

## **Beyond sensorimotor segregation: On mirror neurons and social affordance space tracking**

By Maria Brincker

### **Abstract**

Mirror neuron research has come a long way since the early 1990s, and many theorists are now stressing the heterogeneity and complexity of the sensorimotor properties of fronto-parietal circuits. However, core aspects of the initial ‘mirror mechanism’ theory, i.e. the idea of a symmetric encapsulated mirroring function translating sensory action perceptions into motor formats, still appears to be shaping much of the debate. This article challenges the empirical plausibility of the sensorimotor segregation implicit in the original mirror metaphor. It is proposed instead that the teleological organization found in the broader fronto-parietal circuits might be inherently sensorimotor. Thus the idea of an independent ‘purely perceptual’ goal understanding process is questioned. Further, it is hypothesized that the often asymmetric, heterogeneous and contextually modulated mirror and canonical neurons support a function of multisensory mapping and tracking of the perceiving agents affordance space. Such a shift in the interpretative framework offers a different theoretical handle on how sensorimotor processes might ground various aspects of intentional action choice and social cognition. Mirror neurons would under the proposed “social affordance model” be seen as dynamic parts of larger circuits, which support tracking of currently shared and competing action possibilities. These circuits support action selection processes—but also our understanding of the options and action potentials that we and perhaps others have in the affordance space. In terms of social cognition ‘mirror’ circuits might thus help us understand not only the intentional actions others are actually performing—but also what they could have done, did not do and might do shortly.

### **1. The caricature view of mirror neurons and the ensuing debate**

Mirror neurons were initially discovered by Giacomo Rizzolatti and colleagues in Parma (di Pellegrino et al., 1992, Gallese et al., 1996 and Rizzolatti et al., 1996)[1]. The core finding that inspired the name was that certain single cells in the macaque premotor cortex were modulated both by the execution of some goal-directed actions and by the perception of others performing similar actions. Such action-sensitive sensorimotor modulations were also found in parietal areas known to be highly anatomically and functionally interconnected with the premotor area F5. Additionally, indirect behavioral and imaging findings suggested homologue modulations in humans. The Parma group soon hypothesized that these fronto-parietal neurons together formed a mirror system by which

we understand the perceived actions and perhaps intentions of others by mapping them onto our own motor system. Here a formulation from a 1996 article:

These data suggest that area F5 is endowed with an observation/execution matching system. When the monkey observes a motor action that belongs (or resembles) its movement repertoire, this action is automatically retrieved. The retrieved action is not necessarily executed. It is only represented in the motor system. We speculated that that this observation/execution mechanism plays a role in understanding the meaning of motor events. (Rizzolatti et al., 1996, p. 132)

The central mirroring idea is that the perceived action is 'matched' with the perceiver's movement repertoire. Through the notion of observation/execution 'mirroring', 'matching' 'mapping' or 'translation', grew the idea that mirror neurons provide a relatively symmetric link between respectively (1) perception and action within the perceiver and (2) other and self, thus a social mirroring between subjects. (See also Uito, van Rooij, Bekkering, & Haselager, 2011a). Thus 'mirroring' is seen as relating social and motor cognition, which, as recently suggested by Ferrari and Rizzolatti, has been incredibly important in igniting the interest in mirror neurons. [2]

### **1.1. Motor processes as 'moonlighting' for perception?**

The discovery of mirror neurons and the hypothesized 'mirror mechanism' as sensorimotor mapping and motor simulation of perceived actions of others has generally been seen as a challenge to the classical cognitivist 'input-cognition-output' view<sup>3</sup> and as providing an 'embodied' alternative (e.g. Gallese, 2007). The idea being that mirroring as processes in motor formats (rather than a-modal symbolic representations) functionally appear to serve not just the production of action outputs but social perception and central cognitive action understanding. Hitherto fronto-parietal circuits had mainly been seen as supporting action planning and "perception for action" rather than "perception for understanding"[4]. In other words, the discovery of mirror processes in motor 'output' systems now contradicted the simple conception of forward-flowing information processing from sensory modules to central cognition to action implementation, as motor neurons here might contribute to both action perception and central cognitive intention understanding.

However, the question is to what extent the classic formulations of the mirror theory represent a move away from the modular input-output framework. Is not the output system of motor cognition here merely given an extra and separate job in service of cognition and social perception beyond its primary job in action execution? Is not this extra job theorized as based on a separate mechanism (i.e. mirroring), which might yield a cognitive understanding of goals and intentions behind the perceived action of others? The standard mirror neuron interpretation appears to maintain much of the core cognitivist structure, in particular the neat functional segregation between sensory and motor systems [5] and the idea of the intention somehow being behind the actually performed action. [6]

Over the last decades however, the picture of mirror neurons and their functional place within the broader fronto-parietal sensorimotor circuits has evolved tremendously. Many new studies have appeared, which together alert us to a much more complex and heterogeneous set of neurons and much less symmetric and modular population functions (see Casile, Caggiano, & Ferrari, 2011 for a review). While researchers in interesting ways have made adjustments to the classic mirror hypothesis, I see the basic framework as needing an explicit overhaul that matches the many new findings. I shall in this article first look at the plausibility of separate sensory and motor goal representations and then present some evidence for my proposed alternative social affordance space framework. [7]

## **1.2. Sensorimotor segregation in the current mirror neuron debate**

The original metaphor of mirroring contributed to what I propose is an empirically problematic and yet entrenched set of ideas: E.g. that mirror neurons (1) constitute a more or less encapsulated, non-contextual mechanism which (2) provides a direct inner motor simulation of the actual actions of others and perhaps access motor intentions and meanings (Gallese and Goldman, 1998 and Gallese et al., 1996). As multimodal neurons with self-other symmetric mirror-like features were found also in somatosensory and visceral circuits (Keysers et al., 2004), this simulation frame was proposed as a possible unifying frame for social cognition (Gallese, 2007 and Gallese et al., 2004). The core idea being that via the workings of multiple mirror systems we get something akin to an inner simulative ‘as if’ 1st person access to elements of an observed 3rd person’s actions and perceptions. Several theorists have raised concerns about the encapsulation assumption (e.g. Kilner, Friston, & Frith, 2007) and the simulation assumption (e.g. Gallagher, 2007).

However, an aspect of the original mirror metaphor which has been less discussed is the idea that (3) mirror neurons provide a translation or mapping not only of self and other but also of two independently preexisting action formats (action as perceived vs. action as execution). I argue in the following that this is an empirically problematic idea, and further that these sensorimotor processes might be constitutive of teleological organizations rather than merely acting as bridging translators. I argue that such theoretical revisions of the original mirror hypothesis yield a different picture of the contribution of mirror neurons to goal and intention understanding and social cognition in general.

Many of the core disputes of the current mirror neuron debate center on how we are to conceptualize (1) what is mapped/shared, i.e. the content and level of abstraction of the observation/execution mirror mapping ( de Vignemont & Haggard, 2008), (2) how the information is processed—i.e. what the inputs and outputs and transformations of the motor ‘simulation’ are ( Csibra, 2007, Uitol et al., 2011a, Uitol et al., 2011b and Hickok, 2013), and (3) how a separate function might have evolved/developed to support social cognition ( Heyes, 2010). Lastly there is (4) the dispute over whether mirroring procedurally causes goal and intention understanding, or whether we must already have a perceptual understanding of these that can then be ‘fed into’ the mirror mechanism. Some proponents of the former suggest that there is a simulation process, perhaps activating ‘action chains’ ( Rizzolatti & Sinigaglia, 2010), which gives rise to a motor or ‘embodied’ action understanding that cannot be understood by purely perceptual means ( Ferrari and

Rizzolatti, 2014, Gallese, 2007 and Gallese and Goldman, 1998). Proponents of the latter often suggest that the functional role of mirror neurons has to do with anticipating sensorimotor consequences of own and perceived actions for the purposes of action coordination and execution, and thus that their role in social cognition is accordingly limited. Further, it is highlighted that we can understand actions, which we cannot perform, and thus that mirror neurons and other motor circuits might contribute to but are neither necessary nor sufficient for action understanding (Csibra, 2007, Hickok, 2009, Hickok, 2013, Jacob, 2008 and Jacob and Jeannerod, 2005). [8]

Each of these core disputes seems to rely on aspects of the caricature metaphor of mirroring. Focusing on the last question, about the how mirror neurons contribute to action and intention understanding, we see that both camps typically presume that perceptual processes are fundamentally distinct from motor processes. Further, in part due to this distinction, action intentions are seen as imperceptible [9]. Thus most describe the actions of mirror and other sensorimotor neurons as “translating”, “mapping” or “linking” purely sensory onto purely motor goal representations. But the question is if these metaphoric descriptions are based on assumptions of sensorimotor segregation rather than empirical findings. I discuss the plausibility of the alternative, i.e. that cortical goal representations are inherently sensorimotor, and teleologically integrating actions and outcomes.

The aim of the article is to show how an abandonment of sensorimotor segregation, through e.g. a social affordance model, would change the terms of the current discussion. Firstly, it would challenge the idea of a purely perceptual or purely motor goal understanding mechanism heralded by many within the debate (Csibra, 2007 and Hickok, 2013). Secondly, it would change the hypothesized process of action understanding and also the role of mirror neurons in it. For example, instead of suggesting that mirror neuron simulation would help us see or infer the intentions behind the individual observed actions, the broader circuits might support a more perceptual understanding of the other’s action in the context of their available options—i.e. it would let us see crucial aspects of their decision-making process. Based on empirical findings, a ‘social affordance space’ interpretation of the function of mirror neuron circuits is sketched. Fronto-parietal circuits are here hypothesized as important for both ones own action choices and for the understanding of others processes of intentional action choice. Note this is not simply a question of recognizing an action type or goal as has typically been the experimental focus, but understanding—and in the second person case influencing—the potential actions of others; i.e. their actions in the making.

## **2. Affordances and action selections in fronto-parietal circuits**

The terminology of teleology has had quite a scientific revival over the last decades, as has the Gibsonian concept of affordances (Gibson, 1979). In connection with the sensorimotor literature within neuroscience, the term teleology is typically used to refer to any process that shows goal modulation. I shall use it as applying to any process organized around an expected distribution of outcomes. Thus not restricting the term to explicit representations of final goals or intentions but pertaining to purposiveness and outcome directedness more

generally. In the sensorimotor context this would mean that it encompasses the entire hierarchy of future-directed actions and processes organized around outcomes (Hamilton & Grafton, 2007).

Teleology as goal/target modulation had been documented in pre-motor and parietal cortical areas, well before the discovery of mirror neurons. In terms of the fronto-parietal “reach” circuit where mirror neurons were first discovered, single cell studies had already revealed curiously teleological sensorimotor modulations. For example ‘object sensitive’ or ‘canonical’ neurons, which are multimodal neurons with visio-motor (and often somatosensory) properties, which are modulated both in connection with action execution and during the presentation of complimentary objects or action targets. For example canonical neurons change their firing rate both when presented with a graspable object and when grasping such objects. Further, many such neurons are modulated in the period between stimuli exposure and action (set related) and when no actions are required (sustained activity) (Raos et al., 2006, Rizzolatti and Gentilucci, 1988, Sakata et al., 1995 and Taira et al., 1990).

The ‘affordance’ notion has crept into use, as these canonical neurons seem to contribute to the tracking of perceived objects in the surrounding environment in terms of the actions that they invite or ‘afford’ the subject to do given their relative position and action repertoire (Grèzes, Armony, Rowe, & Passingham, 2003) [10]. Accordingly many findings of tool and learning dependent modulations highlight the roles of both ability and target accessibility (Berti and Frassinetti, 2000, Bonini et al., 2014 and Cardellicchio et al., 2011). Such modulations of single neurons by visual perception of an object, and its unperceived presence in the dark and intentional actions toward such objects suggest that they integrate and/or anticipate the potential teleological relation between the agent and the target—and might therefore support the perceptual categorization and tracking of the ‘afforded’ action in respect to a target. Fagg and Arbib e.g. summarize their concept use as follows: “The term affordance is used to mean that visual cues are mapped directly to parameters that are relevant for motor interaction” (Fagg & Arbib, 1998).

Some might hypothesize canonical neurons as not contributing to affordance perception per se, but rather as guiding the initiation of motor commands. However, as already mentioned, single-cell recordings have shown affordance modulations in many such neurons when no action where required, as well as during delay periods between perception and action (Konen and Kastner, 2008 and Raos et al., 2006). Further, findings of modulation in the dark suggest that this multimodal integration yields a broader tracking of environmental affordances than needed for guidance of actually performed actions.

Hence this affordance-related fronto-parietal activity appears to support processes prior to the actual action initiation. Paul Cisek and John Kalaska have demonstrated that multiple sensorimotor affordances get specified in parallel until the later stages of the action selection process ( Cisek, 2007, Cisek and Kalaska, 2002 and Cisek and Kalaska, 2010) [11]. They proposed an “affordance competition hypothesis” for decision-making in fronto-parietal and related sub-cortical circuits, which hypothesizes that these sensorimotor

processes support not just perceptual attention and action specification but also decision-making processes.

Interestingly, they explicitly contrast this view to traditional input–output information processing views. They highlight the empirical problems of frameworks that segregate perceptual input and motor output systems, as they thereby locate cognition or decision-making processes in some black box between these (Cisek & Kalaska, 2010). Fagg and Arbib and others have also explicitly described parietal areas as crucial for affordance tracking: “Visual information is processed in the posterior parietal cortex for the hypothesized purpose of extracting a variety of affordances for the generation of motor behavior” (Fagg & Arbib, 1998).

Similarly teleological visio-motor properties have been studied and theorized quite intensely in connection with oculomotor attention and saccade tasks in other frontoparietal circuits (FEF-LIP). These studies are generally interpreted as indicating a sensorimotor mapping and tracking of sometimes competing possible targets for intentional saccades in the environment. Further single cells were reported as also showing dynamic modulation according to motivational bias and more general valence features of the target for the subject (Gottlieb, 2007 and Mountcastle et al., 1975).

There are many complexities pertaining to timing and divisions of labor within various premotor and parietal areas, left–right lateralizations, not to mention the intricate massively parallel sub-cortical sections of these circuits (Caligiore, Pezzulo, Miall, & Baldassarre, 2013). However for current purposes I merely stress that by the time of the discovery of mirror neurons much was already known about multiple fronto-parietal circuits supporting processes not only of action initiation but also of selection, and parallel affordance trackings of perceived options. Further the areas have been theorized as involved in spatial attention task and the planning and selection of visually guided actions and saccades (Andersen and Cui, 2009, Cisek and Kalaska, 2010 and Fagg and Arbib, 1998).

Overall, the affordance related findings challenge the idea of perception as depending on relatively modular sensory ‘input’ systems—and the idea that action selection and motor related processes functions uniquely to select and specify ‘outputs’. Many neuroscientists however continue to use a terminology of ‘translation’ or ‘mapping’, indicating separate sensory and motor formats (Bach et al., 2011 and Fagg and Arbib, 1998). They thus fail to appreciate the possibility that such sensorimotor processes might change the very organization of the perception, and serve to constitute the goal representation rather than merely to translate it through linkage.

### **3. Are cortical motor systems inherently sensorimotor and teleological?**

Within the literature, mirror neurons are often referred to as “basically motor neurons” (Ferrari & Rizzolatti, 2014). But what does it mean to say that a neuron is ‘motor’ or that mirror processes are part of the cortical motor system? Are parietal sensorimotor neurons motor neurons? Does not the very discovery of similar multimodal neurons in premotor and parietal areas suggest that the division between sensory and motor areas is a bit more

blurred that previously thought? (Rizzolatti & Luppino, 2001) To understand the weight of the challenge to assumptions about sensory and motor segregation, it is helpful to look beyond both canonical and mirror neuron findings for a moment, to what is known about the organization of fronto-parietal neurons more generally.

Beyond the affordance aspect of so-called canonical neurons Rizzolatti and colleagues proposed that many premotor neurons, also those modulated primarily by the monkey's own movement, had to be conceptualized in terms of goals and outcomes. They write:

We became sure that goal was a necessary concept in order to understand this class of neurons...There is no way to interpret these observations in terms of contractions of single muscles or muscular groups...the concept of aim was indispensable for explaining also the activity of neurons exclusively related to arm movements. (Rizzolatti et al., 1987)

Rizzolatti and colleagues in this way saw their work as challenging the idea of a uniform premotor cortex and also added to the mounting empirical challenges to the standard motor homunculus conceptions resulting from Penfield's famous stimulation studies (Penfield & Rasmussen, 1952). The view, which has now become more or less mainstream (Purves et al., 2012), is that not only premotor areas but even primary motor regions are organized not according to one detailed topological motor map of distal muscle groups and their efferents, but rather by way of several only grossly topological maps, each functionally organized around various sensory afferents (Strick & Preston, 1982). In other words, the anticipated sensory outcomes of actions seem to be key to the cortical motor organization. This view of cortical sensorimotor organization can be seen as at least a partial vindication of William James' proposal from more than a century ago, where he denied Wundt's "feeling of innervation" and wrote:

... I cannot help thinking...that the discharge into the motor nerves is insentient, and that all our ideas of movement, including those of effort which it requires, as well as those of its direction, its extent, its strength, and its velocity, are images of peripheral sensations, either 'remote,' or resident in the moving parts, or in other parts which sympathetically act with them in consequence of the 'diffusive wave.' (James, 1890, chap. 26)

Leaving the question of how we are aware of our actions aside, what I take from James is the question of whether it makes sense to talk about cortical motor commands or 'representations' independently of their anticipated sensory consequences? In other words, what should be the theoretical implications of the findings that cortical motor areas are organized around various anticipated proprioceptive, somatosensory and other more distal sensory outcomes (with James terminology 'resident' and 'remote' peripheral sensations)? [12]

One such implication seems to be that these circuits—both the granular and agranular sections—are inherently and inseparably sensorimotor in their organization. This is a rather important point when dealing with the question of what 'motor cognition' is. I shall

therefore give a little background on the typical anatomical reasons why primary and pre-motor areas have been isolated as the seats of the cortical motor system and parietal regions have been seen as perceptual association areas.

The classic divisions are based in part on electrically evoked behaviors through direct regional stimulation and upon cytoarchitectural evidence of the main distribution of cortico-spinal and thalamic efferents and afferents documented. Interestingly, the classical frontal motor areas are known as the ‘agranular cortex’ due to the relative absence of granular afferents (Solari & Stoner, 2011). What we call primary and premotor cortical areas are thus in a sense defined negatively as cortical areas with a pronounced near absence of direct sensory afferents from the thalamus. However, given an input–output framework the most intuitive way to demarcate motor areas might be to look for efferents to sub-cortical areas and the spinal cord. And most cortico-spinal projections do indeed arise from classical primary motor and premotor areas—however some significant spinal projections also arise directly from within core sensory areas, the most significant of these being from primary somatosensory subdivisions (Matyas et al., 2010 and Rathelot and Strick, 2009).

The claim here is not that we cannot meaningfully distinguish these peripheral afferents and efferents. Rather the point is that at the level of organization, in cortical areas in particular, it becomes much harder to insist on anatomical regions as either pertaining to sensory or motor processes. There are significant functional and anatomical differences between say pre-motor and parietal or somatosensory areas. However, evidence for any cortical pure motor organization appears to be lacking. Accordingly, the notions of ‘motor representations’ and ‘motor cognition’ might be misleading as we might be dealing with inherently sensorimotor conglomerates and indeed products of repeated sensorimotor feedback.

Partially similar proposals have been made by e.g. proponents of the ‘common coding’ theory of action and perception. Schütz-Bosbach and Prinz for example writes that the ideomotor principle implies that actions and perceptions are “coded in a common representational medium” (Hommel et al., 2001 and Schütz-Bosbach and Prinz, 2007). They go on to summarize the association process and its use as follows:

When a certain movement is performed, an association is created between the motor pattern it is generated by and the sensory effects it leads to. This association can then also be used in the reverse direction, such that a movement can be induced by anticipating or perceiving sensory effects (Schütz-Bosbach & Prinz, 2007, p. 349).

The question I have for the common coding theorists is how more precisely we are to understand the ‘associations’ as well as the ‘directions’ of anticipation referred to here. Similarly, among researchers inspired by studies of actions control and sensory feedback based prediction, the formulations of internal models, namely as ‘inverse’ and ‘forward’ simulations, appear to rely on a schematic that still to a large extent keeps cortical sensory and motor formats neatly divided (e.g. Miall, 2003). [13]



To exemplify the logical implications that sensorimotor segregation has for the interpretation of mirror neurons and fronto-parietal circuits I quote from a recent article by Hickok: “...action understanding cannot be achieved by matching or simulating observed actions in one’s own motor system, as was once claimed, but by matching or simulating the goals of the actions” (Hickok, 2013). Hickok thus distinguishes the simulation of actions and movements from goals. This is similar to Csibra’s 2007 analysis, where he distinguishes action-to-goal simulation from goal-to-action and argues like Hickok that movement simulation does not yield goal and teleological reasoning unless we already understand it by other—likely purely perceptual—means. Hickok’s conclusion is similar and his reasoning quite fascinating given our present purposes:

The question then becomes, how and where are the goals of an action coded in the brain? The answer is that the goal is encoded neurally as a sensory state... If the monkey were blindfolded and prevented from receiving somatosensory feedback, no matter how many movements he executed, accurately or not, the monkey would have no way to know whether the goal was achieved. The motor system alone is literally and figuratively blind and in this sense is incapable of understanding. The goals of an action are not in the actions themselves...they are in the consequences of the actions and these consequences are, for the range of actions we are considering here, sensory. Therefore, to understand an action, we must understand the sensory goal(s) of the action. Action understanding is a function of perceptual, not motor systems. (Hickok, 2013, p. 56)

I could not agree more that the monkey needs sensory movement feedback. Similarly, I agree with the Jamesian point made here that the movements themselves are ‘blind’ and that action consequences reveal themselves through re-afferent processes. Hickok is also right in stressing the importance of somatosensory and proprioceptive feedback, which in many mirror neuron studies have been ignored and sensorimotor is often equated with visual-motor [14]. But the question is why Hickok assumes segregated sensory and motor systems? Why suggest that the goal ‘encoding’ is purely sensory? And why assume that cortical motor systems are devoid of afferent organization and thus blind? As highlighted above anatomical evidence does not appear to support such segregations. Note that the distinction between sensory and motor ‘states’ and systems is what carries Hickok’s firm conclusion that goals are encoded in purely sensory non-motor formats. This is an example of how ‘classical sandwich’ assumptions can yield implausible implications even when based on otherwise valuable insights—here about goals and sensory afferents.

In summary, mirror neurons have repeatedly been theorized as some sort of translational interface between action and perception (as well as between self and other). The question however is whether we have two functionally independent kinds of cortical representations or systems—sensory and motor—to translate between. I propose that fronto-parietal circuits might instead support an inherently sensorimotor functional organization that is anticipatory and feedback-based in nature. Thus the evidence of parallel affordance tracking we saw earlier might indeed be “canonical” and revealing something central about the overall teleological organization of fronto-parietal areas.

To evaluate this idea a more detailed look will be needed at how mirror neurons findings contradict the caricature idea of an 'observation/execution mirror matching mechanism'. We turn first to the questions of (1) whether mirror neurons like many other fronto-parietal neurons can be thought of as teleologically organized, and (2) whether the goal modulation in the STS can be seen as purely perceptual. Then we interrogate the idea of (3) a relatively separate 'mirroring' mechanism, and of (4) a symmetrical action-perception self-other modulation. Overall the findings of contextual dynamics, asymmetry and various heterogeneous goal and affordance modulations lead to the hypothesis of a social affordance space mapping function in fronto-parietal circuits.

#### **4. Goal abstraction and intentional action compression**

Though the mirror metaphor suggests that the observed actions are mirrored, reproduced, or simulated in the motor systems of the observer, findings indicate that most of these action sensitive neurons are modulated by the goal or the anticipated outcome of the perceived action at some level of abstraction higher than perceived kinetic details. The idea that fronto-parietal neurons are particularly tuned to goal-oriented and intentional actions fits well with prior knowledge. Many later studies have now supported the hypothesis that most mirror neurons are modulated by the target, goal, sub-goal or expected outcome of actions (Bonini et al., 2009, Ocampo and Kritikos, 2011 and Umiltà et al., 2008). Some findings suggest that different cortical areas are selective for different levels of goal abstraction and multiple parallel circuits have been proposed, of which some might provide a more precise mapping (Rizzolatti & Sinigaglia, 2010). Disparities between humans and non-human primates have also been reported in terms of both transitive (goal directed) vs. intransitive actions (non object directed intentional actions, e.g. gestures), and also in terms of the level of sub-goal detail (Peeters et al., 2009) and tool responses (Cattaneo, Caruana, Jezzini, & Rizzolatti, 2009). However, as argued above even detailed or intransitive action modulations can be thought of as organized teleologically around sensory outcomes or communicative purposes. Lyons and colleagues have introduced the idea of various levels of 'intentional compression', and hypothesized that documented differences in human and monkey sensitivities might relate to differences in what can count as a 'goal' or a meaningful outcome, rather than to a difference in whether mirror neurons are modulated by goal-directed intentional actions. They write:

...one of the potential benefits of construing behavior in intentional terms is that doing so might facilitate more concise representation: rather than encoding the complicated visual features of an action sequence, the sequence can be compressed to a simpler description of the underlying intention. Although such 'intentional compression' would be advantageous in many ways, as with any computational data compression algorithm the disadvantage is that information might be lost. Thus, if mirror neurons are attuned to the intentional structure of behavior, it is possible that non-human primates might simply be unable to encode lower-level visual details of observed actions. (Lyons, Santos, & Keil, 2006, p. 232)

Lyons and colleagues thus suggest that if you have intentional organization at some level of abstraction/generalization then lower-level visual details might be unavailable.

Additionally, there could be a mutually determining relation between what can be intended and what can count as a level of compression. Visual details might accordingly be available for some sub-cortical circuits but fail to be differentiated as intentional goals—i.e. they may not be tracked as differentiated teleological units for cortical sensorimotor planning purposes. Given this ‘intentional compression’ idea, one could further hypothesize that we might only be capable of intentional performance of actions that has been thus compressed in terms of cortical organization and possibly action-outcome expectations [15]. However, this is not to say that actions cannot be organized at many levels in the same subject, but merely that there might be granularities in both ends of the spectrum as well as specific kinds of action meanings that are not available to certain species or individuals. [16]

The developmental psychologist Gergely Csibra has made some points in the same vein as Lyons et al., as he has argued that motor processes always ‘emulates’ actions at some level of abstraction rather than serving as precise ‘mirrors’ or imitators. Interestingly however Csibra, as opposed to Lyons and colleagues, sees this goal modulation as an argument against the role of mirror neuron circuits in goal and intention understanding. A key factor in Csibra’s argument concerns how sensorimotor abstraction and motor simulation are conceptualized and whether one thinks that such processes can underlie the understanding of action goals beyond one’s own motor repertoire. Csibra seems to presume that all motor processes are simulative and much like a covert version of an actual chosen and executed action (i.e. action minus execution). [17] He then reasons that action mirroring must be a ‘goal-to-action’ process where actions are matched at some specific level of description followed by a detailed covert simulation. The idea that sensorimotor processes could encode or simulate any action beyond our action repertoire is dismissed a priori. Referring to a 2005 study by Ferrari et al. showing that some monkey premotor mirror neurons can be trained with purely perceptual exposure to respond to goal-directed actions with tools that are not in the monkey’s own motor repertoire. Csibra concludes:

...MNs responded to the sight of a non-executable action with a different action that the monkey could have used to achieve the same goal. This is exactly what the emulation model of action mirroring predicts for observed actions whose *goals are interpreted outside the motor system and then fed into the observer’s action control system for reconstruction.* (Csibra, 2007, p.446. My italics)

Csibra thus stresses that goals are understood first and then serve as the input ‘fed into’ to mirror systems rather than as their product. Curiously he and his colleague György Gergely are great advocates for the idea that ‘teleological reasoning’ and affordance understanding are crucial for intention and goal understanding, but propose as we see here that these processes are based on purely perceptual processes taking place prior to the involvement of sensorimotor processes (Csibra & Gergely, 2007).

Like Hickok, Csibra relies on assumptions about segregated sensory and motor formats and a feedforward information-processing model. Additionally he appears to hypothesize that fronto-parietal systems always work under the same constraints as overtly chosen and executed actions, and therefore that the selection of a particular action at a particular level of description happens prior to any engagement of the in essence always action simulating

motor system (Csibra, 2007). In brief, the action—and intention—selection must always happen before any sensorimotor ‘mapping’. Note that this theory goes straight against the evidence of multiple competing affordances in parietal areas and of parallel fronto-parietal circuits (Cisek & Kalaska, 2010) [18]. Csibra’s arguments thus rely on empirically implausible assumptions about what sensorimotor processes can and cannot do. If we move away from these assumptions then we can agree with him that actions are emulative and organized around hierarchical goals, and yet maintain that parallel sensorimotor processes support action choice, affordances and goal understanding.

## **5. Goal modulation in the STS – a ‘purely perceptual’ format?**

Csibra and also Hickok’s proposals that purely perceptual analyses underlie our goal, intention and ‘teleological reasoning’ mechanisms are however not empirically unsupported. Well before the discovery of mirror neurons in pre-motor areas, certain cells in the Superior Temporal Sulcus (STS) were found to be modulated by complex visual stimuli of biological action including goal-directed actions and gaze direction (Perrett et al., 1985 and Perrett et al., 1989). Further, these cells did not respond to the monkey’s own movements.

Consequently, the STS has consistently been hypothesized as providing the visual and non-motor input for the mirror neurons mechanism. This also fits with the matching/mirroring metaphor, which implies a process of translation or mapping of two different pre-existing formats and organizations, namely a purely perceptual and a purely motor representation of the same action. Thus, even defenders of the mirror theory of action understanding, generally support the idea of a purely perceptual action representation in the STS, which might be what is ‘matched’ in the motor systems by mirror neurons. Gallese and Goldman describe their preferred hypothesis as follows:

The STS neurons would provide an initial ‘pictorial’ description of actions that would be then fed (most likely through an intermediate step in the posterior parietal cortex) to the F5 motor vocabulary where it would acquire a meaning for the individual. (Gallese & Goldman, 1998, p. 499)

Accordingly, even though Goldman and Gallese want to argue that some lived 1st person meaning is added by sensorimotor processes, they still see the STS as providing a prior and independent ‘pictorial’ action understanding. Further, the background of Mishkin, Ungerleider, and Macko (1983) and Milner and Goodale’s (1995) influential distinctions between two visual processing streams should be kept in mind: The temporal ‘ventral stream’ pertains to the ‘what’, i.e. the semantic understanding of the content of perception, and the parietal ‘dorsal stream’, supports the ‘how’ and ‘where’, i.e. perception for action. Given this division and the STS findings Hickok argues as follows:

The existence of other mechanisms for action understanding is a problem for the mirror neuron theory of action understanding because, it places action understanding on par with “object understanding.” Object responses in F5 are not generally interpreted as the neural basis for object understanding (Rizzolatti &

Gentilucci, 1988), presumably because other neural systems in the ventral visual stream support object recognition/understanding. Object information, processed for “meaning” in the temporal lobe, can gain access to motor programs as appropriate for behaviors such as grasping, thus explaining the object response properties of F5 cells, even though the meaning of the objects is not coded in these motor areas. (Hickok, 2009, p.7)

He makes an analogy between action and object perception—mirror and canonical neurons—and argues that in both cases the “understanding” might have its neural basis in the ventral stream and then “gain access to motor programs” for the purpose of action coordination. Some problems with this ‘access to motor programs’ interpretation of canonical neurons have been discussed above, but note here that both Hickok’s and Goldman and Gallese’s proposals assume classic feed-forward processes over temporal–parietal–premotor areas. That is, both proposals ignore the many documented projections back to the STS from both premotor and parietal regions (Hietanen and Perrett, 1993 and Hietanen and Perrett, 1996)—as well as via subcortical integration loops (Caligiore et al., 2013). The question is if the goal processing in the temporal lobe is respectively (1) prior to and (2) independent of parietal and premotor processes. To this point Schippers and Keysers used a Granger causality analysis of imaging data to explore the flow of information between areas of the ‘putative mirror system’ within respectively the premotor, parietal and temporal regions. They write: “We found predominantly an information flow within the pMNS from premotor to parietal and middle temporal cortices” (Schippers & Keysers, 2011). Hence Hickok’s idea of the STS as an “other mechanism for action understanding” seems to ignore the dynamic modulations and organizational integration between STS and fronto-parietal regions.

Beyond back propagations the findings that intrigue me most pertain to the single cell studies by Hietanen and Perrett. They did indeed find that STS action sensitive neurons were only modulated by the perception of actions of others, and not by the monkeys’ own movements. This finding supports the interpretation of the STS as purely perceptual and non-motor. Interestingly, however they also found that these neurons did not respond to the sight of own movements, and often not even to predictable visual consequences of own movements (Hietanen & Perrett, 1996). Other studies generalized the lack of response to all expected visual change (Mistlin & Perrett, 1990). How is this differentiation between self and other, expected and unexpected, possible? Can we understand this kind of differentiation as ‘purely sensory’? One might instead speculate that the activity in such areas is a product of sensorimotor modulation—a sort of subtraction of self—to reflect the external and surprising elements of perception. Hence, the question is in what sense the STS is ‘non-motor’ and ‘purely perceptual’? Hietanen and Perrett’s own findings appear to leave open the option that the goal-organization in the STS is a product of inherently sensorimotor processes rather than independent from these. If this is the case the translation/mapping notion of mirroring is dealt a significant blow.

## **6. Dynamic and context-dependent properties of mirror neurons**

The next question is whether it makes sense to talk about mirror neurons as forming a separate 'mechanism' independent from the broader fronto-parietal circuits and in particular apart from affordance functions and other sensorimotor neurons with non-symmetric perceptual and movement correlated modulatory activity.

A finding, which is often cited as an example of the goal level modulation of mirror neurons, is from the 2001 study by Umiltà et al. Here the Parma group found that almost half of mirror neurons modulated by various hand-object grasps, were nearly similarly modulated when the object contact took place behind an occluder and therefore was not directly seen but based on prior knowledge of the presence or absence of an object behind the occluder. What is rarely discussed is the fact that this is clear evidence that many mirror neurons must be dynamically integrating contextual knowledge, more specifically knowledge about the presence of the grasp-affording object. How else could these cells show a differential response depending respectively on the unseen presence or absence of the object? This and similar studies support the idea that mirror neurons serve as a functionally dynamic part of the larger affordance space tracking functions of these areas. This kind of finding empirically counters the idea that individual or groups of mirror neurons function context independently as automatic mirroring processes of perceived action types. Similarly one can refer to the findings of differing mirror neuron (Fogassi et al., 2005) and human population level (Iacoboni et al., 2005) modulations given actions toward a specific object according to the larger contextual clues of varying 'end goals' (i.e. in the Fogassi et al. study of whether the monkey is 'grasping to eat' or 'grasping to place'). These studies have been interpreted as showing that mirror neurons are wired as distinct 'action chains' depending on the end-goal and thus the larger intentional hierarchy (Gallese, 2007 and Rizzolatti and Sinigaglia, 2010). A different interpretation is that these dynamic and hierarchical modulations are not simply a matter of mirror neurons wired in chains but rather a product of the larger affordance space tracking and the ongoing dynamic interrelations between object affordances and action interpretations and anticipations.

Such an affordance space interpretation is also supported by a recent study by Bach et al. (2011), which shows an interaction and interference of mirror facilitation when incongruent but irrelevant object affordances are present. They conclude:

These findings demonstrate that the observation of another person's actions automatically evokes sophisticated motor representations that reflect the relationship between actions and objects even when an action is not directed towards an object" (Bach et al., 2011, p. 171).

Bach and colleagues seem to acknowledge that their findings go against the caricature model of mirroring. They write that the "data reveal that action observation not only involves a direct matching of visual to motor features, but also a sophisticated integration of the behavior of the body part with the affordances of the goal object" (Bach et al., 2011, p. 175).

## **7. Social affordances and self-other relational aspects of mirror neurons**

As mentioned, at the heart of the mirror metaphor is the idea of a symmetrical mapping between action and perception. That is, caricature mirror neurons would respond symmetrically to (1) action stimuli whether visually perceived or executed, and thereby to (2) actions of self (executed) and other (perceived). However, already in the first publication of the findings of mirror neurons—and before the use of this term—several asymmetries were documented (di Pellegrino et al., 1992). In effect there was never much evidence of exact action-perception/self-other symmetry even within the sub-group of action perception and execution modulated premotor neurons that would later be categorized and labeled as mirror neurons (Gallese et al., 1996).

The early asymmetries included differences in the intensity for the modulation for execution/self and perception/other, differences that recently was found to be significant (Rochat et al., 2010). ‘Action kind’ differences were also reported: e.g. a subset of mirror neurons would be modulated not by one action type, but by temporally linked or ‘logically connected’ actions, i.e. a sight of grasping and execution of mouth opening. Another subset was simply categorized as ‘non-congruent’ as showing no meaningful relation between effective observed vs. executed actions. Another subgroup of premotor neurons were ‘visually dominant’ but would not qualify as falling under the later ‘mirror neuron’ label as they showed little modulation during action execution. The idea of mirroring was thus based not on all action sensitive neurons reported, but rather on two subgroups labeled ‘congruent’ and ‘broadly congruent’ according to the degree of execution–observation modulatory stimuli overlap. Notably, ‘strictly congruent’ mirror neurons made up only about a third of the premotor neurons classified as mirror—or action sensitive in the early studies (di Pellegrino et al., 1992 and Gallese et al., 1996).

Due to the nearly exclusive focus on effective action types the relational and contextual properties of mirror neurons were rarely tested/reported in early studies. However, asymmetries have now been documented even within the original ‘strictly congruent’ category. For example, a single cell study by Caggiano and colleagues showed that more than half of the tested premotor mirror neurons showed selective modulation according to whether the perceived action took place in the monkey’s peri-personal space (within reach) or in their extra-personal space (beyond reach) (Caggiano, Fogassi, Rizzolatti, Thier, & Casile, 2009). The mirror neurons, thus modulated by the relative distance of other’s perceived action as it relates to the perceiving monkey’s ability based affordance space, do not seem to fit the ‘mirror mechanism’ story. Note that originally perceived action types were thought to be mirrored automatically and ubiquitously. This idea supported the ‘agent neutrality’ of self-other mirroring, and was precisely thought to be important for how the perceiver could gain insight into the action of the other; i.e. how mirroring could serve action understanding rather than action execution. This finding shows that many mirror neurons do not function like modular automatons of action recognition, but rather reflects broader contextual factors.

We have already seen examples of complex contextual modulations in the occlusion study, which can be hypothesized as depending on broader object affordance tracking. Now we see that mirror neurons show a differential response given where the actions of others take place in the affordance space. That is, it is at least consistent with the findings that fronto-

parietal circuits support the tracking of others actions both as they relate to object affordances (Umiltà et al., 2001) and in terms of how they relate to the perceiver as providing social affordances for interactions (Caggiano et al., 2009). A series of other studies, (monkey as well as imaging and behavioral studies of motor facilitation in humans) support the notion that fronto-parietal circuits indeed show differential responses to perceived actions given contextual and relational factors such as e.g. shared versus non-shared pragmatic space and affordances (Fuljii, Hihara, & Iriki, 2007), cooperation–competition (Häberle, Schütz-Bosbach, Laboissière, & Prinz, 2008) complementary vs. imitative interaction (Newman-Norlund et al., 2007 and van Schie et al., 2008), motivation (Cheng, Meltzoff, & Decety, 2007), culture (Molnar-Szakacs, Wu, Robles, & Iacoboni, 2007), social distance and status (Yamakawa, Kanai, Matsumura, & Naito, 2009), self-other distinctions (Schütz-Bosbach, Mancini, Aglioti, & Haggard, 2006) as well as visual-somatosensory receptive fields around the body of others (Ishida, Nakajima, Inase, & Murata, 2010).

## **8. The social affordance space: beyond segregation of action-perception function**

Interestingly Caggiano and colleagues do not see a need for a significant reinterpretation of the caricature mirror theory. Rather they suggest that the new relational and asymmetric modulations of mirror neurons simply point to an additional function of these neurons. They write:

The most accepted interpretation of the function of mirror neurons is that they are involved in action understanding. Here, we investigated whether mirror neurons, *besides playing a role in this function*, also encode aspects of the observed actions that are relevant to subsequent interacting behaviors...Although *completely irrelevant* for “understanding” what the actor is doing, a precise knowledge of the distance at which the observed action is performed is crucial for selecting the most appropriate behavioral reaction. (Caggiano et al., 2009, p. 403, my italics)

In other words they seem to keep a neat distinction in place between knowledge for “understanding” (classic mirroring) and knowledge for action/interaction (new relational social affordance finding). Similarly in an otherwise interesting human TMS study exploring the notion of social affordances for interaction Sartori and colleagues also maintain the idea of mirroring and complementarity as two rather distinct and additive functions (Sartori, Cavallo, Bucchioni, & Castiello, 2012).

My hypothesis, on the contrary, is that these aspects are both procedurally and functionally intertwined in that they contribute to a common physical and social affordance space tracking that provides the foundation for both first person action planning and selection, and second and third person social understanding of the other as they navigate the shared—or simply perceived—affordance space.

This is a crucial aspect of the social affordance space hypothesis. Namely, that the relative contributions of own action plans and the monitoring of the actions of others in the affordance space dynamically interact. It is precisely this dynamic aspect that would



explain the modulatory findings in regards to motivation, task, distance as well as in respect to different observational formats such as video versus live action (Shimada & Hiraki, 2006) [19]. In short, the additive interpretation fails to account for reciprocity, and the difference between 2nd and 3rd person action understanding.

Another important piece of asymmetric evidence is the recent finding that many action sensitive neurons are selectively modulated by the viewpoint angle from which an action is seen. I.e. whether it is frontal or profile view, and also a first person, vs. second or third person view (Caggiano et al., 2011). This represents another single cell example of how the visual properties of mirror neurons seem far from simple ‘action type’ mirrors, and rather are selective for a range of relational properties pertaining to how this action relates to the perceiving individual. Further, Casile and colleagues have used this study to hypothesize the role of perception of self-movement in the development of the action-perception overlap in mirror neurons (Casile et al., 2011). This is an important hypothesis, which points to the largely ignored role of somatosensation and proprioception in the establishment and adaptation of mirror neurons and possibly fronto-parietal affordance tracking more generally (see also Torres et al., 2013 and Torres et al., 2014). However, beyond this developmental role of visual perception of own movements, it seems that sensitivity to the angle of view by which actions are seen also could play an important role in understanding our social affordance space. That is, I would argue that it is highly socially relevant whether the other is facing me or the other way, and not only in terms of my own complimentary action planning, but also in understanding what the other is up to, and the nature of our reciprocal relation.

Last but not least various findings have now documented that we do not simply have a mirroring sensorimotor response to the actually performed actions of others, but often seem to map something like the affordances (Bonini et al., 2014) or anticipated sensorimotor outcomes (Ishida et al., 2010) of the other. In other words, evidence suggests that we track not only our own object-based and social affordances but also those of others in our shared space. Object-related tracking can thus be enhanced by the presence of the capable other [20]. This is a fascinating new area of sensorimotor research, which fits with the predictions of a social affordance hypothesis, but clearly goes against the idea of separate and additive action and social understanding functions.

## **9. The social affordance space model: monitoring the shared ‘here and now’**

We can now turn to the explicit discussion of the social affordance space hypothesis and how it relates to social cognition. I have argued that our frontoparietal circuits support a complex set of physical and social affordance space tracking processes. The complexity has to do with sub-circuits for various limbs and respectively postural, self- vs. other-directed and object-directed actions, gestures, saccades etc. However, the complexity also has to do with our tracking of ‘relations’ and ‘contents’ of the space that we are afforded to act into, so to speak. Here we have discussed the findings of ‘canonical’ object affordance neurons and salience maps for saccades. Further there is the tracking of actions—of self and other—which are currently unfolding in this space. Here we have our classical mirror neuron findings along with more recent findings of asymmetric relational properties, and

modulation in response to the perception of ones own actions, view point, as well as affordance tracking relating to the position of the other [21]. There are thus many relational features, pertaining to action repertoire, object affordances, social affordances and own on-going actions—which all stand in dynamic relations to each other and must be undergoing reciprocal modulation to support our mapping and understanding of the overall affordance space.

I hypothesize that fronto-parietal circuits functionally support affordance understanding and decision-making in our actual current environment. I call this the ‘here and now’ affordance space as I see this affordance tracking as anchored in current and relatively concrete sensorimotor relations to this space. This idea of a present space might not be intuitive to all, and a few aspects need to be stressed.

(1) Inherent teleology: As argued above, fronto-parietal circuits can be seen as organized by way of teleological abstraction and with the characteristic of ‘intentional compression’ and integration of more near and remote sensory outcomes. This abstraction also means that we can track current affordance potentials, which to some extent go beyond our precise bodily position and detailed motor experience.

(2) The social dimension: The presence of others in the affordance space appears to create a further complexity, as the findings suggest that we track affordances as they relate to the body, peri-personal space and known perception–action teleology of the other and their bodily capabilities. I hypothesize that many parallel levels ‘intentional compression’ organization supports this social perspectival dimension, as one might perceive the space through the body of the other via ones own somewhat abstracted sensorimotor teleology. Here there is some overlap to the classical mirror story, however on my model of seeing through the body of the other is always partial and related to the shared affordance space—not a full simulation of their first person perspective or their actual action.

(3) The present affordance space: The notion of a ‘here and now’ affordance space is not meant to be limited to our current perception—i.e. the door as I am looking at it or pen as I am holding it ( Brincker, 2014). Rather, it is crucial that we track affordances beyond current modality-dependent perceptions—but as still present and available in relation to some of our affordance trackings and movement potentials. Recall here the occlusion study and the modulation due to the unseen but tracked object behind the occluder. In other words, things and actions can be currently ‘present’ as affordances in even if they are not continuously perceived.

(4) Limitations of affordance tracking: The fronto-parietal ‘here and now’ affordance space, can be contrasted with what I call navigation of counterfactual spaces. I might e.g. think about what to do tomorrow after I pick up the kids. In this process I imagine myself at the bus stop—i.e. I place my skilled body expectations in relation to a space that I do not actually currently inhabit or have a practical hold on with my physical body, be it imagined or remembered. I hypothesize that this other kind of navigation is a key factor to understand many “mentalizing” and “theory of mind” capabilities and further is likely supported by areas typically implicated in such tasks, as e.g. the default mode network.

Thus, these sorts of processes are beyond the 'here and now', and beyond the sensorimotor functions I here hypothesize for fronto-parietal circuits. [22]

This 'here and now' affordance space is the basis for a new interpretive framework. However, there are many unknowns and questions that I see as empirically tractable but still unexplored, e.g. in terms of the precise reach and depth of the fronto-parietal based affordance space. For example, it is an unanswered and species-specific question exactly how far into the extra-personal space our current affordance space stretches. Thus, one might ask whether the front door of my house is part of my here and now space as I sit at my desk? The answer to this question might depend on the capability of my action hierarchy to command the affordance space and track distal elements as direct action possibilities. Another complexity likely to be clarified empirically has to do with the degree to which we can deal with counterfactual or symbolic content within our concrete current affordance space. That is, do linguistic conversations primarily depend on counterfactual navigation (beyond the fronto-parietal hypothesis) or are many linguistic expressions more akin to toddlers use of pretense play and counterfactuals within the here and now affordance field. These unanswered questions illustrate how the affordance space hypothesis offers a new perspective of core cognitive issues, which open up for new empirical questions.

With this rough sketch of the affordance space hypothesis, we can return to the question of the role of mirror neurons and fronto-parietal circuits in social cognition.

## **10. Fronto-parietal contributions to social cognition**

The debate about the role of mirror neurons in intentional action understanding is often based upon the assumption that intentions are hidden mental states. Many reiterate that 'prior intentions' are underdetermined by their present behavioral expression (e.g. Jacob & Jeannerod, 2005). For the most part, this fact is used to argue that processes supporting the observation and understanding of the observable behavior are not essential to the understanding of other's intentional and mental states. As mirror neurons are generally thought to mirror and anticipate the overt action in the concrete context, it is argued that they are not at the core of our 'mind-reading' abilities. Further, many critics of mirroring as supporting action understanding take the affordance properties and asymmetric evidence discussed above to suggest that mirror neuron circuits simply are 'for action', as the classical dorsal stream hypothesis suggests. Thus, it is often argued that mirror neuron circuits might help us anticipate others' actions for the purposes of better interaction and appropriate action selection, but that these circuits hold little promise of supporting more sophisticated action understanding and social cognition (Hickok, 2013).

Given an affordance space interpretation, I see the possibility space differently. One initial question is whether the neat distinction between hidden mental states and overt behavior is the most useful. I agree that the minds of others always transcend my current perception, i.e. there are always aspects of others mental life that is perceptually unavailable—also when the other is present in a shared affordance space. In a sense this is what it means to be a minded creature and to know that one is facing another minded creature, namely that

not everything is revealed in the present. However, it is crucial to see how the affordance space hypothesis brings in alternative categories, which go beyond concrete bodies and hidden minds. If my proposal is right then the fronto-parietal areas are deeply teleologically organized—and thus any modulation of these areas to some extent takes us beyond the present and the actual to the realm of the possible and potential. Sensorimotor-based perception thus allows the perceiving agent to go beyond the concretely given as these experience integrating processes can alert us to the potential futures nestled in the concrete present. Notably, potentialities are anchored in present intentional actions and affordance structures. But the ‘present’ situation does not mean a momentary temporal time slice, but rather an ongoing experienced environment and our evolving teleological tracking of it. Accordingly, as seen in the occlusion study, some pre-motor neurons are modulated by prior knowledge of the intentional context. Similarly, the studies by Fogassi et al. (2005) and Iacoboni et al. (2005) indicate that many parietal mirror neurons are modulated by the broader intentional context and thereby a judgment about the ultimate goal of the action observed.

In short, the fronto-parietal circuits are not just modulated by overt behavior, but monitoring and judging the present environment given both prior and contextual knowledge. Further, we do not only monitor our own affordance relations to this present action space, but also how others appear in this space and how they relate to their own and our shared affordances in it. We perceive not only the actual actions that others perform, but rather we perceive them as they make their action selections. We see both the options and the decisions made. We might see what they could have done but didn’t do, as well as what they might do, and in reciprocal scenarios we even see what we could do to make them do something else.

As we perceive and relate to others the affordance space understanding accordingly seem to take on a profound level of social knowledge. The mirror focus on the actually performed actions misses the larger picture—it misses the point that fronto-parietal areas might support how we see others think, evaluate, deliberate, explore, poke, manipulate, ignore and chose. Further, most of the social meanings in a shared space are not only observed from a third person perspective but as a second person interlocutor. This mutual reciprocity serves as a crucial source of social affordances; the key being that it is an ongoing and open-ended morphable affordance source. We constantly interrogate, guide and manipulate each other’s actions and action choices through language, gaze, gestures and goal-directed and other intentional actions. Our own actions do not only reveal ourselves to the perceiving other but the reciprocity can also be used to purposively set the constraints that furthers the understanding (De Jaegher, Di Paolo, & Gallagher, 2010). Many of our more spontaneous, non-intentional and automatically driven movements—e.g. the posture adjustments in emotional contagion—are also important for this social reciprocity and our judgment of the others’ emotions, sensitivities, social capabilities, status etc. Given the teleological organization found in fronto-parietal areas I speculate however, that such processes are largely unconscious and might primarily depend on subcortical processes (Torres, 2011).

In terms of understanding the intentions of others, the hypothesis is that the affordance space tracking allows us a significant but always partial view. I cannot now understand all your intentions based on our current shared affordance space. But in so far as your behavior, bodily capabilities and contextual agency is perceptually available and we share an affordance space, I do see many of your intentional options and choices and your mind is by no means entirely hidden or imperceptible. Further, the partial nature of the access to the minds of others is itself is a sort negative and situated knowledge and therefore often presents a social affordance of dynamic interrogation—which if resisted of course in itself presents us with new perceptible social knowledge.

## **11. Concluding summary**

This article challenges certain lingering assumptions about the ‘mechanism’ and function of mirror neuron circuits; particularly the model of mirroring as modular processes of symmetric and simulative matching of observed actions, and as linking independent perceptual and motor action representations. It was argued that the assumption of segregated cortical sensory and motor organizations is central to the original functional hypothesis of mirror neurons, where action is ‘moonlighting’ for perception. However, it is hard to defend given current empirical knowledge, which rather points to intertwined sensorimotor processes that might be constitutive of teleological organizations, and not merely acting to bridge already existing goal representations.

I attempted to show how these theoretical revisions of the original mirror hypothesis also yields a different picture of the contribution that mirror neurons might have for goal and intention understanding and social cognition more generally. It was thus hypothesized that fronto-parietal areas support inherently sensorimotor and teleologically organized processes, which helps us understand, track and navigate our ‘here and now’ affordance space. Under this ‘social affordance space model’ the social function pertains to understanding others and their relation to this affordance space, and—if the space is shared—our reciprocal actions and affordances. This is a profound part of our social cognition because it gives us a platform for understanding and influencing decisions and actions in the making. The current sketch is an attempt to change the focus and framework of the existing debate, and to open up new empirical and theoretical questions not tackled in this current paper. There are many already known empirical details and theoretical implications that I had to leave out, as well as future directions and relations between the affordance theory and existing theories of action and social cognition, which deserve to be explored. However, I hope to have shown that if we let go of the stubborn and with Cecilia Heyes words “mesmerizing” mirror metaphor (Heyes, 2010), and its broader cognitivist roots in segregated sensorimotor processes, then sensorimotor circuits might be seen as important for teleological understanding and social cognition for rather different reasons that what has typically been assumed.

## **Endnotes**

1. I shall for reasons of simplicity refer to this group of researchers collectively as “the Parma group”.
2. The discovery of mirror neurons has indeed been one of the most influential events in neuroscience in recent decades. Ramachandran has perhaps been the least shy about his expectations, as he hypothesized that “mirror neurons will do for psychology what DNA did for biology” (2000). Ferrari and Rizzolatti write on the question why the notion of mirror neurons has had such an impact across fields: “Two reasons are the most likely. The first is that their discovery put the problem of how we understand others at the forefront of neuroscience. The second is that, by showing that mirror neurons were basically motor neurons, they suggested a rather unexpected solution to this problem: the motor system is involved in understanding the actions and intentions of others.” (Ferrari & Rizzolatti, 2014)
3. Susan Hurley has famously dubbed this cognitivist information processing view “the classical sandwich” as cognitive processes are conceived as sandwiched between input and output modules (Hurley, 1998). I shall in the following refer to this view as either the sandwich or input–output view.
4. E.g. there is a wide range of evidence that multisensory–motor integration and pragmatic and spatial functions depends on parietal areas, whereas e.g. object and facial recognition depend on temporal areas (Milner & Goodale, 1995).
5. See also Dewey’s (1896) classic critique of sensorimotor segregation and simple feedforward analyses.
6. See also Gallagher, 2008, Gallagher, 2007 and Zahavi, 2008 for a critique of simulational interpretations of mirror neurons and the assumption that intentions cannot be perceived.
7. This article focuses narrowly on the properties of the cortical parts of circuits related to goal-directed limb actions. The larger issues and literatures relevant to sensorimotor organization are enormous, and many important issues will be left aside. Most criminally I shall bracket the issues of how development, and adaptation of these circuits relates to their sub-cortical basal ganglia, thalamic and cerebellar connections, and thereby inadvertently continue the prevalent “current dualism of peripheral and central structures and functions” (Dewey, 1896), which needs its own re-interpretation (Brincker & Torres, 2013). Further, beyond fronto-parietal limb circuitry three other parallel cortical-basal ganglia-thalamic loops has been reported, pertaining to emotional and sensorimotor response navigation in respectively limbic/temporal, pre-frontal and facial fronto-parietal cortical areas (Purves et al., 2012). These show differences in function and maturation, as well as different levels of plasticity and associative vs. genetically based organization (Casile et al., 2011 and Heyes, 2010). Further I follow the current literature and focus entirely on the observation of intentional and goal-directed actions, though more spontaneous action segments (Torres, 2011) also are very important to social cognition and in particular emotional judgements. Lastly, I shall also ignore many of the complexities in comparing single cell studies of macaque monkeys and behavioral and imaging studies, which supply the main human data (Brincker, 2010 and Fabbri-Destro and Rizzolatti, 2008). Hopefully these simplifications will be justified in the context of the overall project of highlighting basic integrative and teleological features of sensorimotor processes, and how current findings challenge core theoretical assumptions.
8. A separate analysis is needed for the bayesian predictive coding account presented e.g. Kilner et al. (2007) as this theory breaks the classical input–output frame in interesting ways. How this account might be seen as compatible and incompatible with the social affordance view presented here deserves careful attention in the future. However, theorists like Hickok, Jacob, and Csibra appear to combine a classical input–output frame with the idea that mirror neuron processes can serve as internal simulators that help us anticipate action outcomes, which then can serve as additive information for “purely perceptual” goal and action understanding mechanisms.
9. For present purposes I shall not argue for or against but just highlight that the mirror neuron literature often simply assumes the imperceptibility of intention. This idea might seem intuitive precisely due to assumptions about separate sensory and motor systems and a notion of intentions as mental states, which can be neatly distinguished from sensorimotor processes (e.g. Spaulding, 2015). Debates over the perceptibility of intentions also show the usefulness of a discussion of whether sensorimotor affordance perception and integrative tracking can be seen as part of the perceptual process or as a later and more additive component (see also Gallagher, 2008).
10. I here follow the way the affordance concept has been used by researchers, though this use in many ways is inconsistent and theoretically wanting. See Rietveld and Kiverstein (2014) for an excellent recent discussion and reinterpretation of the affordance concept. Following their analysis we might want to say that what is being tracked by ‘canonical’ neurons and similar sensorimotor processes are affordance solicitations rather than affordances per se.

11. For the motor/sensorimotor rather than merely perceptual role in such parallel target and affordance tracking see also Stewart, Gallivan, Baugh, & Flanagan, 2014.
12. See here also Elizabeth Torres' recent re-interpretation and applications of the concept of re-afference (Torres and Choi, 2014, Torres et al., 2014 and Torres et al., 2013). The two most recent articles are incredibly important for the question of not only sensory feedback in general for intentional and teleological action organization in parietal cortex but the specific role of proprioception. A future and fuller social affordance framework would have to include an analysis of proprioception, interoception and the role of body schemas in fronto-parietal circuits.
13. Kilner and colleageagues seem with their 'predictive coding' account to avoid the feedforward aspect of the classical sandwich by not even talking about perceptions and action choices but merely about "predictions" and "prediction errors" (Kilner et al., 2007). Their computational model of error minimization relies on a preset hierarchy of modules and one question is how to model an autonomous acting and perceiving system given such constraints. However as mentioned a satisfying negotiation between the predictive coding model and the affordance model is beyond my current scope.
14. Neurons have for example often been categorized as 'motor dominant' without controlling for somatosensory and proprioceptive modulation.
15. Torres (2011) documented systematic kinesthetic differences in target-directed vs. spontaneous withdrawl movements. Such differences can be hypothesized as being due to involvement of different cortical and subcortical processes.
16. As Michael Wheeler (2010) has argued, humans might be particularly contextually 'plastic', flexible and adaptive in their behavior and in what can come to count as a goal as compared to other species.
17. Mark Jeannerod (2006) wrote a book about motor cognition based on this simulative definition. See also Brincker, 2010 and Brincker, 2012 for critical discussion of this view.
18. This is by no means the only empirical inconsistency for Csibra and other theorists with a narrow view of the motor system. A range of other sensorimotor findings of e.g. viewer independent object shape perception in the dorsal stream (Konen & Kastner, 2008) seem in need of some explanation that goes beyond action simulation.
19. See also Brincker (2015) for theoretical discussion.
20. Note that the very division between canonical neurons as related to object affordances and mirror neurons as related to action mirroring breaks down under the social affordance model and a much more messy and heterogeneous array of teleological sensory motor neurons are predicted by the model (Brincker, 2010), which also fits with above mentioned asymmetric affordance space related mirror neuron propoties (Caggiano et al., 2009) as well as e.g. recent findings of "canonical mirror neurons" (Bonini et al., 2014).
21. See also Footnote 20.
22. For a discussion of the distinction and development of the ability to navigate the 'here and now' versus counterfactual spaces see Brincker (2014).

## References

- Andersen, R. A., & Cui, H. (2009). Intention, action planning, and decision making in parietal–frontal circuits. *Neuron*, 63(5), 568–583.
- Bach, P., Bayliss, A. P., & Tipper, S. P. (2011). The predictive mirror: Interactions of mirror and affordance processes during action observation. *Psychonomic Bulletin and Review*, 18(1), 171–176.
- Berti, A., & Frassinetti, F. (2000). When far becomes near: Remapping of space by tool use. *Journal of Cognitive Neuroscience*, 12(3), 415–420.
- Bonini, L., Rozzi, S., Ugolotti Serventi, F., Simone, L., Ferrari, P. F., & Fogassi, L. (2009). Ventral Premotor and inferior parietal cortices make distinct contribution to action organization and intention understanding. *Cerebral Cortex*, 20, 1372–1385.

- Bonini, L., Maranesi, M., Livi, A., Fogassi, L., & Rizzolatti, G. (2014). Space-dependent representation of objects and other's action in monkey ventral premotor grasping neurons. *The Journal of Neuroscience*, 34(11), 4108–4119.
- Brincker, M. (2010). *Moving beyond mirroring – A social affordance model of sensorimotor integration during action perception*. City University of New York.
- Brincker, M. (2012). If the motor system is no mirror. In *Connected minds: Cognition and interaction in the social world* (pp. 158–182). Cambridge Scholars Publishing.
- Brincker, M. (2014). Navigating beyond 'here & now' affordances – On sensorimotor maturation and 'false belief' performance. *Frontiers Psychology*, 5.
- Brincker, M. (2015). The Aesthetic Stance – On the conditions and consequences of becoming a beholder. In A. Scarinzi (Ed.), *Aesthetics and the embodied mind: Beyond art theory and the cartesian mind-body dichotomy*. New York: Springer.
- Brincker, M., & Torres, E. B. (2013). Noise from the periphery in autism. *Frontiers in Integrative Neuroscience*, 7, 34.
- Caggiano, V., Fogassi, L., Rizzolatti, G., Pomper, J. K., Thier, P., Giese, M. A., et al. (2011). View-based encoding of actions in mirror neurons of area f5 in macaque premotor cortex. *Current Biology*, 21(2), 144–148.
- Caggiano, V., Fogassi, L., Rizzolatti, G., Thier, P., & Casile, A. (2009). Mirror neurons differentially encode the interpersonal and extrapersonal space of monkeys. *Science*, 324(5925), 403–406.
- Caligiore, D., Pezzulo, G., Miall, R. C., & Baldassarre, G. (2013). The contribution of brain sub-cortical loops in the expression and acquisition of action understanding abilities. *Neuroscience & Biobehavioral Reviews*, 37(10), 2504–2515.
- Cardellicchio, P., Sinigaglia, C., & Costantini, M. (2011). The space of affordances: A TMS study. *Neuropsychologia*, 49(5), 1369–1372.
- Casile, A., Caggiano, V., & Ferrari, P. F. (2011). The mirror neuron system: A fresh view. *The Neuroscientist*, 17(5), 524–538.
- Cattaneo, L., Caruana, F., Jezzini, A., & Rizzolatti, G. (2009). Representation of goal and movements without overt motor behavior in the human motor cortex: A transcranial magnetic stimulation study. *The Journal of Neuroscience*, 29(36), 11134–11138.
- Cheng, Y., Meltzoff, A. N., & Decety, J. (2007). Motivation modulates the activity of the human mirror-neuron system. *Cerebral Cortex*, 17(8), 1979–1986.
- Cisek, P. (2007). Cortical mechanisms of action selection: The affordance competition hypothesis. *Philosophical Transactions of the Royal Society London B: Biological Sciences*, 362(1485), 1585–1599.
- Cisek, P., & Kalaska, J. F. (2002). Simultaneous encoding of multiple potential reach directions in dorsal premotor cortex. *Journal of Neurophysiology*, 87(2), 1149–1154.
- Cisek, P., & Kalaska, J. F. (2010). Neural mechanisms for interacting with a world full of action choices. *Annual Review of Neuroscience*, 33, 269–298.



- Csibra, G., & Gergely, G. (2007). 'Obsessed with goals': Functions and mechanisms of teleological interpretation of actions in humans. *Acta Psychologica*, 124, 60–78.
- Csibra, G. (2007). Action mirroring and action understanding: An alternative account. In P. Haggard, Y. Rosetti, & M. Kawato (Eds.), *Sensorimotor foundations of higher cognition. Attention and performance XXII*. Oxford: Oxford University Press.
- De Jaegher, H., Di Paolo, E., & Gallagher, S. (2010). Can social interaction constitute social cognition?. *Trends in Cognitive Sciences* 14(10), 441–447. de Vignemont, F., & Haggard, P. (2008). Action observation and execution: What is shared? *Social Neuroscience*, 3(3&4), 421–433.
- Dewey, J. (1896). The reflex arc concept in psychology. *Psychological Review*, 3(4), 357.
- di Pellegrino, G., Fadiga, L., Fogassi, L., Gallese, V., & Rizzolatti, G. (1992). Understanding motor events: A neurophysiological study. *Experimental Brain Research*, 91, 176–180.
- Fabbri-Destro, M., & Rizzolatti, G. (2008). Mirror neurons and mirror systems in monkeys and humans. *Physiology*, 23(3), 171–179.
- Fagg, A. H., & Arbib, M. A. (1998). Modeling parietal–premotor interactions in primate control of grasping. *Neural Networks*, 11(7), 1277–1303.
- Ferrari, P. F., & Rizzolatti, G. (2014). Mirror neuron research: The past and the future. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 369(1644), 20130169.
- Fogassi, L., Ferrari, P. F., Gesierich, B., Rozzi, S., Chersi, F., & Rizzolatti, G. (2005). Parietal lobe: From action organization to action understanding. *Science*, 308, 662–667.
- Fuljii Hihara & Iriki (2007). Dynamic social adaptation of motor-related neurons in primate parietal cortex. *PLoS One*, 4, e397.
- Gallagher, S. (2007). Simulation trouble. *Social Neuroscience*, 2(3–4), 353–365.
- Gallagher, S. (2008). Direct perception in the intersubjective context. *Consciousness and Cognition*, 17(2), 535–543.
- Gallese, V. (2007). Before and below 'theory of mind': Embodied simulation and the neural correlates of social cognition. *Philosophical Transactions of the Royal Society B*, 362, 659–669.
- Gallese, V., Fadiga, L., Fogassi, L., & Rizzolatti, G. (1996). Action recognition in the premotor cortex. *Brain*, 119(2), 593–609.
- Gallese, V., & Goldman, A. (1998). Mirror neurons and the simulation theory of mind reading. *Trends in Cognitive Sciences*, 12, 493–501.
- Gallese, V., Keysers, C., & Rizzolatti, G. (2004). A unifying view of the basis of social cognition. *Trends in Cognitive Sciences*, 8(9), 396–403.
- Gibson, J. J. (1979). *The ecological approach to visual perception*. Boston: Houghton Mifflin.
- Gottlieb, J. (2007). From thought to action: The parietal cortex as a bridge between perception, action, and

cognition. *Neuron*, 53(1), 9–16.

Grezes, J., Armony, J. L., Rowe, J., & Passingham, R. E. (2003). Activations related to “Mirror” and “Canonical” neurons in the human brain: A fMRI study. *Neuroimage*, 18, 928–937.

Haberle, A., Schutz-Bosbach, S., Laboissie`re, R., & Prinz, W. (2008). Ideomotor action in cooperative and competitive settings. *Social Neuroscience*, 3(1), 26–36 (1747-0927).

Hamilton, A. F., & Grafton, S. T. (2007). The motor hierarchy: From kinematics to goals and intentions. In Y. Rosetti, M. Kawato, & P. Haggard (Eds.), *Attention and performance xxii*. Oxford: OxfordUniversity Press.

Heyes, C. (2010). Mesmerising mirror neurons. *Neuroimage*, 51, 789–791.

Hickok, G. (2009). Eight problems for the mirror neuron theory of action understanding in monkeys and humans. *Journal of Cognitive Neuroscience*, 21(7), 1229–1243.

Hickok, G. (2013). Do mirror neurons subserve action understanding? *Neuroscience Letters*, 540, 56–58.

Hietanen, J. K., & Perrett, D. I. (1993). Motion sensitive cells in the macaque superior temporal polysensory area. *Experimental Brain Research*, 93(1), 117–128.

Hietanen, J. K., & Perrett, D. I. (1996). A comparison of visual responses to object-and ego-motion in the macaque superior temporal polysensory area. *Experimental Brain Research*, 108(2), 341–345.

Hommel, B., Musseler, J., Aschersleben, G., & Prinz, W. (2001). The theory of event coding (TEC): A framework for perception and action planning. *Behavioral and Brain Sciences*, 24, 849–937.

Hurley, S. (1998). *Consciousness in action*. Cambridge, MA: Harvard University Press.

Iacoboni, M., Molnar-Szakacs, I., Gallese, V., Buccino, G., Mazziotta, J. C., et al. (2005). Grasping the intentions of others with one’s own mirror neuron system. *PLoS Biology*, 3(3), e79.  
<http://dx.doi.org/10.1371/journal.pbio.0030079>.

Ishida, H., Nakajima, K., Inase, M., & Murata, A. (2010). Shared mapping of own and others’ bodies in visuotactile bimodal area of monkey parietal cortex. *Journal of Cognitive Neuroscience*, 22(1), 83–96.

Jacob, P. (2008). What do mirror neurons contribute to human social cognition? *Mind and Language*, 23(2), 190–223.

Jacob, P., & Jeannerod, M. (2005). The motor theory of social cognition: A critique. *Trends in Cognitive Sciences*, 9(1), 21–25.

James, W. (1890/1950). *The principles of psychology*. Dover Publications.

Jeannerod, M. (2006). *Motor cognition: What actions tell the self* (No. 42). Oxford: Oxford University Press.

Keysers, C., Wicker, B., Gazzola, V., Anton, J. L., Fogassi, L., & Gallese, V. (2004). A touching sight: SII/PV activation during the observation and experience of touch. *Neuron*, 42(2), 335–346.

Kilner, J. M., Friston, K. J., & Frith, C. D. (2007). Predictive coding: An account of the mirror neuron system. *Cognitive Processing*, 8, 159–166.14.

- Konen, C. S., & Kastner, S. (2008). Two hierarchically organized neural systems for object information in human visual cortex. *Nature Neuroscience*, 11(2), 224–231.
- Lyons, D. E., Santos, L. R., & Keil, F. C. (2006). Reflections of other minds: How primate social cognition can inform the function of mirror neurons. *Current Opinion in Neurobiology*, 16, 230–234.
- Matyas, F., Sreenivasan, V., Marbach, F., Wacongne, C., Barsy, B., Mateo, C., et al. (2010). Motor control by sensory cortex. *Science*, 330(6008), 1240–1243.
- Miall, R. C. (2003). Connecting mirror neurons and forward models. *Neuroreport*, 14(17), 2135–2137.
- Milner, A. D., & Goodale, M. A. (1995). *The visual brain in action* (Vol. 27).
- Mishkin, M., Ungerleider, L. G., & Macko, K. A. (1983). Object vision and spatial vision: Two cortical pathways. *Trends in Neurosciences*, 6, 414–417.
- Mistlin, A. J., & Perrett, D. I. (1990). Visual and somatosensory processing in the macaque temporal cortex: The role of ‘expectation’. *Experimental Brain Research*, 82(2), 437–450.
- Molnar-Szakacs, I., Wu, A. D., Robles, F. J., & Iacoboni, M. (2007). Do you see what I mean? Corticospinal excitability during observation of culture-specific gestures. *PLoS One*, 2(7), e626.
- Mountcastle, V. B., Lynch, J. C., Georgopoulos, A., Sakata, H., & Acuña, C. (1975). Posterior parietal association cortex of the monkey: Command functions for operations within extrapersonal space. *Journal of Neurophysiology*, 38, 871–908.
- Newman-Norlund, R. D., van Schie, H. T., van Zuijlen, A. M. J., & Bekkering, H. (2007). The mirror neuron system is more active during complementary compared with imitative actions. *Nature Neuroscience*, 10(7), 817–818.
- Ocampo, B., & Kritikos, A. (2011). Interpreting actions: The goal behind mirror neuron function. *Brain Research Reviews*, 67(1), 260–267.
- Peeters, R., Simone, L., Nelissen, K., Fabbri-Destro, M., Vanduffel, W., Rizzolatti, G., et al. (2009). The representation of tool use in humans and monkeys: Common and uniquely human features. *Journal of Neuroscience*, 29(37), 11523–11539.
- Penfield, W., & Rasmussen, T. (1952). *The cerebral cortex of man* (2<sup>nd</sup> ed.). New York: MacMillan Co.
- Perrett, D. I., Harries, M. H., Bevan, R., Thomas, S., Benson, P. J., Mistlin, A. J., et al. (1989). Frameworks of analysis for the neural representation of animate objects and actions. *Journal of Experimental Biology*, 146(1), 87–113.
- Perrett, D. I., Smith, P. A. J., Potter, D. D., Mistlin, A. J., Head, A. S., Milner, A. D., et al. (1985). Visual cells in the temporal cortex sensitive to face view and gaze direction. *Proceedings of the Royal Society of London Series B: Biological Sciences*, 223(1232), 293–317.
- Purves, D., Augustine, G. J., Fitzpatrick, D., Hall, W. C., LaMantia, A., & White, L. E. (2012). *Neuroscience* (5th ed.). Sunderland, MA: Sinauer Associates, Inc.

- Raos, V., Umiltà, M. A., Murata, A., Fogassi, L., & Gallese, V. (2006). Functional properties of grasping-related neurons in the ventral premotor area F5 of the macaque monkey. *Journal of Neurophysiology*, 95(2), 709–729.
- Rathelot, J. A., & Strick, P. L. (2009). Subdivisions of primary motor cortex based on cortico-motoneuronal cells. *Proceedings of the National Academy of Sciences of the United States of America*, 106(3), 918–923.
- Rietveld, E., & Kiverstein, J. (2014). A rich landscape of affordances. *Ecological Psychology*, 26(4), 325–352.
- Rizzolatti, G., Fadiga, L., Fogassi, L., & Gallese, V. (1996). Premotor cortex and the recognition of motor actions. *Cognitive Brain Research*, 3, 131–141.
- Rizzolatti, G., & Gentilucci, M. (1988). Motor and visual-motor functions of the premotor cortex. In P. Rakic & W. Singer (Eds.), *Neurobiology of neocortex* (pp. 269–284). Chichester: Wiley.
- Rizzolatti, G., & Luppino, G. (2001). The cortical motor system. *Neuron*, 31(6), 889–901.
- Rizzolatti, G., & Sinigaglia, C. (2010). The functional role of the parietofrontal mirror circuit: Interpretations and misinterpretations. *Nature Reviews Neuroscience*, 11(4), 264–274.
- Rochat, M. J., Caruana, F., Jezzini, A., Escola, L., Intskirveli, I., Grammont, F., et al. (2010). Responses of mirror neurons in area F5 to hand and tool grasping observation. *Experimental Brain Research*.
- Sakata, H., Taira, M., Murata, A., & Mine, S. (1995). Neural mechanisms of visual guidance of hand action in the parietal cortex of the monkey. *Cerebral Cortex*, 5(5), 429–438.
- Sartori, L., Cavallo, A., Buccioni, G., & Castiello, U. (2012). From simulation to reciprocity: The case of complementary actions. *Social Neuroscience*, 7(2), 146–158.
- Schippers, M. B., & Keysers, C. (2011). Mapping the flow of information within the putative mirror neurons system during observation. *Neuroimage*, 57, 37–44.
- Schutz-Bosbach, S., Mancini, B., Aglioti, S. M., & Haggard, P. (2006). Self and other in the human motor system. *Current Biology*, 16, 1830–1834.
- Schutz-Bosbach, S., & Prinz, W. (2007). Perceptual resonance: Action-induced modulation of perception. *Trends in Cognitive Sciences*, 11(8), 349–355.
- Shimada, S., & Hiraki, K. (2006). Infant's brains respond differently to live and televised action. *Neuroimage*, 32, 930–939.
- Solari, S. V. H., & Stoner, R. (2011). Cognitive consilience: Primate nonprimary neuroanatomical circuits underlying cognition. *Frontiers in Neuroanatomy*, 5, 65.
- Spaulding, S. (2015). On whether we can see intentions. *Pacific Philosophical Quarterly*.
- Stewart, B. M., Gallivan, J. P., Baugh, L. A., & Flanagan, J. R. (2014). Motor, not visual, encoding of potential reach targets. *Current Biology*, 24(19), R953–R954.
- Strick, P. L., & Preston, J. B. (1982). Two representations of the hand in area 4 of a primate. II. Somatosensory input organization. *Journal of Neurophysiology*, 48(1), 150–159.

- Taira, M., Mine, S., Georgopoulos, A. P., Murata, A., & Sakata, H. (1990). Parietal cortex neurons of the monkey related to the visual guidance of hand movement. *Experimental Brain Research*, 83(1), 29–36.
- Torres, E. B. (2011). Two classes of movements in motor control. *Experimental Brain Research*, 215(3–4), 269–283.
- Torres, E. B., Brincker, M., Isenhower, R. W., Yanovich, P., Stigler, K. A., Nurnberger, J. I., et al. (2013). Autism: The micro-movement perspective. *Frontiers in Integrative Neuroscience*, 7, 32.
- Torres, E., & Choi, K. (2014). A neural correlate of intentionality persists in the parietal cortex of a patient without proprioception. *Journal of Vision*, 14(10), 1102.
- Torres, E. B., Cole, J., & Poizner, H. (2014). Motor output variability, deafferentation, and putative deficits in kinesthetic reafference in Parkinson's disease. *Frontiers in Human Neuroscience*, 8.
- Torres, E. B., Quiroga, R. Q., Cui, H., & Buneo, C. A. (2013). Neural correlates of learning and trajectory planning in the posterior parietal cortex. *Frontiers in Integrative Neuroscience*, 7.
- Uitot, S., van Rooij, I., Bekkering, H., & Haselager, P. (2011a). Understanding motor resonance. *Social Neuroscience*, 6(4), 388–397.
- Uitot, S., van Rooij, I., Bekkering, H., & Haselager, P. (2011b). What do mirror neurons mirror? *Philosophical Psychology*, 24(5), 607–623.
- Umiltà, M. A., Escola, L., Intskirveli, I., Grammont, F., Rochat, M., Caruana, F., et al. (2008). When pliers become fingers in the monkey motor system. *Proceedings of the National Academy of Sciences of the United States of America*, 105, 2209–2213.
- Umiltà, M. A., Kohler, E., Gallese, V., Fogassi, L., Fadiga, L., Keysers, C., et al. (2001). I know what you are doing: A neurophysiological study. *Neuron*, 32, 91–101.
- van Schie, H. T., van Waterschoot, B. M., & Bekkering, H. (2008). Understanding action beyond imitation: Reversed compatibility effects of action observation in imitation and joint action. *Journal of Experimental Psychology: Human Perception and Performance*, 34, 1493–1500.
- Wheeler, M. (2010). Plastic machines: Behavioural diversity and the Turing test. *Kybernetes*, 39(3), 466–480.
- Yamakawa, Y., Kanai, R., Matsumura, V., & Naito, E. (2009). Social distance evaluation in human parietal cortex. *PLoS One*, 4(2), e4360.
- Zahavi, D. (2008). Simulation, projection and empathy. *Consciousness and Cognition*, 17, 514–522.