

19 Complementary Actions

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Abstract

Human beings come into the world wired for social interaction. At the fourteenth week of gestation, twin fetuses already display interactive movements specifically directed towards their co-twin. Readiness for social interaction is also clearly expressed by the newborn who imitates facial gestures, suggesting that there is a common representation mediating action observation and execution. While actions that are observed and those that are planned seem to be functionally equivalent, it is unclear if the visual representation of an observed action inevitably leads to its motor representation. This is particularly true with regard to *complementary* actions (from the Latin *complementum*; i.e. that fills up), a specific class of movements which differ, while interacting, with observed ones. In geometry, angles are defined as complementary if they form a right angle. In art and design, complementary colors are color pairs that, when combined in the right proportions, produce white or black. As a working definition, complementary actions refer here to any form of social interaction wherein two (or more) individuals complete each other's actions in a balanced way. Successful complementary interactions are founded on the abilities: (1) to simulate another person's movements; (2) to predict another person's future action/s; (3) to produce an appropriate congruent/incongruent response that completes the other person's action/s; and (4) to integrate the predicted effects of one's own and another person's actions. It is the neurophysiological mechanism that underlies this process which forms the main theme of this chapter.

Introduction

As has been observed in mimicry, priming and automatic imitative actions (Heyes, 2011), humans are remarkably efficient at resonating with one another (Box 19.1). In specific contexts that require incongruent, complementary rather than imitative forms of interaction, motor resonance with

action observation can, nevertheless, be an unsuitable response (for review, see Knoblich, Butterfill, & Sebanz, 2011). In the case, for example, that someone hands us a mug by its handle, we will automatically, without thinking, grab the mug using a whole-hand grasp (the most appropriate grasping gesture in this particular situation). The types of grasp adopted here by the two interacting agents are incongruent, but in this case they are appropriate and complementary. This example illustrates the functional importance of complementary actions in the context of the action–perception domain (Graf, Schütz-Bosbach, & Prinz, 2009), and it encourages us to take a look at what is taking place behind the scenes and to question the mechanisms involved in producing this outcome. Preliminary data addressing this question have been provided by recent studies utilizing different research methods.

The first part of the chapter will be dedicated to providing behavioral and neuroimaging data illustrating the processes and specific activation underlying complementary actions. The focus of the second, neurophysiologic part, will be to specifically describe, in spatial and temporal terms, the shift from imitative to reciprocal forms of interaction. Additionally, these processes will be explained in computational terms, and a novel theoretical framework will be proposed to elucidate this kind of social interaction.

Box 19.1 Motor resonance

In humans, a large number of neurophysiological studies have demonstrated that a *motor resonance* mechanism in the motor, premotor and the posterior parietal cortices is at work when individuals observe goal-directed actions being executed by other persons (for review, see Fadiga, Craighero, & Olivier, 2005; Heyes, 2011; Rizzolatti, Cattaneo, Fabbri-Destro, & Rozzi, 2014). Gallese (2001), in fact, explained that: ‘when we observe actions performed by other individuals our motor system “resonates” along with that of the observed agent’ (pp. 38–39). The discovery of mirror neurons in the monkey provided the physiological model for the basic perception–action coupling mechanism (Rizzolatti & Craighero, 2004). Located in the ventral premotor cortex (area F5) and posterior parietal cortex, it was seen that mirror neurons fire *both* when a monkey carries out a goal-directed action and when it observes that same action being performed by another subject (di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992). Neuroimaging studies have likewise provided evidence that a fronto-parietal perception–action system is implicated in coupling the representations of executed and observed actions in humans (for review, see Fabbri-Destro & Rizzolatti, 2008; Giorrello & Sinigaglia, 2007; Keysers, 2009; Molenberghs, Cunning-

ton, & Mattingley, 2012; Rizzolatti & Sinigaglia 2010; Turella, Tubaldi, Erb, Grodd, & Castiello, 2012). Taken together, monkey and human data have been interpreted to favor the *direct matching hypothesis*, which states that we understand observed actions by mapping their visual representation onto our motor representation (Rizzolatti, Fogassi, & Gallese 2001), and that the similarity between the observer's and the agent's action representations determines the degree to which motor resonance occurs in the former. Motor resonance seems to pre-activate our own motor system in order to represent and interpret the movements of someone else even when the go signal is not given and pre-activation remains unconscious (Costantini, Committeri, & Sinigaglia 2011b).

Behavioral Studies of Complementary Actions

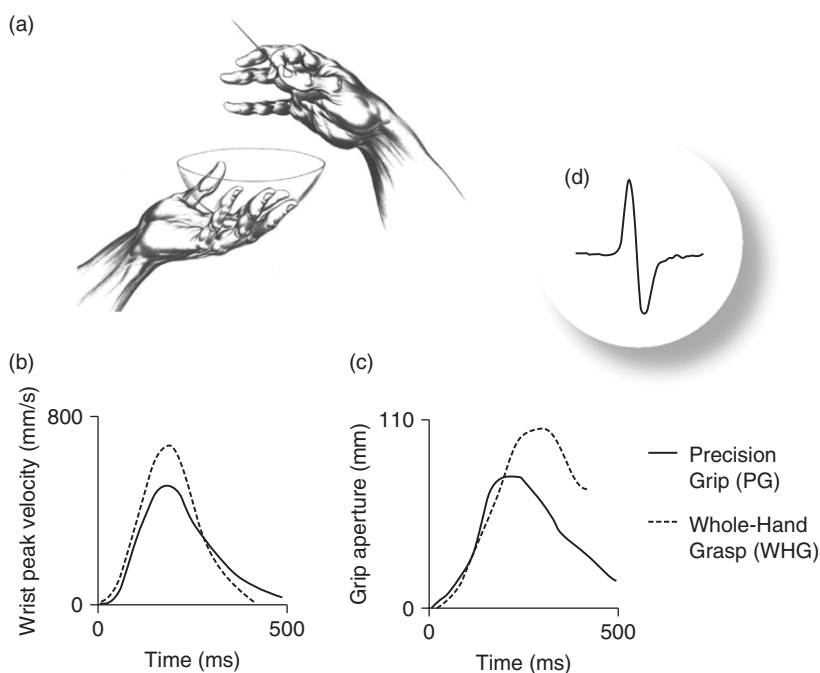
The British evolutionary biologist John Napier (1956), who pioneered the modern study of human hand movements, explained that how our hands interact with objects depends not only on the object's features but also on the intentions guiding the action. Capitalizing on this insight, reach-to-grasp actions have been utilized as an experimental window in a variety of behavioral and neurophysiologic studies (Box 19.2). Available evidence indicates that different kinds of social object-oriented actions (e.g. passing an object to someone else) involve specific and often distinct movement parameterizations depending on whether the situation implies manipulating an object in order to cooperate or to compete against an opponent (Becchio, Sartori, Bulgheroni, & Castiello, 2008a, 2008b; Georgiou, Becchio, Glover, & Castiello, 2007; Sacheli, Tidoni, Pavone, Aglioti, & Candidi, 2013; Sartori, Becchio, Bara, & Castiello, 2009a; Sartori, Becchio, Bulgheroni, & Castiello, 2009b; Sartori, Becchio, & Castiello, 2011a). According to this perspective, direct perception of intentions underlying actions seems to afford specific action plans (Gangopadhyay & Schilbach, 2012). Moving an empty hand to unexpectedly ask for an object, for instance, possesses the power to override an observer's initial motor plan and to induce a complementary response, regardless of any previously imparted instructions (Sartori et al., 2009b). Evidence that the action context plays a pivotal role in shaping complementary actions has also been provided by a series of studies (Newman-Norlund, van Schie, van Zuijlen, & Bekkering, 2007b; Poljac, van Schie, & Bekkering, 2009; van Schie, van Waterschoot, & Bekkering, 2008b) in which participants were explicitly instructed to imitate or complement a virtual actor's grasp on a manipulandum using either a precision or a whole-hand grasp (grips are defined by the position of the thumb and the fingers; see Box 19.2). As expected, within the context of an imitation task, participants were faster at initiating a predefined action if their own action was congruent

with the observed behavior, and their response was relatively delayed when they observed dissimilar actions. But the reverse pattern was found during complementary action tasks: the participants responded with greater rapidity when they observed dissimilar rather than similar actions. The need to maintain a task representation (imitative versus complementary) temporarily overruled existing long-term stimulus–response (S–R) associations, influencing the way that action–perception coupling took place. Further evidence on this flexible perception–action coupling came from a motion capture study (Ocampo & Kritikos, 2010) in which reaching and grasping parameters of identical responses were improved in imitative contexts, but the opposite was true for complementary contexts. Consistent with these findings, Longo, Kosobud, and Bertenthal (2008) reported that automatic imitation is modulated by top-down influences. They demonstrated that the level of action coding can be changed (e.g. towards coding in terms of movements) depending on task requirements. Taken together, these data challenge the idea that action observation automatically leads to imitation in the observer (i.e. direct matching hypothesis) and suggest that observed actions can prime non-identical responses depending on the context.

Box 19.2 Prehensile actions as an experimental window

Throughout any ordinary day we routinely reach for objects, grasp, lift and manipulate them while interacting with others. Reaching to grasp an object is, in fact, probably one of the most common human manual activities. Classic kinematic studies have distinguished and defined two main types of grasping action depending on intrinsic properties (e.g. the size and shape) of the object to be grasped: precision grip (PG; i.e. opposition between the index finger and thumb; see top right of panel (a) in the figure below) and whole-hand grasp (WHG; i.e. opposition of the thumb with the other fingers; (a), bottom left). Precise actions towards small objects are typically associated with lower wrist velocity profiles than whole-hand prehension movements due to the extra time needed to control accurate hand shaping in relation to a small object (Gentilucci et al., 1991; (b) in figure). The maximum amplitude of the index finger–thumb distance (maximum grip aperture, MGP) is also related to the object size, allowing the careful and smooth positioning of the fingers as the hand approaches the target. MGP is significantly larger when grasping is being performed to carry out whole-hand with respect to precision tasks ((c) in figure). Capitalizing on the differences between hand postures, neurophysiologic studies have demonstrated how observing different muscular activations leads to specific motor facilitation effects in the onlooker’s corresponding muscles (Cavallo,

Becchio, Sartori, Bucchioni, & Castiello, 2012; Cavallo, Sartori, & Castiello, 2011; Fadiga, Craighero, & Olivier, 2005; Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995; Sartori & Castiello, 2013; Sartori, Bucchioni, & Castiello, 2012a; Urgesi, Candidi, Fabbro, Romani, & Aglioti, 2006). In particular, observing another person grasping a large object induces motor facilitation in both the first dorsal interosseus (FDI; the muscle serving index finger flexion/extension) and the abductor digiti minimi (ADM; the muscle serving little finger abduction) because those are the muscles involved in a WHG. Conversely, only motor-evoked potentials (MEPs; (d) in figure) recorded from the FDI muscle show a markedly increased activation when an individual observes someone grasping a small object, because the ADM muscle is not implicated in a PG grasp.



Box 19.2 Precision grip and whole-hand grasp characterization.

Notes: (a) Graphic drawing of an WHG (left) and a PG (right). (b) Wrist peak velocity profile for PG and WHG actions. (c) Grip aperture profile for PG and WHG actions. (d) TMS-induced MEP recorded in a hand muscle.

Neuroimaging Studies of Complementary Actions

Very few studies have examined the circuitry behind joint actions, and in particular the human mirror neuron system's (hMNS; [Box 19.1](#)) involvement in complementary forms of social interaction. In a pioneering experiment, the response of the hMNS was specifically investigated in imitative and complementary action contexts using fMRI ([Newman-Nordlund et al., 2007b](#)). Signals were recorded while the participants prepared to grasp a manipulandum in one of two ways (with a WHG or a PG) after they viewed an actor doing it ([Figure 19.1a](#)). With respect to imitative actions, preparation of complementary ones resulted in an increased blood-oxygen-level-dependent (BOLD) signal in the right inferior frontal gyrus (IFG) and bilateral inferior parietal lobule (IPL), two core components of the mirror system ([Figure 19.1b](#)). This has been explained in terms of different kinds of mirror neuron: strictly congruent mirror neurons, which respond to identical observed and executed actions, and broadly congruent mirror neurons, which respond to non-identical observed and executed actions upon the same object, possibly involving complementary actions ([Fogassi & Gallese, 2002](#)). Alternatively, another explanation could be that in the complementary condition, the participants observed an action that drew attention to an object eliciting a different action. This might have determined an interplay between mirror and canonical neurons: the latter type of neuron responds both during action execution and during the perception of the objects that are related to those behaviors ([Rizzolatti & Craighero, 2004](#)). Canonical motor neurons that become active during PG movements are, for instance, also activated when a small object that can be grasped using a PG is simply presented. Conversely, canonical neurons that become active during a WHG are selectively activated when a large object is shown ([Murata et al., 1997](#)). The need to perform a complementary action involving a different object might then imply a combination of mirror and canonical neurons coding for different types of action at different times. The hypothesis that different sets of mirror neurons might serve to integrate observed and executed actions during complementary kinds of social interaction is indeed an appealing one. Moreover, [Newman-Nordlund et al. \(2007b\)](#) and [Newman-Nordlund, Bosga, Meulenbroek, and Bekkering \(2008\)](#) hypothesized that a joint action could preferentially recruit right lateralized components of the mirror system since right inferior frontal activations are linked to inhibition processes ([Brass, Derrfuss, & von Cramon, 2005](#)). Planning and executing complementary actions in this framework would mean, first of all, actively inhibiting the natural tendency to imitate observed actions. It is also possible that right hemisphere components of the mirror system serve to integrate information regarding actions being generated by multiple actors and to determine an appropriate response, which is then forwarded to left hemisphere areas which are better suited to support

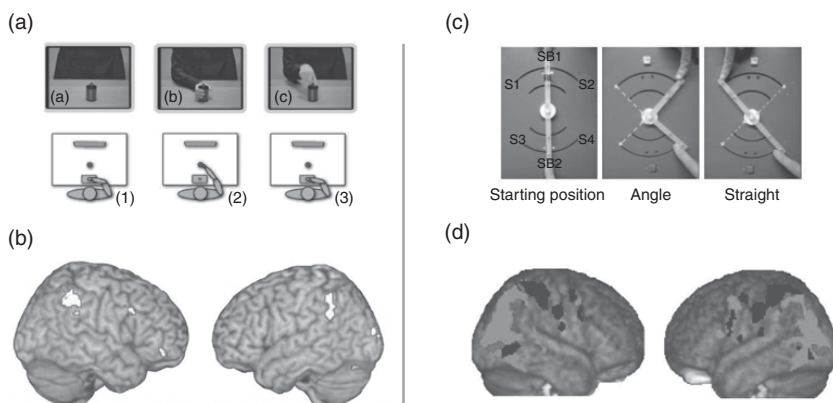


Figure 19.1 Brain structures that are involved in imitative and complementary actions.

Notes: (a) Investigations into the neural basis of joint actions have yielded partially converging results from functional imaging studies in normal individuals. Subjects participated in an ‘imitation’ and a ‘complementary’ action task with a manipulandum that could be grasped in two ways. The top-side of the object allowed a PG from above; the bottom side afforded a full-grip from the side. During the imitation task, subjects imitated the grasping behavior of a virtual actor viewed on a computer screen; during the complementary action condition, subjects performed the opposite action. In some (40%) of the trials a color cue indicated that the subjects were to execute a predefined grasp of the manipulandum (either WHG or PG), regardless of the actor’s behavior. (b) Brain areas with a greater BOLD signal for complementary actions include the right IFG (pars opercularis) and bilateral IPL. (c) Participants were engaged in real-time joint actions with an experimenter who was standing next to them by performing an action similar or opposite to the one observed to achieve a common goal on a response box (the experimenter’s and the participant’s finger could either form an angle or a straight line). Participants also performed the same actions individually (execution) and observed the experimenter’s actions (observation). (d) Rendering of the average brain of participants with hMNS (blue), superadditive voxels in joint actions (green) and overlap between hMNS and JA (red). Voxels common to both networks were restricted to the superior parietal lobule and higher-level visual areas.

Sources: (a) Set up and procedures adapted from Newman-Norlund et al. (2007b). (c) Set up and procedures adapted from Kokal and Keysers (2010) and Kokal et al. (2009).

execution of specific movement trains (Newman-Norlund et al., 2008). In the light of recent debates concerning the interpretation of the mirror mechanism (de Bruin & Gahhagher, 2012; Gallese & Sinigaglia, 2011), some have theorized that mirror neurons would transform perceptual information regarding

an intentional action in terms of the observer's own action possibilities. In the case of aplasic patients born without arms or hands, observation of hand actions activated regions generally attributed to the hMNS, but involved in the execution of foot or mouth actions (Gazzola et al., 2007).

The idea that the hMNS would link perceived actions with appropriate motor plans was confirmed by an fMRI study carried out by Ocampo, Kritikos, and Cunnington (2011), who investigated if performing actions that are dissimilar to ones we observe activates core regions of the hMNS (namely, IPL and IFG) or general control mechanisms responsible for selecting and preparing conflicting responses. Consistent with the direct matching hypothesis, activity within right IPL and right IFG regions in the imitative context was greatest when participants responded with similar actions to observed hand actions. Interestingly, activity within these regions increased also when performing dissimilar responses, reflecting increased demands in the remapping of stimulus–response associations. In a similar way, Shibata, Inui, and Ogawa (2011) found that the right IFG was involved in mediating higher-order action understanding linked to a requested complementary action. Overall, these findings seem to suggest that there are two separate processes both supported by fronto-parietal brain regions. The first process operates at a simple motor level within contexts that require similar responses. The second process allows an observer to inhibit those responses and prepare the most compatible with task demands.

A more integrated account of the neural circuits underlying joint actions (both imitative and complementary) was recently proposed by Kokal, Gazzola, and Keysers (2009) and Kokal and Keysers (2010). Participants in an interactive fMRI study were required to carry out complementary and imitative actions in real-time cooperation with an experimenter ('joint action'), to perform the same actions individually ('execution'), or to simply observe the experimenter's actions (observation; Figure 19.1c).

This experiment brought our understanding of social interactions to a new level by specifically mapping the contribution of the hMNS (i.e. common voxels for both execution and observation) together with the areas specifically involved in the joint actions (i.e. voxels exceeding the sum of execution and observation). The areas responsible for this integration process were located bilaterally in the IFG, IPL, precentral gyrus, superior parietal lobule, middle and temporal occipital gyri and cerebellum (Figure 19.1d).

Two anatomically separate networks were thus delineated: one that would transform observed and executed actions into a single code (Etzel, Gazzola, & Keysers, 2008) and another that would integrate this information to achieve common goals. These findings show that, although the hMNS plays a critical role in coordinating two-party efforts by translating all actions into a common code, the flexible remapping of these actions seems to be performed somewhere else.

Neurophysiologic Studies of Complementary Actions

Action observation automatically activates corresponding motor representations in an observer, and this seems to be an essential step in coordinating actions with others. A direct way to examine this link is by using single-pulse transcranial magnetic stimulation (spTMS) over the primary motor cortex (M1) and concomitant electromyography (EMG) (e.g. [Fadiga et al., 1995](#)). This method allows for the investigation of modulations of the observer's corticospinal (CS) excitability while he watches an agent performing an action. A statistically significant modulation of TMS-induced MEP amplitudes in the corresponding muscles indicates that observers are specifically attuned to the observed action.

The CS facilitation phenomenon provided the first physiological evidence for a direct matching in humans between action perception and action execution (for a review, see [Fadiga et al., 2005](#)), and made it possible to explore motor system reactions in interactive contexts. A series of recent neurophysiologic studies were indeed designed to assess CS facilitation while participants observed video-clips evoking imitative and incongruent complementary gestures (Sartori, Betti, & Castiello, 2013b, 2013c, 2013d; Sartori, Cavallo, Buccioni, & Castiello, 2011b, 2012b).

CS Excitability is Specifically Modulated by the Social Dimension of Observed Actions

In order to investigate whether the CS facilitation phenomenon is modulated depending on contextual factors, TMS-induced MEPs were recorded from participants' right hand muscles in response to either an observed action *explicitly* calling for a complementary response or the same action performed in a context which did not imply any social interaction ([Sartori et al., 2011b](#)). As the participants were instructed to remain motionless throughout the task, the degree to which the motor system was activated provided an index of the CS activity elicited by action preparation. In the experimental condition, seeing an actor in a frontal position with an open hand signaling a request near a salient object strategically placed out of her reach induced a modulation in the observer's MEP amplitudes that was consistent with the intention to accept the request (i.e. reaching for and grasping the object in question) rather than with the tendency to resonate with the observed action ([Figure 19.2a](#)). Notably, placing the object in the observer's peripersonal space is a crucial factor for inducing a function-related affordance (Costantini, Ambrosini, Scorolli, & Borghi, 2011a; Costantini, Ambrosini, Tieri, Sinigaglia, & Committeri, 2010; De Stefani et al., 2014; see [Box 19.3](#)). In this case, the type of grasp observed and the one that was planned were crucially mismatched (i.e. an open hand versus a WHG).

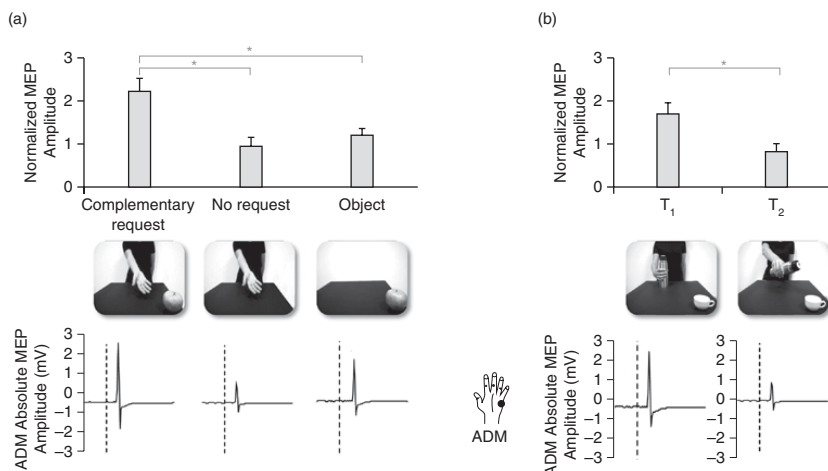


Figure 19.2 Experimental stimuli and TMS-induced mean MEP amplitude recorded in a participant's right ADM muscle.

Notes: (a) Three frames extracted from the experimental video-clips show: an actor extending an arm toward the viewer and unfolding her hand as if to explicitly request an out-of-reach apple ('complementary request'), the same actor extending her arm toward the viewer and unfolding her hand without the apple ('no-request') and the out-of-reach apple alone ('object'). Notably, only in the first condition is the out-of-reach apple present in the direction of the extended hand and the actor's open hand can readily be interpreted as a request addressed to the viewer to hand over the object. The normalized (top panel) and absolute (low panel) mean MEP amplitude indicates a significant pre-activation of ADM muscle in the 'complementary request' condition with respect to the other control conditions. This suggests that the complementary action disposition is contingent on perceiving the social gesture in connection to an object. (b) Two frames extracted from one of the experimental video-clips show an actor grasping a thermos with a whole-hand grasp (T₁), and then extending her arm toward the viewer as she attempts to pour something into the out-of-reach coffee cup (T₂). Notably, the gesture can readily be interpreted as a request to move the cup closer to the actor. The normalized (top panel) and absolute (low panel) mean MEP amplitude indicates an imitative pattern during the first part of the video (T₁) followed by a disposition toward executing the complementary grip in the second part (T₂), in preparation to hand the object over.

Sources: (a) Visual stimuli and results adapted from Sartori et al. (2011b). (b) Visual stimuli and results adapted from Sartori et al. (2012b).

As no explicit instructions were imparted to the participants, the effect uncovered spontaneous tendencies to fulfill the request embedded in a social interaction. This experiment was indeed particularly enlightening in view of

the fact that most studies typically ask participants to perform actions that are *not* associated with any meaningful behavior in real life or tasks that are likely to uncover dispositions formed during the execution of the experimental task itself (e.g. in imitation versus complementary blocks), rather than spontaneous tendencies.

To further strengthen these data, another experiment was designed to ascertain if the effect was intrinsically social or might be elicited even by non-social cues (i.e. an arrow cue pointing towards the object). It is well known, indeed, that the mere sight of an object activates the representation of the action that can be performed on it even in the absence of explicit intentions to act (Craighero, Fadiga, Rizzolatti, & Umiltà, 1998; Jeannerod, 1994; Tucker & Ellis, 1998; Box 19.3). The results showed that the presence of either the object or the arrow had the ability to determine MEP activation, but to a lesser extent than when the context was characterized by a request gesture toward the object. Taken together, these findings corroborate the idea that it is the social nature of an observed gesture along with the coding of object affordances (Box 19.3) that determine the observed effect. This was the first neurophysiologic evidence that the mechanisms underlying action observation are flexible, and spontaneously respond to contextual factors guiding social interactions above and beyond imitation.

The Functional Shift of Complementary Actions

A fundamental requirement for successful complementary actions is the capacity to smoothly and efficiently switch from observing another person's gestures to planning a corresponding reciprocal action, the so-called *functional shift* (Sartori et al., 2012b). Observed actions embedding a complementary request were studied in experimental trials to investigate the succession of these mechanisms. TMS-induced MEPs were recorded from participants' hand muscles in response to observing an actor grasping an object and then trying vainly to fulfill a task (e.g. pouring coffee) in a cup that was strategically placed out of her reach but in the video foreground, close to the observer's right hand (Figure 19.2b). The movement of the actor's hand was interpreted as a request to move the out-of-reach cup closer to the actor, so that she could complete the action. The type of grasp observed and the one that was required to carry out what was requested were reciprocally mismatched in all the videos (i.e. a WHG performed by the actor versus a PG requested of the observer, and vice versa). Results showed that a matching mechanism at the beginning of the action sequence turned into a complementary one as long as the request for a reciprocal action became evident (functional shift). The muscle-specificity of MEP amplitude highlighted an interplay between the initial tendency to resonate with what was observed and the implicit preparation for a dissimilar complementary action. This functional switch generated a modulation in grasp

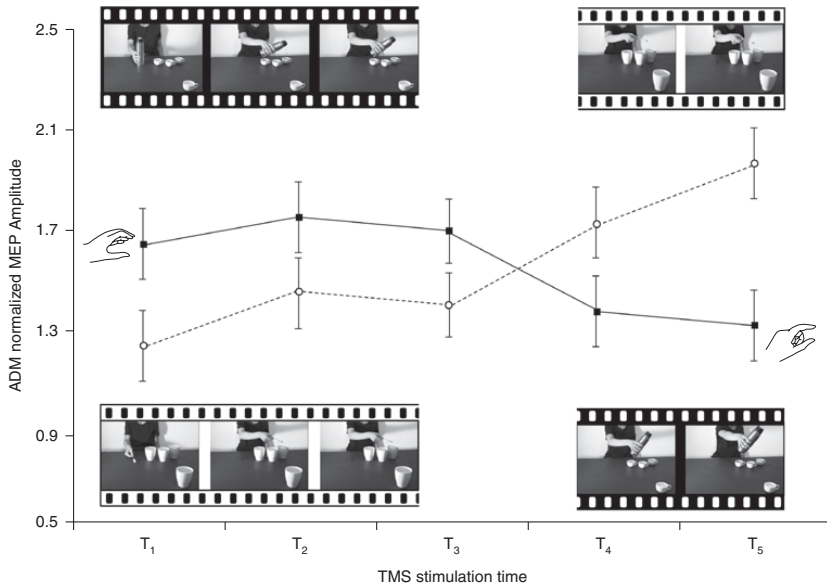


Figure 19.3 The time-course of complementary actions.

Notes: Visual stimuli and corresponding mean MEP amplitude recorded in a participant's ADM muscle show the time-course of the functional shift from motor resonance to reciprocity. spTMS was delivered at: T₁ (the time the hand made contact with the object), T₂ (when the model finished pouring), T₃ (when the model raised her hand from the third cup/mug), T₄ (the onset of the complementary request gesture) and T₅ (the end of the complementary request gesture). Social precision grip movements requiring a WHG (white) and social whole-hand grasp movements requiring a PG (black) are illustrated. Bars represent the standard error of means. Note that a measurable variation in the observer's MEP amplitude occurred 240 ms after the actor completed the first of a two-step sequence (T₄), at a time when it was still difficult to predict the course of action the actor would take.

Source: From Sartori et al. (2013d).

planning, immediately reflected in the activation of different hand muscles (Chinellato & del Pobil 2009).

Interestingly, the observer's handedness also seems to shape complementary interactions (Sartori, Begliomini, Panozzo, Garolla, & Castiello, 2014). In particular, observers tend to translate the complementary motor activation to their most functional effector (i.e. left-handers pre-activate the left hand and right-handers the right hand). These results confirm the hypothesis of a functional tuning of the action observation–execution system enabling left-handers living in a right-handed world to correctly plan movements in a highly efficient action-specific modality (Sartori, Begliomini, & Castiello, 2013a).

The Time-Course of Complementary Actions

The functional shift, as previously shown, indicates the ability to untie the automatic tendency to mirror another's actions and prepare for appropriate, complementary movements. The next question was then at what point this phenomenon occurs. A new experiment was then designed in which TMS was delivered at *five* different time points corresponding to five kinematic landmarks characterizing the observed action (Sartori et al., 2013c, 2013d; Figure 19.3). The most important was the fourth (T_4) time point when the actor's hand trajectory began to significantly move towards the out-of-reach object. A TMS pulse was specifically delivered at that time to investigate whether participants were able to predict the moment's trajectory relevance even before the action became explicit. The results showed that the participants were able to quickly discriminate between an action driven by a social goal and one that was not, simply by observing the kinematic cues signaling the direction of the actor's hand (Figure 19.3). Interestingly, the control condition consisted of the actor bringing her hand back to its initial position – with the out-of-reach object still visible in the foreground (Figure 19.3). This control condition made it possible to disentangle the role of *complementary affordances* (see Box 19.3).

These findings have direct implications with regard to action representation theories as they suggest that intention attribution (i.e. social versus individual) is sensitive to kinematic constraints. As different types of intentional actions have different motion signatures, observers seem to take note of precocious differences in kinematics during action observation to predict the actor's intentions (Becchio, Manera, Sartori, Cavallo, & Castiello, 2012a; Becchio, Sartori, & Castiello, 2010; Becchio et al., 2012b; Kilner et al., 2007; Manera, Becchio, Cavallo, Sartori, & Castiello, 2011; Sartori et al., 2009b, 2011a). Advance information gained while an action sequence is being observed allows observers not only to mirror an observed action but also to see behind the what and the why of an action and how to interact appropriately. It would seem, then, that any potential discrepancy between an observed action and a non-identical, complementary response is resolved flexibly in a two-step manner by the system itself. During the first step, the observed action is processed in order to predict its goal. During the second step, associations are made between the observed action and an appropriate action needed to accomplish a complementary goal. In line with this, it is tempting to assume that the motor system can mediate both automatic and flexible action–perception coupling. Erlhagen et al. (2006) recently proposed a model implementing both a direct (automatic) and a flexible route. The model involves four interconnected brain areas, namely, the superior temporal sulcus (STS), area PF, area F5 and the prefrontal cortex (PFC). The STS–F5 connection, allowing for the matching between a visual description

of an action and its motor representation, would represent the neural basis of the direct route for the automatic imitation of an observed action. More importantly, when required, the flexible action–perception coupling is realized in the model by the connection between the PF area and the PFC through which goal representations from the PFC can modulate and set the coupling between visual (STS) and motor (F5) representations (ibid).

Box 19.3 Complementary affordances

Perception is an active process that highlights particular properties of the environment called ‘affordances’ (Gibson, 1979). Affordances can be defined as action possibilities, associations between environmental properties and abilities (Chemero, 2003). Crucially, some affordances are more relevant than others. *Complementary affordances* are a specific subcategory, referring to all those possibilities for interaction provided by others that activate appropriate motor programs aiming to bring a common goal to completion. We are selectively responsive to a world of relevant affordances, including complementary ones. We directly perceive, for instance, the ‘meaning’ of a cup’s handle, which, of course, is used to pick it up, and this perception results from past experience. In a similar way, complementary requests can be understood in terms of the potential for the interactive involvement they elicit, even in situations in which the involvement does not take place. Complementary affordances depend on a number of variables, such as the presence of objects in a space that are necessary for an action to occur, gaze information (the relational orientation between the actor and the perceiver allowing for joint action; i.e. facing rather than behind or to the side), and the willingness to engage in a collaborative task. The concept of *readiness to interact* describes the disposition to engage in socially meaningful situations (Di Paolo & De Jaegher, 2012). The readiness to interact has been identified in the increased CS excitability of M1 as an index of a covert disposition to respond to a social gesture (Sartori et al., 2011b, 2012b, 2013b, 2013c, 2013d). In those studies, the functional shift from imitative to complementary action inclinations was contingent on perceiving a social gesture in connection to an object and was not likely to be mediated by inferential mechanisms. In this respect, *social signals* (e.g. instrumental gestures), whose function is to alter a recipient’s behavior by triggering a range of opportunities for action, deserve special attention (Dezecache, Conty, & Grèzes, 2013; Gallagher & Frith, 2004). Depending on its posture and context, for example, an extended open hand can lead to a handshake or other actions (see figure). As demonstrated by social interactive paradigms, engaging in complementary actions is made possible by



Box 19.3 Social signals such as an extended open hand can alter a recipient's behavior by triggering a range of opportunities for actions.

immediate apprehension of another person's goals (Sartori et al., 2009b). The activation of a complementary affordance is extremely powerful, and suggests that in our everyday interactions the automatic and rapid decoding of social cues influences our intentional behavior, maximizing the efficiency of our responses.

*Predictive Simulation in Social Contexts Calling for
Reciprocity: A Computational Model*

One of the motor system's basic functions is to predict another person's actions (Blakemore & Frith, 2005; Prinz, 2006; Wilson & Knoblich, 2005). Some evidence suggests that motor resonance would indeed support action prediction (Kilner, Vargas, Duval, Blakemore, & Sirigu, 2004), allowing individuals to extend the temporal horizon of their motor planning and anticipating another person's actions rather than simply responding to them.

The simulation theory (Gallese & Goldman, 1998) specifically argues that our ability to predict the actions of others depends on our capacity to simulate

(i.e. to internally reproduce) their actions. From this perspective, the same predictive mechanisms used to anticipate the sensory consequences of one's own movement/s may be employed to predict what others will do next (Wolpert & Flanagan, 2001). Indeed, observing another person's action is not simply a post-hoc reconstruction of visual input but an intrinsically predictive activity. When we observe another person's actions, we automatically anticipate their future ones. At the most basic level, humans can predict how a movement will evolve simply by watching how it was begun (Aglioti, Cesari, Romani, & Urgesi, 2008; Knoblich & Flach, 2001). In this vein, motor simulation seems to be called into play to solve fundamental computational dilemmas posed by action perception in those cases where information is missing or ambiguous (Aglioti & Pazzaglia, 2011; Avenanti & Urgesi, 2011; Schütz-Bosbach & Prinz, 2007; Wilson & Knoblich, 2005). Notably, predicting another person's behavior has immediate implications for one's own action selection system because, depending on the output of action simulation, a suitable action can be selected from a multiplicity of possible alternatives (Bekkering et al., 2009; Sartori et al., 2012c).

In contexts calling for complementary responses, the initially observed motor act must be coded from the very beginning in terms of the subsequent steps required to fulfill the action goal. This issue has been tackled in computational terms. Kinematic data linked to videos filmed by Sartori and colleagues (2013d) were utilized to implement a model identifying the switching point from the resonance to the social response phases (Chinellato, Ognibene, Sartori, & Demiris, 2013). Depending on the actor's hand trajectory, the model is capable of detecting a changeover even before the movement has come to an end. Once validated, one of the research project's long-term goals is to provide an artificial system, such as a humanoid robot, with more advanced social skills as it interacts with human partners.

In general terms, these studies have proposed a novel framework for modeling social interactions. The functional switch that has been previously described (Sartori et al., 2013c, 2013d) would be part of a dynamic interplay between the Action Observation System (AOS) and the Action Planning System (APS). The AOS is in charge of monitoring the actions of the person being observed, mainly by matching them to the observer's own motor repertoire. The APS is, instead, the neural system that plans and monitors the execution of all types of action. In social scenarios requiring non-identical joint actions, the APS takes control over the AOS, overriding automatic imitation behavior with a complementary social response (Chinellato et al., 2013). Notably, when the APS takes control over the AOS, monitoring the other person's actions is still performed by the AOS, and could directly affect on-line action execution. The process of selecting the appropriate action, therefore, does not necessarily

bypass resonating behavior but seems to proceed in an intermingled way. The following section focuses on this process.

Temporal Coupling of Congruent and Non-Congruent Motor Resonance during Action Observation

What are the basic mechanisms facilitating complementary actions? At first glance, it would seem that complementary actions can be successfully performed by an observer only if activation of motor representations of observed actions is suppressed. [Brass, Zysset, and von Cramon \(2001\)](#) pointed out that the automatic tendency to imitate needs, first of all, to be inhibited if we want to generate a response that is different from the one that was observed. Recent computational and electrophysiological data seem, however, to suggest that motor resonant and associative processes can work side-by-side ([Chinellato et al., 2013](#); Sartori, Bulgheroni, Tizzi, & Castiello, 2015b). Motor simulation of another person's actions during complementary interactions is particularly critical to success. An experiment combining spTMS and EMG recordings from multiple effectors was designed to examine if observing another person's actions priming for an incongruent reaction can lead to a motor-resonant response in the observer's corresponding muscles as well as a predictive activation and a simultaneous preparation of effectors necessary for a non-congruent response (Sartori, Betti, Chinellato, & Castiello, 2015a; [Figure 19.4](#)). CS modulation was assessed in the upper and lower limb muscles of participants observing a soccer player performing: (1) a penalty kick straight in their direction and then coming to a full stop, (2) a penalty kick straight in their direction and then continuing to run, (3) a penalty kick to the side and then continuing to run. The results showed a modulation of the observer's CS excitability in different effectors at different times, reflecting a multiplicity of motor coding: the internal replica of the observed action, the predictive activation and the adaptive integration of congruent and non-congruent responses to the actions of others.

A Working Memory Hypothesis

Taking the findings described a step further raises another interesting question: if observing an action performed using a specific effector can trigger responses in different ones, what mechanism selects the effectors needing to be activated for an appropriate response? A dual process seems to lie behind joint actions: a low-level motor resonance would store and analyze information on observed actions (allowing the onlooker to experience what is being observed), while a high-level simulation would flexibly integrate the individual's actions with those of others and select the most appropriate course to achieve joint

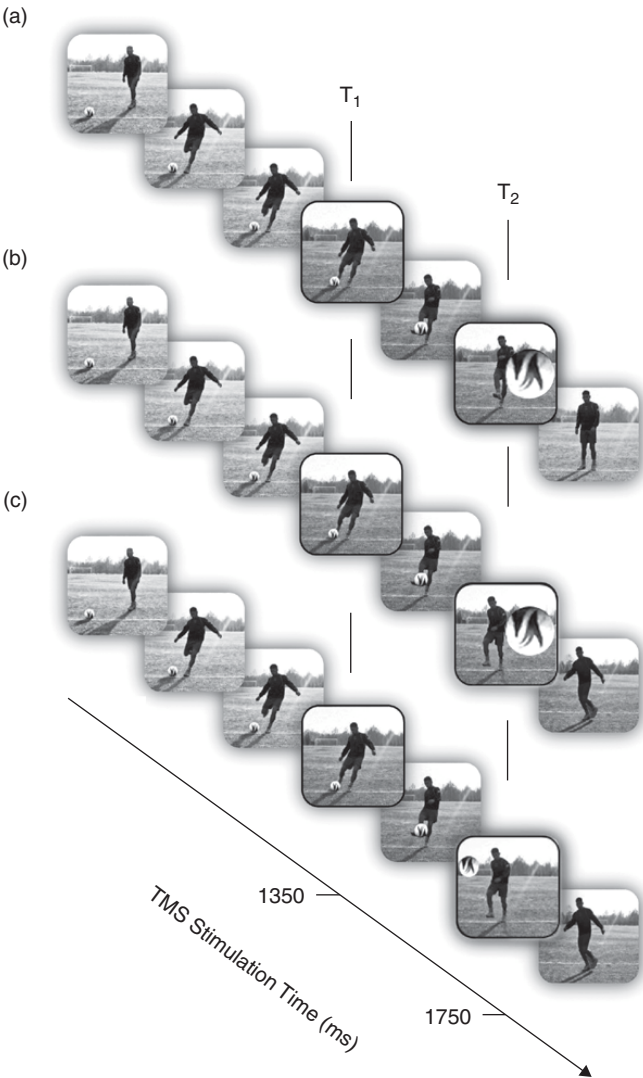


Figure 19.4 Video-clips and timing of TMS pulses.

Notes: The continuous oblique line represents the entire presentation of the three video-clips: (a) still, (b) running, (c) side. The vertical lines denote the time points when single TMS pulses were delivered: at T_1 (when the player's foot makes contact with the ball) and at T_2 (when the ball trajectory reaches its highest peak).

Source: From Sartori et al. (2013d).

goals (van Schie et al., 2008a). It can be hypothesized, then, that the hMNS' function is similar to that of a working memory, but specifically tailored for action. The hMNS's primary role is, as demonstrated by studies outlining its multisensory nature, to keep the neuronal activation linked to the visual, auditory or imaging aspects of motor actions (Kohler et al., 2002) on hold. As in the case of the working memory, distinct elements are kept on-line while others are being processed (Gibson, 2000).

Complementary actions are the ideal way to test this hypothesis. During complex social interactions, an individual needs to keep information relative to the observed action available while the attempt is being made to process its relative response. The working memory permits an individual to manipulate distinct components of a scene to extract meaning from it in view of a final goal. In the same way, during social interactions, the mirror system may be involved in keeping action-related information on hold to enable other brain areas to extract the meaning of an observed action to achieve a joint goal. The relation between observed and executed actions could be coordinated by a *social associative memory*, which would match certain actions to their natural social responses, irrespective of who is actually performing the action (Chinellato et al., 2013). If action B (e.g. take) usually follows action A (e.g. give), observing an actor executing A elicits pre-planning of B in the observer. If, instead, an actor executes A, she expects to see the observer perform B in response. A response that differs from the expected one could either be classified as an anomaly to discard or be considered an important new reaction that needs to be kept in our filing system. It is the comparison between predicted and observed stimuli, both with regard to individual and social movements, which directs the use and plastic modification of action components and their relations. The nature of the linkage between perception and action continues to be debated: is learning how to interact with other persons treated in the same way as stimulus–response (S–R) associations, or is it treated as a special way? Notably, there is a huge difference between basic and complex forms of complementary action. The former involve coordination without representation of the other persons' intentions and may be sub-served by the hMNS. The latter require a specific form of interdependence of the individual's intentions, as described by Bratman (1992), and the supplementary intervention of specific brain networks. Future research on complementary action may prove critical in clarifying how humans learn to interact with other persons.

Summary

The basic idea behind the research outlined here is that motor resonance elicited by action observation is modulated depending on the context: when an observed gesture is socially relevant (i.e. there is an implicit or explicit request),

anticipatory complementary activations follow. The theory that observing an action automatically triggers an inclination to execute it was largely based on the fact that most studies did not explicitly challenge the automaticity and flexibility of the visuomotor transformation process. It is nevertheless undeniable that successful interactions often require complementary rather than imitative actions. A series of neurophysiologic studies have, in fact, demonstrated that an observed action characterized by a complementary request evokes a shift from motor resonance to reciprocity in the observer's motor system (Sartori et al., 2011b, 2012b, 2013b, 2013c, 2013d).

The data outlined here have contributed to shedding light on the functioning of the human motor system in social contexts and have increased knowledge on forms of social behavior frequently occurring in daily life situations. Defining the conditions and the modalities by which motor-resonant responses to action observation can be modulated may prove to have specific translational implications leading to the development of novel neuro-rehabilitation protocols for patients with localized lesions to cortical motor areas (e.g. ischemic stroke) and for pathologies such as autism. More distant horizons may include developing models of brain mechanisms underlying social interactions in view of endowing artificial agents such as robots with the ability to perform meaningful responses to observed actions.

References

- Aglioti, S. M., Cesari, P., Romani, M., & Urgesi, C. (2008). Action anticipation and motor resonance in elite basketball players. *Nature Neuroscience*, 11, 1109–1116.
- Aglioti, S. M., & Pazzaglia, M. (2011). Sounds and scents in (social) action. *Trends in Cognitive Sciences*, 15 (2011), 47–55.
- Avenanti, A. & Urgesi, C. (2011). Understanding ‘what’ others do: Mirror mechanisms play a crucial role in action perception. *Social Cognitive and Affective Neuroscience*, 6, 257–259.
- Becchio, C., Cavallo, A., Begliomini, C., Sartori, L., Feltrin, G., & Castiello, U. (2012b). Social grasping: From mirroring to mentalizing. *NeuroImage*, 61, 240–248.
- Becchio, C., Manera, V., Sartori, L., Cavallo, A., & Castiello, U. (2012a). Grasping intentions: From thought experiments to empirical evidence. *Frontiers in Human Neuroscience*, 6, 1–6.
- Becchio, C., Sartori, L., Bulgheroni, M., & Castiello, U. (2008a). The case of Dr. Jekyll and Mr. Hyde: A kinematic study on social intention. *Consciousness and Cognition*, 17, 557–564.
- (2008b). Both your intention and mine are reflected in the kinematics of my reach to grasp movement. *Cognition*, 106, 894–912.
- Becchio, C., Sartori, L., & Castiello, U. (2010). Towards you: The social side of actions. *Current Directions in Psychological Science*, 19, 183–188.
- Bekkering, H., de Bruijn, E., Cuijpers, R., Newman-Norlund, R., van Schie, H., & Meulenbroek, R. (2009). Joint action: Neurocognitive mechanisms supporting human interaction. *Topics in Cognitive Science*, 1, 340–352.

- Blakemore, S. J., & Frith, C. (2005). The role of motor contagion in the prediction of action. *Neuropsychologia*, 43, 260–267.
- Brass, M., Derrfuss, J., & von Cramon, D. Y. (2005). The inhibition of imitative and overlearned responses: A functional double dissociation. *Neuropsychologia*, 43, 89–98.
- Brass, M., Zysset, S., & von Cramon, D. Y. (2001). The inhibition of imitative response tendencies. *NeuroImage*, 14, 1416–1423.
- Bratman, M. E. (1992). Shared cooperative activity. *Philosophical Review*, 101, 327–341.
- Bruin, L. de, & Gallagher, S. (2012). Embodied simulation, an unproductive explanation: Comment on Gallese and Sinigaglia. *Trends in Cognitive Sciences*, 16, 98–99.
- Castiello, U., Becchio, C., Zoia, S., Nelini, C., Sartori, L., et al. (2010). Wired to be social: The ontogeny of human interaction. *PLoS One*, 5, e13199.
- Cavallo, A., Becchio, C., Sartori, L., Bucchioni, G., & Castiello, U. (2012). Grasping with tools: Corticospinal excitability reflects observed hand movements. *Cerebral Cortex*, 22, 710–716.
- Cavallo, A., Sartori, L., & Castiello, U. (2011). Corticospinal excitability modulation to hand muscles during the observation of appropriate versus inappropriate actions. *Cognitive Neuroscience*, 2, 83–90.
- Chemero, A. (2003). An outline of a theory of affordances. *Ecological Psychology*, 15, 181–195.
- Chinellato, E., & del Pobil, A. P. (2009). The neuroscience of vision-based grasping: A functional review for computational modeling and bio-inspired robotics. *Journal of Integrative Neuroscience*, 8, 223–254.
- Chinellato, E., Ognibene, D., Sartori, L., & Demiris, Y. (2013). Time to change: Deciding when to switch action plans during a social interaction. In N. F. Lepora, A. Mura, H. G. Krapp, P. F. M. J. Verschure, & T. J. Prescott (Eds.), *Biomimetic and biohybrid systems*. London: Springer, 47–58.
- Costantini, M., Ambrosini, E., Scroli, C., & Borghi, A. M. (2011a). When objects are close to me: Affordances in the peripersonal space. *Psychonomic Bulletin and Review*, 18, 302–308.
- Costantini, M., Ambrosini, E., Tieri, G., Sinigaglia, C., & Comitteri, G. (2010). Where does an object trigger an action? An investigation about affordances in space. *Experimental Brain Research*, 207, 95–103.
- Costantini, M., Comitteri, G., & Sinigaglia, C. (2011b). Ready both to your and to my hands: Mapping the action space of others. *PLoS One*, 6, e17923.
- Craigheo, L., Fadiga, L., Rizzolatti, G., & Umiltà, C. (1998). Visuomotor priming. *Visual Cognition*, 5, 109–125.
- De Stefani, D., Innocenti, A., De Marco, D., Busiello, M., Ferri, F., et al. (2014). The spatial alignment effect in near and far space: A kinematic study. *Experimental Brain Research*, 1–8.
- Dezechache, G., Conty, L., & Grèzes, J. (2013). Social affordances: Is the mirror neuron system involved? *Behavioral and Brain Sciences*, 36, 417–418.
- Di Paolo, E., & De Jaegher, H. (2012). The interactive brain hypothesis. *Frontiers in Human Neuroscience*, 6, 1–16.
- Erlhagen, W., Mukovskiy, A., Bicho, E., Panin, G., Kiss, A., et al. (2006). Goal-directed imitation for robots: A bio-inspired approach to action understanding and skill learning. *Robotics and Autonomous Systems*, 54, 353–360.
- Etzel, J. A., Gazzola, V., & Keysers, C. (2008). Testing simulations theory with cross-model multivariate classification of fMRI data. *PLoS One*, 3, 1–6.

- Fabbri-Destro, M., & Rizzolatti, G. (2008). Mirror neurons and mirror systems in monkeys and humans. *Physiology*, 23, 171–179.
- Fadiga, L., Craighero, L., & Olivier, E. (2005). Human motor cortex excitability during the perception of others' action. *Current Opinion in Neurobiology*, 15, 213–218.
- Fadiga, L., Fogassi, L., Pavesi, G., & Rizzolatti, G. (1995). Motor facilitation during action observation: A magnetic stimulation study. *Journal of Neurophysiology*, 73, 2608–2611.
- Fogassi, L., & Gallese, V. (2002). The neural correlates of action understanding in non-human primates. *Advances in Consciousness Research*, 42, 13–36.
- Gallagher, H. L., & Frith, C. D. (2004). Dissociable neural pathways for the perception and recognition of expressive and instrumental gestures. *Neuropsychologia*, 42, 1725–1736.
- Gallese, V. (2001). The shared manifold hypothesis. From mirror neurons to empathy. *Journal of Consciousness Studies*, 8, 5–7.
- Gallese, V., & Goldman, A. (1998). Mirror neurons and the simulation theory of mind-reading. *Trends in Cognitive Sciences*, 2, 493–501.
- Gallese, V., & Sinigaglia, C. (2011). What is so special about embodied simulation? *Trends in Cognitive Sciences*, 15, 512–519.
- Gangopadhyay, N., & Schilbach, L. (2012). Seeing minds: A neurophilosophical investigation of the role of perception–action coupling in social perception. *Social Neuroscience*, 7, 410–423.
- Gazzola, V., van der Worp, H., Mulder, T., Wicker, B., Rizzolatti, G., & Keysers, C. (2007). Aplasics born without hands mirror the goal of hand actions with their feet. *Current Biology*, 17, 1235–1240.
- Gentilucci, M., Castiello, U., Corradini, M. L., Scarpa, M., Umiltà, C., & Rizzolatti, G. (1991). Influence of different types of grasping on the transport component of prehension movements. *Neuropsychologia*, 29, 361–378.
- Georgiou, I., Becchio, C., Glover, S., & Castiello, U. (2007). Different action patterns for cooperative and competitive behaviour. *Cognition*, 102, 415–433.
- Gibson, E. (2000). The dependency locality theory: A distance-based theory of linguistic complexity. In Y. Miyashita, A. Marantz, & W. O'Niel (Eds.), *Image, language, brain*. Cambridge, MA: MIT Press, 95–126.
- Gibson, J. J. (1979). *The ecological approach to visual perception*. Boston, MA: Houghton Mifflin.
- Giorello, G., & Sinigaglia, C. (2007). Perception in action. *Acta Biomedica*, 78, 49–57.
- Graf, M., Schütz-Bosbach, S., & Prinz, W. (2009). *Motor involvement in action and object perception: Similarity and complementarity*. New York: Psychology Press.
- Heyes, C. (2011). Automatic imitation. *Psychological Bulletin*, 137, 463–483.
- Jeannerod, M. (1994). The representing brain: Neural correlates of motor intention and imagery. *Behavioral Brain Sciences*, 17, 187–245.
- Keysers, C. (2009). Mirror neurons. *Current Biology*, 19, R971–R973.
- Kilner, J. M., Friston, K. J., & Frith, C. D. (2007). Predictive coding: An account of the mirror neuron system. *Cognitive Processes*, 8, 159–166.
- Kilner, J. M., Vargas, C., Duval, S., Blakemore, S. J., & Sirigu, A. (2004). Motor activation prior to observation of a predicted movement. *Nature Neuroscience*, 7, 1299–1301.
- Knoblich, G., Butterfill, S., & Sebanz, N. (2011). Psychological research on joint action: Theory and data. In B. Ross (Ed.), *The psychology of learning and motivation*. Burlington, VT: Academic Press, 59–101.

- Knoblich, G., & Flach, R. (2001). Predicting the effects of actions: Interactions of perception and action. *Psychological Science*, 2, 467–472.
- Kohler, E., Keysers, C., Umiltà, M. A., Fogassi, L., Gallese, V., & Rizzolatti, G. (2002). Hearing sounds, understanding actions: Action representation in mirror neurons. *Science*, 297, 846–848.
- Kokal, I., Gazzola, V., & Keysers, C. (2009). Acting together in and beyond the mirror neuron system. *NeuroImage*, 47, 2046–2056.
- Kokal, I., & Keysers, C. (2010). Granger causality mapping during joint actions reveals evidence for forward models that could overcome sensory-motor delays. *PLoS One*, 5, e13507.
- Longo, M. R., Kosobud, A., & Bertenthal, B. I. (2008). Automatic imitation of biomechanically possible and impossible actions: Effects of priming movements versus goals. *Journal of Experimental Psychology: Human Perception and Performance*, 34, 489–501.
- Manera, V., Becchio, C., Cavallo, A., Sartori, L., & Castiello, U. (2011). Cooperation or competition? Discriminating between social intentions by observing prehensile movements. *Experimental Brain Research*, 211, 547–556.
- Meltzoff, A. N. (2005). Imitation and other minds: The ‘like me’ hypothesis. In S. Hurley & N. Chater (Eds.), *Perspectives on imitation: From cognitive neuroscience to social science*, Volume 2. Cambridge, MA: MIT Press, 55–77.
- Molenberghs, P., Cunnington, R., & Mattingley, J. B. (2012). Brain regions with mirror properties: A meta-analysis of 125 human fMRI studies. *Neuroscience and Biobehavioral Reviews*, 36, 341–349.
- Murata, A., Fadiga, L., Fogassi, L., Gallese, V., Raos, V., & Rizzolatti, G. (1997). Object representation in the ventral premotor cortex (area F5) of the monkey. *Journal of Neurophysiology*, 78, 2226–2230.
- Napier, J. R. (1956). The prehensile movements of the human hand. *Journal of Bone and Joint Surgery*, 38, 902–913.
- Newman-Norlund, R. D., Bosga, J., Meulenbroek, R. G., & Bekkering, H. (2008). Anatomical substrates of cooperative joint-action in a continuous motor task: Virtual lifting and balancing. *NeuroImage*, 41, 169–177.
- Newman-Norlund, R. D., Noordzij, M. L., Meulenbroek, R. G., & Bekkering, H. (2007a). Exploring the brain basis of joint action: Co-ordination of actions, goals and intentions. *Social Neuroscience*, 2, 48–65.
- Newman-Nordlund, R. D., van Schie, H. T., van Zuijlen A. M., & Bekkering, H. (2007b). The mirror neuron system is more activated during complementary compared with imitative action. *Nature Neuroscience*, 10, 817–818.
- Ocampo, B., & Kritikos, A. (2010). Placing actions in context: Motor facilitation following observation of identical and non-identical manual acts. *Experimental Brain Research*, 201, 743–751.
- Ocampo, B., Kritikos, A., & Cunnington, R. (2011). How frontoparietal brain regions mediate imitative and complementary actions: An fMRI study. *PLoS One*, 6, e26945.
- Pellegrino, G. di, Fadiga, L., Fogassi, L., Gallese, & Rizzolatti, G. (1992). Understanding motor events: A neurophysiological study. *Experimental Brain Research*, 91, 176–180.
- Poljac, E., van Schie, H. T., & Bekkering, H. (2009). Understanding the flexibility of action–perception coupling. *Psychological Research*, 73, 578–586.

- Prinz, W. (2006). What re-enactment earns us. *Cortex*, 42, 515–517.
- Rizzolatti, G., Cattaneo, L., Fabbri-Destro, M., & Rozzi, S. (2014). Cortical mechanisms underlying the organization of goal-directed actions and mirror neuron-based action understanding. *Physiological Reviews*, 94, 655–706.
- Rizzolatti, G., & Craighero, L. (2004). The mirror-neuron system. *Annual Review of Neuroscience*, 27, 169–192.
- Rizzolatti, G., Fogassi, L., & Gallese, V. (2001). Neurophysiological mechanisms underlying the understanding and imitation of action. *Nature Review Neuroscience*, 2, 661–670.
- Rizzolatti, G., & Sinigaglia, C. (2010). The functional role of the parieto-frontal mirror circuit: Interpretations and misinterpretations. *Nature Reviews Neuroscience*, 11, 264–274.
- Sacheli, L. M., Tidoni, E., Pavone, E. F., Aglioti, S. M., & Candidi, M. (2013). Kinematic fingerprints of leader and follower role-taking during cooperative joint actions. *Experimental Brain Research*, 226, 473–486.
- Sartori, L., & Castiello, U. (2013). Shadows in the mirror. *Neuroreport*, 24, 63–67.
- Sartori, L., Becchio, C., Bara, B. G., & Castiello, U. (2009a). Does the intention to communicate affect action kinematics? *Consciousness and Cognition*, 18, 766–772.
- Sartori, L., Becchio, C., Bulgheroni, M., & Castiello, U. (2009b). Modulation of the action control system by social intention: Unexpected social requests override preplanned action. *Journal of Experimental Psychology: Human Perception and Performance*, 35, 1490–1500.
- Sartori, L., Becchio, C., & Castiello, U. (2011a). Cues to intention: The role of movement information. *Cognition*, 119, 242–252.
- Sartori, L., Begliomini, C., & Castiello, U. (2013a). Motor resonance in left- and right-handers: Evidence for effector-independent motor representations. *Frontiers in Human Neuroscience*, 13, 7–33.
- Sartori, L., Begliomini, C., Panozzo, C., Garolla, A., & Castiello, U. (2014). The left side of motor resonance. *Frontiers in Human Neuroscience*, 8, 702.
- Sartori, L., Betti, S., & Castiello, U. (2013b). When mirroring is not enough: That is, when only a complementary action will do (the trick). *Neuroreport*, 24, 601–604.
- (2013c). Corticospinal excitability modulation during action observation. *Journal of Visualized Experiments*, 82, e51001.
- Sartori, L., Betti, B., Chinellato, E., & Castiello, U. (2015a). The multiform motor cortical output: Kinematic, predictive and response coding. *Cortex*, 70, 169–178.
- Sartori, L., Bucchioni, G., & Castiello, U. (2012a). Motor cortex excitability is tightly coupled to observed movements. *Neuropsychologia*, 50, 2341–2347.
- (2013d). When emulation becomes reciprocity. *Social Cognitive and Affective Neuroscience*, 8, 662–669.
- Sartori, L., Bulgheroni, M., Tizzi, R., & Castiello, U. (2015b). A kinematic study on (un)intentional imitation in bottlenose dolphins. *Frontiers in Human Neuroscience*, 5(9), 446.
- Sartori, L., Cavallo, A., Bucchioni, G., & Castiello, U. (2011b). Corticospinal excitability is specifically modulated by the social dimension of observed actions. *Experimental Brain Research*, 211, 557–568.

- Sartori, L., Cavallo, A., Buccioni, B., & Castiello, U. (2012b). From simulation to reciprocity: The case of complementary actions. *Social Neuroscience*, 7, 146–158.
- Sartori, L., Xompero, F., Buccioni, G., & Castiello, U. (2012c). The transfer of motor functional strategies via action observation. *Biology Letters*, 8, 193–196.
- Schütz-Bosbach, S., & Prinz, W. (2007). Perceptual resonance: Action-induced modulation of perception. *Trends in Cognitive Sciences*, 11, 349–355.
- Sebanz, N., Bekkering, H., & Knoblich, G. (2006). Joint action: Bodies and minds moving together. *Trends in Cognitive Sciences*, 10, 70–76.
- Shibata, H., Inui, T., & Ogawa, K. (2011). Understanding interpersonal action coordination: An fMRI study. *Experimental Brain Research*, 211, 569–579.
- Schie, H. T. van, Koelewijn, T., Jensen, O., Oostenveld, R., Maris, E., & Bekkering, H. (2008a). Evidence for fast, low-level motor resonance to action observation: An MEG study. *Social Neuroscience*, 3, 213–228.
- Schie, H. T. van, Waterschoot, B. M., & Bekkering, H. (2008b). 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.
- Tucker, M., & Ellis, R. (1998). On the relations between seen objects and components of potential actions. *Journal of Experimental Psychology: Human Perception and Performance*, 24, 830–846.
- Turella, L., Tubaldi, F., Erb, M., Grodd, W., & Castiello, U. (2012). Object presence modulates activity within the somatosensory component of the action observation network. *Cerebral Cortex*, 22, 668–679.
- Urgesi, C., Candidi, M., Fabbro, F., Romani, M., & Aglioti, S. M. (2006). Motor facilitation during action observation: Topographic mapping of the target muscle and influence of the onlooker's posture. *European Journal of Neuroscience*, 23, 2522–2530.
- Wilson, W., & Knoblich, G. (2005). The case for motor involvement in perceiving conspecifics. *Psychological Bulletin*, 131, 460–473.
- Wolpert, D. M. & Flanagan, J. R. (2001). Motor prediction. *Current Biology*, 11, R729–R732.