. Kohler, V. Gallese, L. Fogassi, L. Fadiga, C. Keysers & G. Rizzolatti. "I Know What You Are Doing: A Neurophysiological Study." *Neuron* 32 (2001): 91–101.

Van Schie, H., B. van Waterschoot & H. Bekkering. "Understanding Action Beyond Imitation." *Brain Research* (forthcoming).

Wilson & Knoblich. "The Case for Motor Involvement in Perceiving Conspecifics." *Psychological Bulletin* 131 (3) (2005): 460–473.

If the Motor System is No Mirror…