Intentions in the Brain: The Unveiling of Mister Hyde

(Article begins on next page)

23 April 2024

Intentions in the brain: the unveiling of Mister Hyde

Ansuini C[1], Cavallo A[2], Bertone C[2], Becchio C[1,2]

[1]Department of Robotics, Brain and Cognitive Sciences, Italian Institute of Technology, Genova, Italy
[2]Centre for Cognitive Science, Department of Psychology, University of Torino, Torino, Italy

Corresponding Author: Cristina Becchio, RBCS, Fondazione Istituto Italiano di Tecnologia, Via Morego 30, 16163 Genova, Italy. Email: cristina.becchio@unito.it

Abstract

Is it possible to understand the intentions of others by merely observing their movements? Current debate has been mainly focused on the role that mirror neurons and motor simulation may play in this process, with surprisingly little attention being devoted to how intentions are actually translated into movements. Here, we delineate an alternative approach to the problem of intention-from-movement understanding, which takes "action execution" rather than "action observation" as a starting point. We first consider whether and to what extent, during action execution, intentions shape movement kinematics. We then examine whether observers are sensitive to intention information conveyed by visual kinematics and can use this information to discriminate between different intentions. Finally, we consider the neural mechanisms that may contribute to intention-from-movement understanding. We argue that by reframing the relationship between intention and movement, this evidence opens new perspectives into the neurobiology of how we know other minds and predict others' behavior.

Suppose an observer, say Dr. Watson, watches Dr. Jekyll/Mr. Hyde taking hold of a scalpel to apply it to a human body. The action is the same for both actors; however, in one case, Dr. Jekyll is using the scalpel to cure a patient, and in the other case, Mr. Hyde grasps the scalpel to inflict pain. Would it be possible for Dr. Watson to discriminate their intentions by simply observing the way they grasp the scalpel?

Current accounts of intention understanding assume that no "one-to-one mapping" exists between intention and movements: the same intention can be achieved with different movements, and more problematically, the same movement can be used for different goals and intentions (Csibra 2007; Kilner and others 2007a; see also Jacob 2013; Jacob and Jeannerod 2005). On this assumption, an "intractable nonspecificity" problem arises. To elaborate, if movement kinematics is equivocally related to intention, then it would not provide an adequate basis for understanding others' intentions. "For example, if, while walking along the street, someone suddenly waves his arm, is he hailing a taxi or swatting a wasp?" (Kilner and others 2007a). Predictive coding models foresee that observers watching this scene may estimate the agent's intention based on contextual information (e.g., the presence of a taxi approaching). In the absence of contextual information, however, given the nonspecificity of the observed kinematics, they would not be able to differentiate between the two intentions (Kilner 2011) (Fig. 1A).
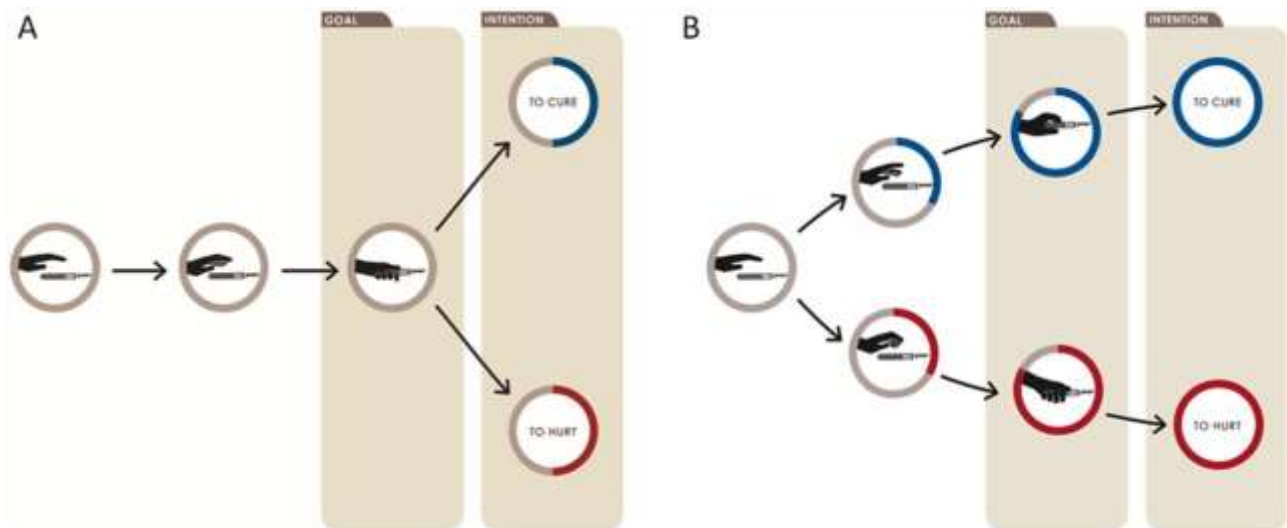
Figure 1. (A) Example of the predictive coding account of action observation. Assuming that the intention "to cure" (blue) and the intention to "hurt" (red) lead to the same goal and kinematics, the prediction error is identical in both schemes. It follows that under these circumstances, the model cannot differentiate between the intentions causing the action. (B) In contrast, we propose that intentions influence action planning so that although the to-be-grasped object is the same, different kinematic features and goals are selected depending on the intention "to cure" or "to hurt." Even in the absence of contextual information, it is thus possible for Dr. Watson to discriminate Dr. Jekyll/Mr. Hyde's intention solely on the basis of the kinematics of the observed movements.

Here, we question the plausibility of these predictions. We propose that even in the absence of contextual information, observers can access others' intentions from the way they move (Fig. 1B). The argument will be made in three moves. First, we show that intentions influence response properties and shape movement kinematics during movement execution (Ansuini and others 2006, 2008; Becchio and others 2008a,2008b, 2012; Sartori and others 2009a; Schuboe and others 2008). Second, we demonstrate that observers are sensitive to early differences in visual kinematics and can use them to discriminate between movements performed with different intentions (Manera and others 2011a; Sartori and others 2011; Stapel and others 2012;Vingerhoets and others 2010). Finally, we show that the activity in neural networks implicated in intention understanding is modulated by intention information conveyed by visual kinematics. We conclude by putting forward the hypothesis that movement kinematics rather than context form the basis for action prediction: even if Mr. Hyde's action would be seen taking place within an operating theater, Dr. Watson would nonetheless be able to discriminate his intention by observing the way he reaches toward and grasps for the scalpel.

## First Move: Intentions Shape Movement Kinematics

Since the seminal work by Marteniuk and others (1987), a plethora of studies have investigated how prior intention (i.e., intention representing the action as a whole, from now on "intention"; Searle 1983) influences the execution of reach-to-grasp movements (e.g., Ansuini and others 2006, 2008; Armbrüster and Spijkers 2006). The logic of these studies was to "manipulate" the intention while keeping the object to be grasped (i.e., goal) as well as the situational requirements (i.e., context) constant. If within the same context, the same object is handled differently depending on the agent's intention, this would indicate that the intention influences the kinematics.

To quantify this influence, Ansuini and others (2008) asked participants to reach, grasp, and accomplish one of the four possible actions (i.e., pouring, displacing, throwing, or passing) on a bottle. Kinematic assessment revealed that when the bottle was grasped with the intent to pour, both the middle and the ring fingers were more extended than in all the other considered intentions. Interestingly, intentions have an effect on hand kinematics not only during the unfolding of the reach-to-grasp movement but also at contact. For example, it has been shown that participants place their thumb and index in a higher position when the bottle is grasped with the intention to pour than when it is grasped with the intention to lift (Crajé and others 2011).

Further studies have extended these effects to the domain of social intention. For instance, it has been shown that participants' maximal finger aperture is smaller and peak grip closing velocity increases when an object is reached and grasped with the intent to move it than to pass it to another person (Becchio and others 2008a). Similarly, actions performed with a communicative intent exhibit different kinematics than those performed with a purely individual intent (Sartori and others 2009a, 2009b).

These data showing intention-related differences in grasping movements suggest that actions are planned and executed as a whole action chain. At a neurobiological level, this intention-related chained organization of actions has been ascribed to a parietal-premotor circuit endowing individuals with predictive representations of the forthcoming action (Bonini and others 2010; Fogassi and others 2005). In particular, it has been shown that motor neurons within both the inferior parietal lobule (IPL; specifically area PFG) and the ventral premotor cortex (PMv; specifically area F5) discharge differently during grasping depending on the intention to be achieved (i.e., grasp-to-eat vs. grasp-to-place) (Fig. 2) (Bonini and others 2010; Fogassi and others 2005). A detailed analysis of the temporal dynamics of end-goal selectivity revealed that the activity of these grasping neurons, particularly in the parietal area PFG, reflected first "how" the object is to be grasped (i.e., type of grip), then "why"

the action is performed (i.e., intention), very likely to facilitate the motor acts following grasping (Bonini and others 2012).
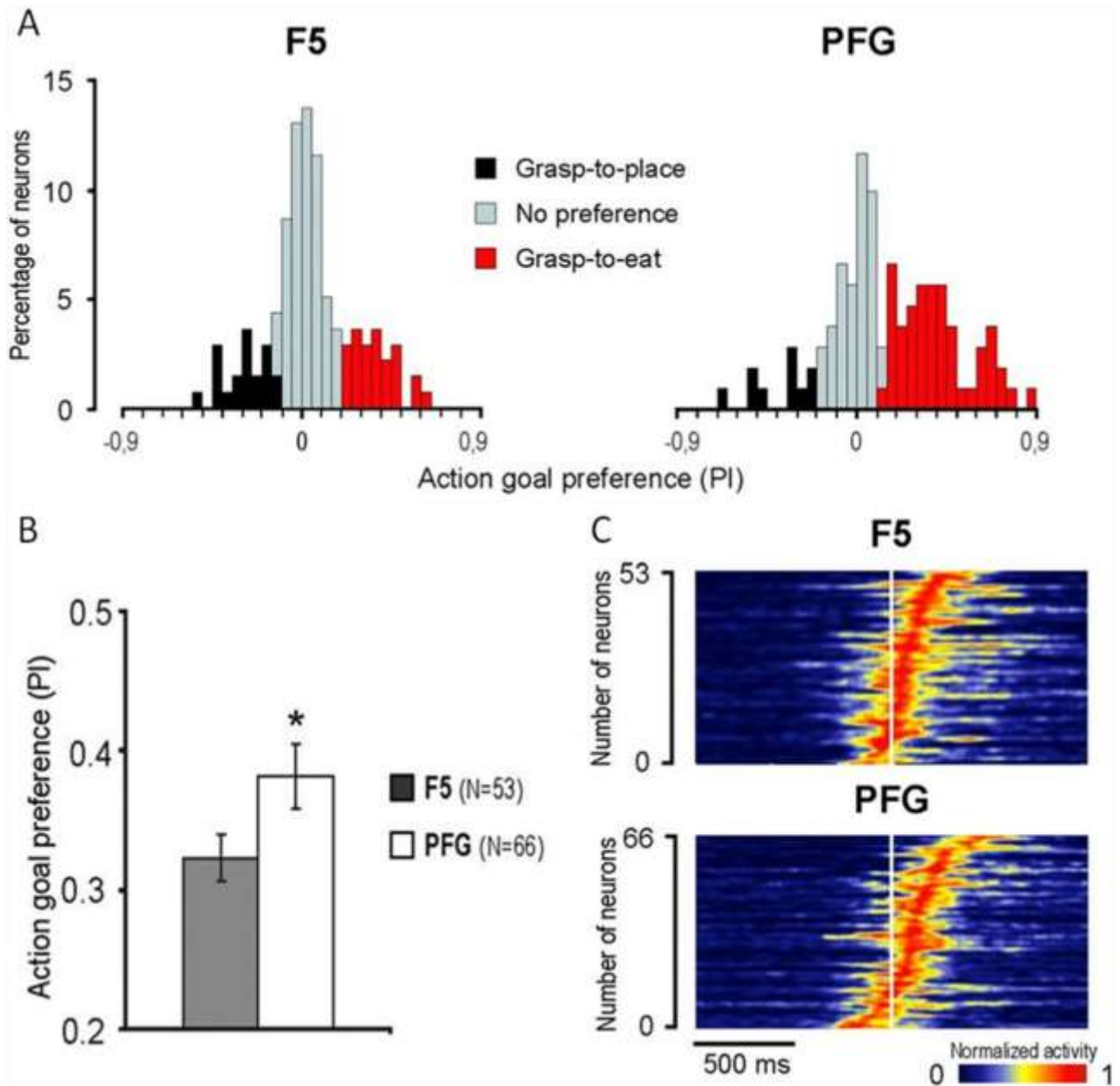
Figure 2. (A) Comparison between the distribution of F5 and PFG neurons according to their preference index (PI; calculated from the average response of the neuron in grasp-to-eat and grasp-to-place condition, respectively). (B) Comparison between average PIs (absolute values) of F5 and PFG for neurons discharging differently during grasping when this act was embedded into actions aimed at different goals. (C) Time course of the activity of F5 and PFG grasping neurons in their "preferred condition", aligned with the moment when the monkey touched the food to be grasped (white line). The discharge intensity over time of each neuron is represented as a change in color along horizontal lines. Neurons have been ordered from bottom to top, based on their peak of activity timing (data adapted from Bonini and others 2010).

Second Move: Observers Discriminate Intentions from Movement Observation

The above findings suggest that intentions influence action planning so that although the to-be-grasped object is the same, different kinematic features are selected depending on the overarching intention. Yet the question remains whether, during action observation, visual kinematics provide a sufficient basis for discriminating intentions. In other words, are observers sensitive to intention information conveyed by movement kinematics? Are they able to pick up and use early differences in visual kinematics to discriminate different intentions in grasping an object?

At a behavioral level, one approach for probing the contribution of visual kinematics to intention understanding is progressive temporal occlusion, where multiple occlusion points are used so as to form a progressive series of time windows within the event of interest (Farrow and others 2005). Naish and others (2013) adapted this approach to test how much of a two-step action sequence participants needed to see to correctly predict the outcome of the action—either eating or placing. The duration of the movement viewed by participants on each trial was determined by their (correct or incorrect) response on the previous trial according to an adaptive staircase procedure. This procedure revealed that participants needed to see at least part of the postgrasp phase to correctly distinguish between grasp-to-eat and grasp-to-place movements. However, because kinematic information was not used to select the video stimuli (and it is thus not possible to determine whether pregrasp kinematics actually differed between grasp-to-eat and grasp-to-place movements), these findings provide no conclusive evidence as to whether observers can pick up early differences in visual kinematics.
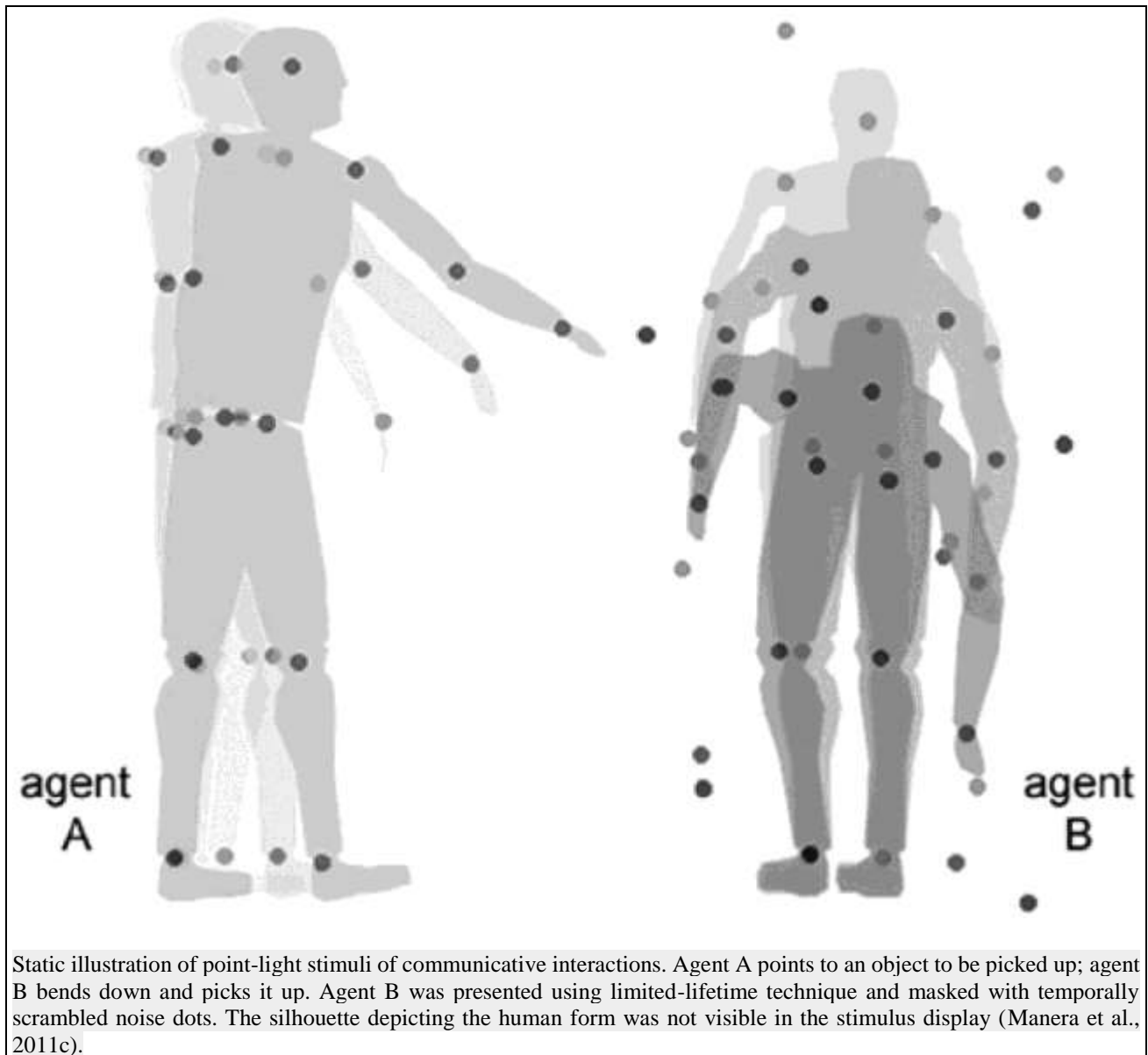
To address this confound, Sartori and others (2011) first analyzed the kinematics of reach-to-grasp movements performed with different intents: cooperate with a partner, compete against an opponent, or perform an individual action at natural or fast speed. Next, to assess attunement to kinematic information, they selected video clips representative of each type of intention to be included in an intention discrimination task. The results revealed that despite the lack of contextual information, observers were able to discriminate cooperative, competitive, and individual movements (Sartori and others 2011).

But *what* specific cues did participants use to make their anticipation judgments? To determine whether arm/hand information could be used in isolation to discriminate intention, in a second experiment, video clips were spatially occluded so that only the arm and forearm of the model were visible. As the spatial occlusion procedure had no substantial impact on the accuracy of the discrimination performance, these findings suggest that arm kinematics was sufficient to discriminate between movements performed with different intentions (Sartori and others 2011). This conclusion was further confirmed by Manera and others (2011a) in a study comparing intention discrimination from video and point-light clips (Box 1). Though in the point-light clips, the display was reduced to only three disconnected points of light corresponding to the moving position of landmarks on the wrist, the index finger, and the thumb of the agent's hand, participants were able to discriminate between social and individual movements.

Box 1. Tools to Study Intention-From-Movement Understanding: The Point-Light Technique

A method employed to isolate the contribution of visual kinematics is the point-light technique (Johansson 1973). With this method, the movements of a body are represented by a small number of point-lights indicating the major joints of a moving person. Despite the "degraded" nature of point-light stimuli, observers report a clear and compelling perception of the precise actions performed by the dynamic point-light actor (e.g., walking; see Blake and Shiffrar 2007 for a review). For example, they can easily recognize instrumental and noninstrumental actions (Vanrie and Verfaillie 2004), discriminate different variations of a particular action (e.g., Pollick and others 2001), and discern activities involving two individuals (Neri and others 2006). Moreover, they are able to identify the point-light actor's identity (e.g., Loula and others 2005), gender (e.g., Kozlowski and Cutting 1977), age (Montpare and Zebrowitz-McArthur 1988), and emotional state (e.g., Atkinson and others 2004). In the study of intention understanding, the use of point-light stimuli is especially suitable to quantify the contribution of kinematic information (Manera and others 2010). In natural settings, the movement patterns of an agent provide kinematic information in conjunction with other sources of information. Being devoid of all the contour, texture, shape, and color cues, point-light displays allow ascertaining to what extent intention-from-movement understanding relies on visual kinematics. Following this logic, point-light displays have been employed in studies conducted in sport settings to investigate whether observers are able to anticipate the direction and the depth of a badminton or a tennis stroke (Abernethy and others 2008;Abernethy and Zawi 2007) or to determine whether a basketball player is about to throw a ball or mimic a throw (Sebanz and Shiffrar 2009). Recently, Manera and others (2011b; see also Manera and others 2011c; Manera and others 2013) demonstrate that observers are able to discriminate the communicative intent of a point-light agent in the context of social interaction. More important, they showed that information extracted from communicative gestures influences the concurrent processing of biological motion by prompting visual detection of a second agent (Manera and others 2011c). This suggests that information extracted from kinematics can be used not only to anticipate what an agent will do next, but also in the context of a social interaction between two agents, to make predictions about the other agent's action.

Static illustration of point-light stimuli of communicative interactions. Agent A points to an object to be picked up; agent B bends down and picks it up. Agent B was presented using limited-lifetime technique and masked with temporally scrambled noise dots. The silhouette depicting the human form was not visible in the stimulus display (Manera et al., 2011c).

Third Move: Intention Information Conveyed by Visual Kinematics Modulates Activation within Mirror and Mentalizing Neural Networks

What neural mechanisms contribute to intention-from-movement understanding? Ever since their discovery, mirror neurons have been proposed to underlie our ability to understand actions "transforming visual information into knowledge" about others' goals and intentions (Gallese and Goldman 1998). The specific role played by visual kinematics in this process has, however, received little attention. In particular, whereas a number of studies have evaluated the impact of contextual information in the cortical representation of grasping actions (e.g., Iacoboni and others 2005; Ortigue and others 2010), only a few studies have directly attempted to assess the contribution of kinematics.

Mirror neuron sensitivity to early differences in visual kinematics is compatible with the finding that during action observation of grasp-to-place and grasp-to-eat actions, the majority of F5 and PFG mirror neurons show differential activity at hand contact (Bonini and others 2010; Fogassi and others 2005; see also Bonini and others 2013). However, because in these studies the presence/absence of a

container acted as contextual cue allowing the monkey to predict the experimenter's most likely motor act following the grasping, the possibility that precontact modulation reflected context, rather than early differences in visual kinematics, cannot be ruled out.

In humans, initial evidence that *how* an object is grasped may influence intention processing within the mirror circuit was provided by Kaplan and Iacoboni (2006) by using fMRI. Here, subjects watched precision grips and whole-hand grasps embedded in a drinking or a cleaning context. Activity within the right PMv, a mirror neuron area, was higher when the type of grasp (e.g., precision grip) and the context (drinking context) conveyed the same intention, suggesting that PMv is sensitive to congruency of contextual and kinematic cues (Kaplan and Iacoboni 2006).

What remained unclear from this study, however, was the specific contribution of kinematics to intention discrimination. It has been proposed that mirror neurons discharge during action observation not because they are driven by visual kinematics, but because they are part of a generative model that is predicting the sensory input (Kilner 2011; Kilner and Lemon 2013; Kilner and others 2007a; see Box 2). Within this framework, the most probable intention of the observed action would be estimated from context, in areas outside the mirror neuron circuit. In this view, the PMv would not encode the intention, but the most probable action within a given context. With respect to the study by Kaplan and Iacoboni (2006), this means that the increased BOLD signal in PMv when the context (e.g., drinking) and the type of grasp (e.g., precision grip) were congruent could reflect the fact that given the intention to drink (as estimated from the context), a precision grip is the most probable action to occur.

Box 2. The Predictive Coding Account of the Mirror Neuron System

Predictive coding is based on minimizing prediction error though recurrent or reciprocal interactions among levels of a cortical hierarchy. In the predictive coding framework, each level of a hierarchy employs a generative model to predict representations in the level below. This generative model uses backward connections to convey the prediction to the lower level where it is compared to the representation of this subordinate level to produce a prediction error. This prediction error is then sent back to the higher level, via forward connections, to adjust the neuronal representation of sensory causes, which in turn change the prediction. Reciprocal exchange of signals continues until prediction error is minimized and the most likely cause of the input has been generated. The predictive coding account of the mirror neuron system proposed by Kilner and colleagues (Kilner 2011; Kilner and others 2007a, 2007b) suggests that during action observation, the generative model starts with a prior prediction of the intention of the person we are observing. Given this prior expectation, we can predict their motor commands. Given their motor commands, we can predict the kinematics on the basis of our own action system (Kilner and others 2007a). The comparison of this predicted kinematics with the observed kinematics generates a prediction error, which is then used via forward connections to update our representation of the person's motor commands and goals. By minimizing the prediction error at all levels of the hierarchy, the most likely intention will finally be inferred. But where and how is the intention prior generated? Kilner (2011) proposes that in this framework, the most probable prediction of the intention of the observed action is estimated from the *context* in which the action is observed, in areas outside the mirror neuron system (Kilner 2011). Assuming that kinematics is not specific to intention, intention discrimination should thus only be possible when the context allows a correct estimation of the intention prior (Kilner and others 2007a, 2007b), that is, when the action intention is achieved in a congruent context. In line with that noted by Clark (2013), this hierarchical predictive coding delivers a processing regime in which context sensitivity is fundamental and pervasive: context rather than kinematics should always form the basis for action prediction.
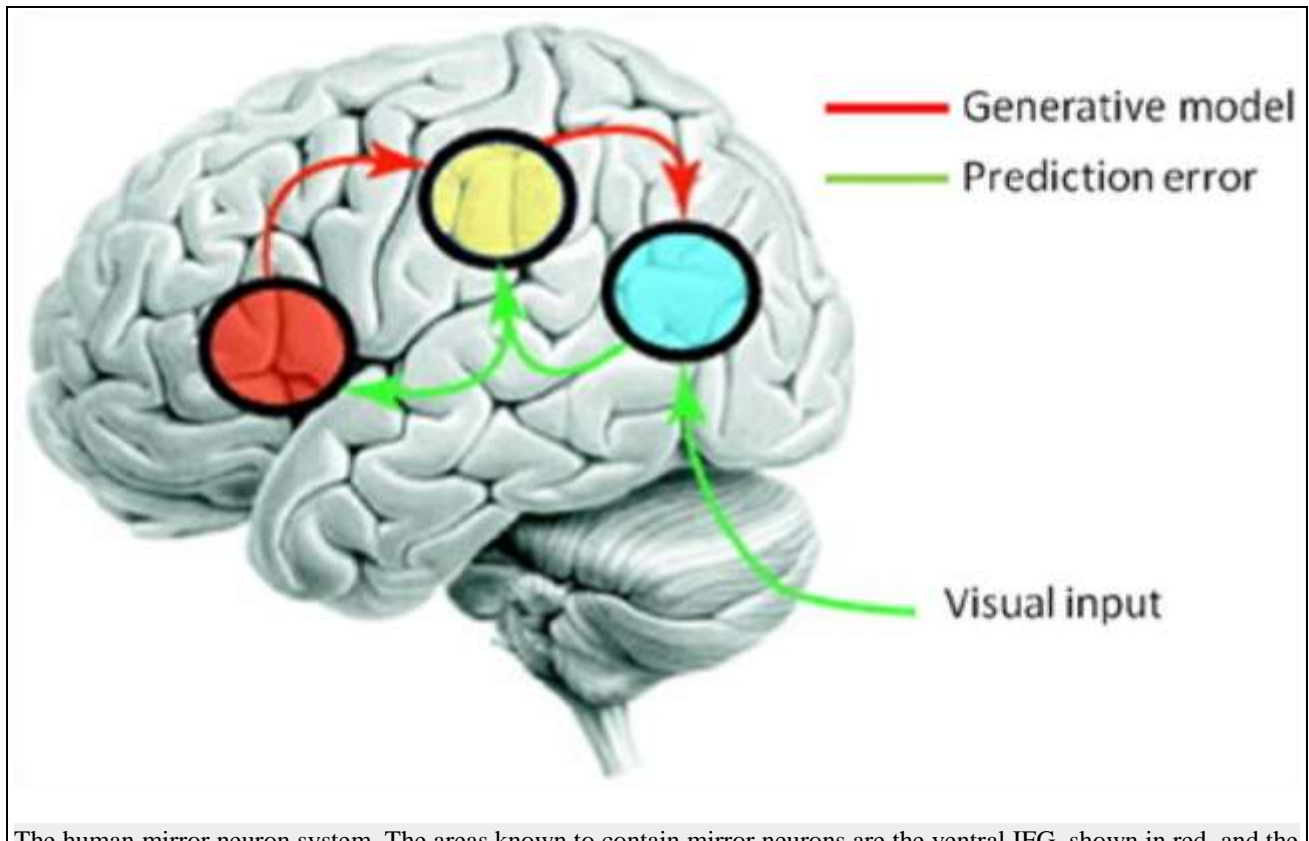
The human mirror neuron system. The areas known to contain mirror neurons are the ventral IFG, shown in red, and the IPL, shown in yellow. These two areas are reciprocally connected (Luppino and others 1999), creating a premotor-parietal mirror system. Neurons within the STS, highlighted in blue, have also been shown to respond selectively to biological movements, both in monkeys (Oram and Perrett 1994) and in humans (Grossman and others 2000). The STS is reciprocally connected to the IPL (Seltzer and Pandya 1994) and therefore provides visual input to the mirror system. In the predictive coding model, generative models use backward connections, shown in red, to convey the prediction to the lower levels. The prediction error is then sent back to the higher level, via forward connections, shown in green, to adjust the neuronal representation of sensory causes (adapted from Kilner 2011).

One way to circumvent this problem is to eliminate the context and see whether, in the absence of contextual guidance, visual kinematics modulates intention processing within mirror neuron areas. To probe this, Lestou and colleagues (2008) used kinematic morphs (i.e., point-light displays manipulated to produce parametric temporal morphs) of different types of arm movements within an fMRI repetition suppression paradigm. Rebound effects of movements that differed in their kinematics were observed within the PMv as well as within parietal mirror regions, including IPL and superior parietal lobules (SPL). However, whereas PMv was shown to encode differences between movements regardless of whether the goal of the movements was different or similar, rebound effects in IPL and SPL were only observed for movements with different goals, suggesting that these areas may be specifically involved in coding kinematic features relevant for intention discrimination.

Further evidence that parietal regions may be sensitive to intention information conveyed by movement kinematics was provided by Vingerhoets and others (2010). This study employed stimuli consisting of single-tool objects that were grabbed by an actor who intended either to use or to displace the tool. By viewing the way in which the object was seized, participants had to decide whether the intention of the actor was to use or to move the object. Results revealed that discrimination of actor's intention involved multifocal activations within the anterior bank of the intraparietal sulcus (aIPS), a region that is also involved in planning of grasp-related actions (Tunik and others 2007).

Relying on the same logic, Becchio and others (2012) investigated whether and to what extent the activity within the mirror neuron system discriminates between social and individual intended movements. Participants observed isolated reach-to-grasp movements performed with the intent to cooperate, compete, or perform an individual movement, followed by a static test picture (see Fig. 3). They were required to judge whether the test picture depicted a continuation of the observed movement or not. Despite the lack of contextual information, observing prehensile movements performed with a social intent relative to prehensile movements performed with an individual intent activated mirror areas, including the PMv and the IPL (Fig. 3). Interestingly, comparison of social versus individual movements also revealed differential activations at the temporoparietal junction (TPJ) and within the dorsal medial prefrontal cortex (dMPFC), two regions traditionally associated with explicitly thinking about the state of minds of other individuals (i.e., "mentalizing"). This result has been taken to suggest that the activity within these areas might as well be bottom-up driven by intentionally salient kinematic features. Both the mirror and the mentalizing circuits (as far as social intentions are concerned) thus appear to be sensitive to intention information conveyed by movement kinematics.
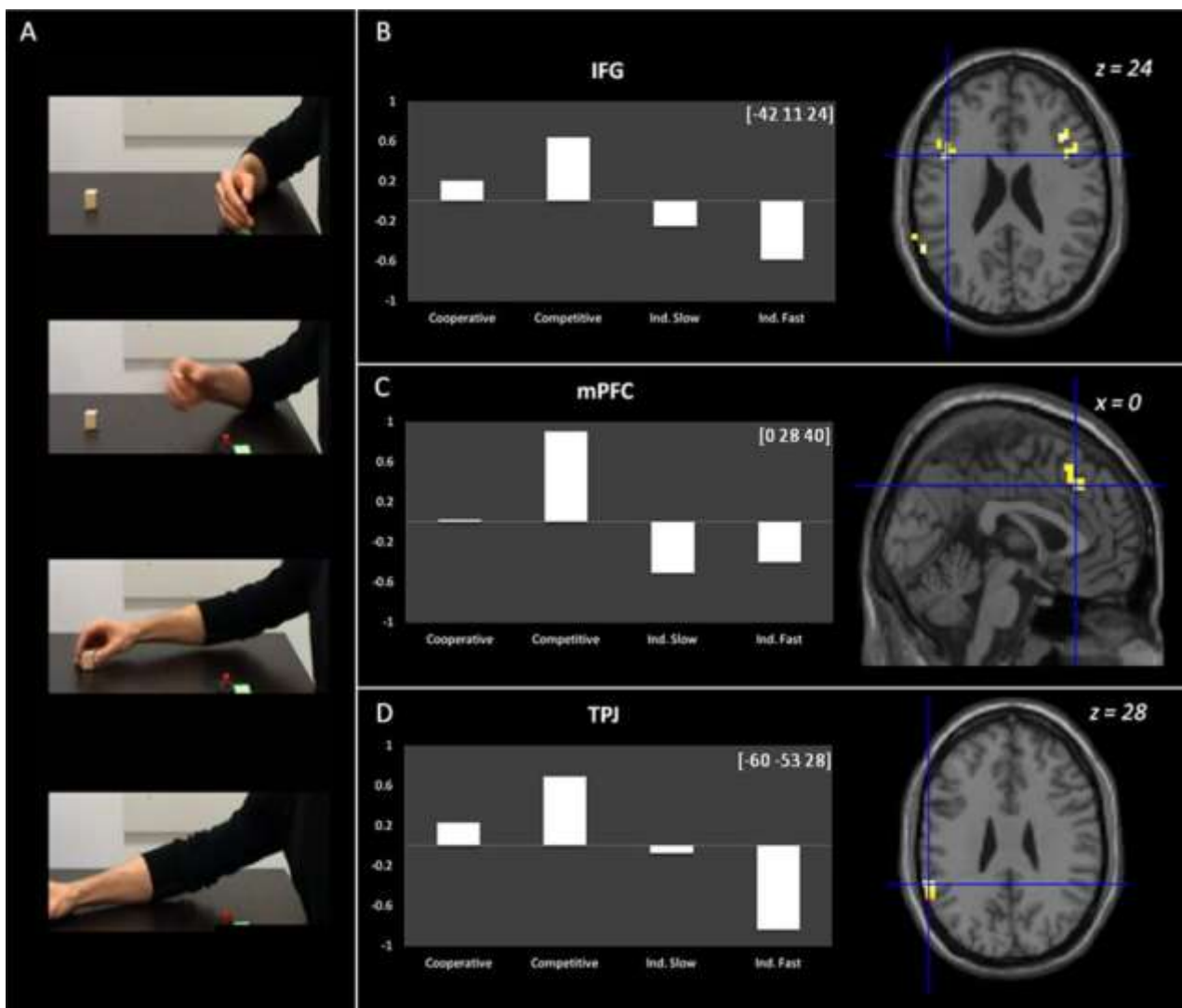
Figure 3. (A) Exemplar schematic representation of event sequencing during a competitive action sequence. A trial started with a video clip depicting the model's arm and forearm reaching toward and grasping for an object. The last visible frame of each clip showed the model's hand disappearing behind a black screen after grasping the object. Then, a test

picture showing the model's hand placing the object in its final position was presented. Participants were instructed to decide whether or not the test picture was a continuation of the observed action. Observing reach-to-grasp movements performed with a social intent [(competitive + cooperative) > (individual fast + individual slow)] increased activity in the left IFG (B), in the dorsal sector of the medial prefrontal cortex (mPFC) (C), and within the supramarginal gyrus (D), extending inferiorly to encompass the TPJ (data adapted from Becchio and others 2012).

Conclusions and Future Directions

All in all, the results reviewed in this article indicate that during action execution, intentions shape movement kinematics. Observers are attuned to early differences in visual kinematics and can use these differences to discriminate between movements performed with different intentions. Even when no contextual information is available, they are able to estimate others' intentions from the way they move. In everyday life, however, actions are embedded within a context and it is plausible that contextual information—the objects available in the scene at the moment, but also preexisting contextual information, such as knowing that the person you are seeing just stole the scalpel from an unlocked cabinet—is used to constrain the expectation of others' goals and intentions (Zaki and Ochsner 2009). But how does movement kinematics combine with context in the prediction of others' actions?

Predictive coding models propose that the context in which the action is embedded forms the basis for action prediction. For example, if the action of grasping a scalpel is seen in an operating theater, then the context will cause a larger prediction error for the intention "to hurt" and a smaller prediction error for the intention "to cure." On the assumption that the kinematics does not specify intention, an observer would then infer that the intention of the observed movement was "to cure." When the action sequence takes place within an operating theater, Mr. Hyde could thus be mistaken for Dr. Jekyll.

Based on the reviewed evidence, we suggest that this is unlikely. Even if the action would be seen taking place within an operating theater, Dr. Watson would nonetheless be able to discriminate Mr. Hyde's intention. He would be able to do so from the kinematic patterning characterizing his reach-to-grasp movements (see Fig. 4). Before movement onset, the intention estimated from the context would be "to cure." However, during movement unfolding, the intention information specified in the visual kinematics would be taken into account and would override the initial intention representation. Despite the context, the intention "to hurt" would thus be correctly discriminated on the basis of how the action is performed and this would finally allow the unveiling of Mr. Hyde: "Elementary, my dear Watson."
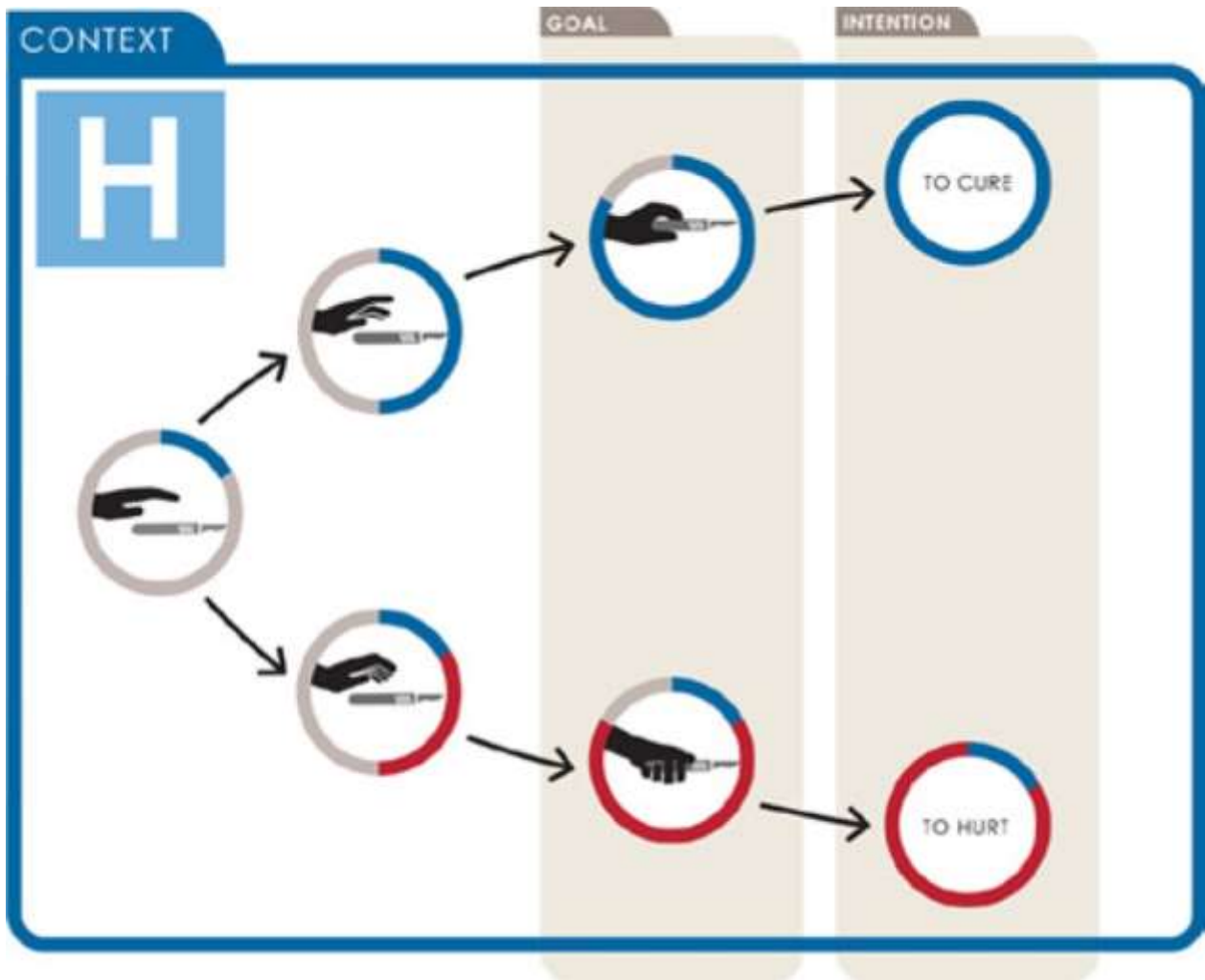
Figure 4. Schematic representation of intention from movement understanding in the presence of an action context, that is, operating theater. As the action is taking place in an operating theater, we foresee that at the very beginning of the movement, the system would "preferentially" load the "to cure" intention. However, as soon as the movement unfolds, the kinematics and the goal might either reveal that the prediction was correct (upper stream) or indicate that the actual intention is "to hurt" (lower stream). Despite the context suggesting that the intention is "to cure," Dr. Watson would thus be able to unveil Mr. Hyde, as disclosed by his kinematics, and correctly understand his actual intent to hurt.

References

Abernethy B, Zawi K. 2007. Pickup of essential kinematicsunderpins expert perception of movement patterns. J Motor Behav 39(5):353–67.

Abernethy B, Zawi K, Jackson RC. 2008. Expertise and attunement to kinematic constraints. Perception 37(6):931–48.

Ansuini C, Giosa L, Turella L, Altoè GM, Castiello U. 2008. An object for an action, the same object for other actions: effects on hand shaping. Exp Brain Res 185(1):111–19.

Ansuini C, Santello M, Massaccesi S, Castiello U. 2006. Effects of end-goal on hand shaping. J Neurophysiol 95:2456–65.

Armbrüster C, Spijkers W. 2006. Movement planning in prehension: do intended actions influence the initial reach and grasp movement? Motor Control 10(4):311–29.

Atkinson AP, Dittrich WH, Gemmell AJ, Young AW. 2004. Emotion perception from dynamic and static body expressions in point-light and full-light displays. Perception 33(6):717–46.

Becchio C, Cavallo A, Begliomini C, Sartori L, Feltrin G, Castiello U. 2012. Social grasping: from mirroring to mentalizing. Neuroimage 61(1):240–8.

Becchio C, Sartori L, Bulgheroni M, Castiello U. 2008a. Both your intention and mine are reflected in the kinematics of my reach to grasp movement. Cognition 106(2):894–912.

Becchio C, Sartori L, Bulgheroni M, Castiello U. 2008b. The case of Dr. Jekyll and Mr. Hyde: a kinematic study on social intention. Conscious Cogn 17(3):557–64.

Blake R, Shiffrar M. 2007. Perception of human motion. Annu Rev Psychol 58:47–73.

Bonini L, Ferrari PF, Fogassi L. 2013. Neurophysiological bases underlying the organization of intentional actions and the understanding of others' intention. Conscious Cogn 22(3):1095–1104.

Bonini L, Rozzi S, Serventi FU, Simone L, Ferrari PF, Fogassi L. 2010. Ventral premotor and inferior parietal cortices make distinct contribution to action organization and intention understanding. Cerebr Cortex 20(6):1372–85.

Bonini L, Serventi FU, Bruni S, Maranesi M, Bimbi M, Simone L, and others. 2012. Selectivity for grip type and action goal in macaque inferior parietal and ventral premotor grasping neurons. J Neurophysiol 108(6):1607–19.

Clark A. 2013. Whatever next? Predictive brains, situated agents, and the future of cognitive science. Behav Brain Sci 36(3):181–204.

Crajé C, Lukos JR, Ansuini C, Gordon AM, Santello M. 2011. The effects of task and content on digit placement on a bottle. Exp Brain Res 212(1):119–24.

Csibra G. 2007. Action mirroring and action interpretation: an alternative account. In: Haggard P, Rosetti Y, Kawato M, editors. Sensorimotor foundations of higher cognition. Attention and performance XXII. Oxford, England: Oxford University Press. p. 435–59.

Farrow D, Abernethy B, Jackson RC. 2005. Probing expert anticipation with the temporal occlusion paradigm: experimental investigations of some methodological issues. Motor Control 9(3):332–51.

Fogassi L, Ferrari PF, Gesierich B, Rozzi S, Chersi F, Rizzolatti G. 2005. Parietal lobe: from action organization to intention understanding. Science 308(5722):662–7.

Gallese V, Goldman A. 1998. Mirror neurons and the simulation theory of mind-reading. Trends Cogn Sci 2(12):493–501.

Grossman E, Donnelly M, Price R, Pickens D, Morgan V, Neighbor G, and others. 2000. Brain areas involved in perception of biological motion. J Cogn Neurosci 12(5):711–20.

Iacoboni M, Molnar-Szakacs I, Gallese V, Buccino G, Mazziotta JC, Rizzolatti G. 2005. Grasping the intentions of others with one's own mirror neuron system. PLoS Biol 3(3):e79.

Jacob P. 2013. How from action-mirroring to intention-ascription? Conscious Cogn 22(3):1132–41.

Jacob P, Jeannerod M. 2005. The motor theory of social cognition: a critique. Trends Cogn Sci 9(1):21–5.

Johansson G. 1973. Visual perception of biological motion and a model for its analysis. Percept Psychophys 14:201–11.

Kaplan JT, Iacoboni M. 2006. Getting a grip on other minds: mirror neurons, intention understanding, and cognitive empathy. Soc Neurosci 1(3–4):175–83.

Kilner JM. 2011. More than one pathway to action understanding. Trends Cogn Sci 15(8):352–7.

Kilner JM, Friston KJ, Frith CD. 2007a. Predictive coding: an account of the mirror neuron system. Cogn Process 8(3):159–66.

Kilner JM, Friston KJ, Frith CD. 2007b. The mirror-neuron system: a Bayesian perspective. Neuroreport 18(6):619–23.

Kilner JM, Lemon RN. 2013. What we know currently about mirror neurons. Curr Biol 23(23):R1057–R1062.

Kozlowski LT, Cutting JE. 1977. Recognizing the sex of a walker from a dynamic point-light display. Percept Psychophys 21(6):575–80.

Lestou V, Pollick FE, Kourtzi Z. 2008. Neural substrates for action understanding at different description levels in the human brain. J Cogn Neurosci 20(2):324–41.

Loula F, Prasad S, Harber K, Shiffrar M. 2005. Recognizing people from their movement. J Exp Psychol Hum Percept Perform 31(1):210–20.

Luppino G, Murata A, Govoni P, Matelli M. 1999. Largely segregated parietofrontal connections linking rostral intraparietal cortex (areas AIP and VIP) and the ventral premotor cortex (areas F5 and F4). Exp Brain Res 128(1–2): 181–7.

Manera V, Becchio C, Cavallo A, Sartori L, Castiello U. 2011a. Cooperation or competition? Discriminating between social intentions by observing prehensile movements. Exp Brain Res 211(3–4):547–56.

Manera V, Becchio C, Schouten B, Bara BG, Verfaillie K. 2011b. Communicative interactions improve visual detection of biological motion. PLoS One 6(1):e14594.

Manera V, Del Giudice M, Bara BG, Verfaillie K, Becchio C. 2011c. The second-agent effect: communicative gestures increase the likelihood of perceiving a second agent. PloS One 6(7):e22650.

Manera V, Shouten B, Becchio C, Bara BG, Verfaillie K. 2010. Inferring intentions from biological motion: A stimulus set of point-light communicative interactions. Behav Res Methods 42(1): 168-178.

Manera V, Schouten B, Verfaillie K, Becchio C. 2013. Time will show: real time predictions during interpersonal action perception. PloS One 8(1):e54949.

Marteniuk RG, MacKenzie CL, Jeannerod M, Athenes S, Dugas C. 1987. Constraints on human arm movement trajectories. Can J Psychol 41(3):365-378.

Montpare JM, Zebrowitz-McArthur L. 1988. Impressions of people created by age-related qualities of their gaits. J Pers Soc Psychol 55(4):547–56.

Naish KR, Reader AT, Houston-Price C, Bremner AJ, Holmes NP. 2013. To eat or not to eat? Kinematics and muscle activity of reach-to-grasp movements are influenced by the action goal, but observers do not detect these differences. Exp Brain Res 225(2):261–75.

Neri P, Luu JY, Levi DM. 2006. Meaningful interactions can enhance visual discrimination of human agents. Nat Neurosci 9(9):1186–92.

Oram MW, Perrett DI. 1994. Responses of anterior superior temporal polysensory (STPa) neurons to "biological motion" stimuli. J Cogn Neurosci 6(2):99–116.

Ortigue S, Sinigaglia C, Rizzolatti G, Grafton ST. 2010. Understanding actions of others: the electrodynamics of the left and right hemispheres. A high-density EEG neuroimaging study. PLoS One 5(8):e12160.

Pollick FE, Fidopiastis C, Braden V. 2001. Recognising the style of spatially exaggerated tennis serves. Perception London 30(3):323–38.

Sartori L, Becchio C, Bara BG, Castiello U. 2009a. Does the intention to communicate affect action kinematics? Conscious Cogn 18(3):766–72.

Sartori L, Becchio C, Bulgheroni M, Castiello U. 2009b. Modulation of the action control system by social intention: unexpected social requests override preplanned action. J Exp Psychol Hum Percept Perform 35(5):1490–500.

Sartori L, Becchio C, Castiello U. 2011. Cues to intention: the role of movement information. Cognition 119(2):242–52.

Schuboe A, Maldonado A, Stork S, Beetz M. 2008. Subsequent actions influence motor control parameters of a current grasping action. In: Robot and Human Interactive Communication, RO-MAN 2008. The 17th IEEE International Symposium. p. 389–94.

Searle JR. 1983. Intentionality: an essay in the philosophy of mind. Cambridge, England: Cambridge University Press.

Sebanz N, Shiffrar M. 2009. Detecting deception in a bluffing body: the role of expertise. Psychon Bull Rev 16(1):170–5.

Seltzer B, Pandya DN. 1994. Parietal, temporal, and occipital projections to cortex of the superior temporal sulcus in the rhesus monkey: a retrograde tracer study. J Comp Neurol 343(3):445–63.

Stapel JC, Hunnius S, Bekkering H. 2012. Online prediction of others' actions: the contribution of target object, action, context, and movement kinematics. Psychol Res 76(4):434–45.

Tunik E, Rice NJ, Hamilton A, Grafton ST. 2007. Beyond grasping: representation of action in human anterior intraparietal sulcus. Neuroimage 36(Suppl 2):T77–T86.

Vanrie J, Verfaillie K. 2004. Perception of biological motion: a stimulus set of human point-light actions. Behav Res Meth Ins C 36(4):625–9.

Vingerhoets G, Honoré P, Vandekerckhove E, Nys J, Vandemaele P, Achten E. 2010. Multifocal intraparietal activation during discrimination of action intention in observed tool grasping. Neuroscience 169(3):1158–67.

Zaki J, Ochsner K. 2009. The need for a cognitive neuroscience of naturalistic social cognition. Ann N Y Acad Sci 1167:16–30.