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Action simulation in the human brain: Twelve questions

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A B S T R A C T

Although the idea of action simulation is nowadays popular in cognitive science, neuroscience and robotics, many aspects of the simulative processes remain unclear from empirical, computational, and neural perspectives. In the first part of the article, we provide a critical review and assessment of action simulation theories advanced so far in the wider literature of embodied and motor cognition. We focus our analysis on twelve key questions, and discuss them in the context of human and (occasionally) primate studies. In the second part of the article, we describe an integrative neuro-computational account of action simulation, which links the neural substrate (as revealed in neuroimaging studies of action simulation) to the components of a computational architecture that includes internal modeling, action monitoring and inhibition mechanisms.

1. Introduction

The concept of *action simulation* (AS) is gaining momentum in cognitive science, neuroscience, and robotics, and in particular within the study of grounded, embodied and motor cognition, which we take here as our starting point; see Barsalou (2008) and Jeannerod (2006) for recent reviews of the field.

Although many theories emphasize prediction and simulation in the brain, we mainly focus on the simulation of actions and its neural underpinnings. A key tenet of action simulation theories is that the brain employs the same (or similar) neural resources and dynamic representations for executing, imagining, and perceiving actions. In other words, an agent can use the brain structures normally employed for executing goal-directed actions to simulate these actions within his or her mind, without executing them overtly (Jeannerod, 2001). Action simulations thus have the same content as overtly executed actions, and use the same "central" brain mechanisms for processing, but an inhibitory mechanism blocks their overt execution downstream in the motor hierarchy. This may also be the case for more complex cognitive operations, such as problem solving and thinking, which could re-create and mentally manipulate possible actions.

Theories of action simulation touch both the individual and social domains of cognition. In individual action and cognition, early research on imagery (Crammond, 1997; Jeannerod, 1995) and mental rotation (Wexler, Kosslyn, & Berthoz, 1998; Wohlschlaeger & Wohlschlaeger, 1998) showed that these processes are influenced by concurrent action performance, which indicates that they make use of motor mechanisms, and in particular visuomotor prediction. A famous experiment performed by Shepard and Metzler (1971) shows that the time required for actually rotating objects is comparable to the time required for imagining and mentally rotating the same objects, implicating a common process that recruits sensorimotor representations.

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Seminal work by Jeannerod and collaborators has provided evidence of a similar neural substrate underlying executed, perceived and imagined actions (Decety, 1996; Decety & Grèzes, 1999; Jeannerod & Decety, 1995; see also Miller et al., 2010; Raos, Evangeliou, & Savaki, 2007). Taken together, these studies (along with subsequent work, such as Moulton & Kosslyn, 2009; that explicitly links imagery and emulation) have provided evidence that action simulation and imagery could be neurally realized by the same brain mechanisms that control the execution of overt actions. In doing so, they have contributed to blurring the traditional separation between perceptual, cognitive, and motor domains, and assigned sensorimotor simulation a prominent role in higher cognition.

In the domain of social cognition, many studies have probed the use of simulative mechanisms in perceiving and understanding actions executed by other people; here the idea is that the representations that we use for action planning are also used to guide perceptual processing and action understanding in social domains. A nice demonstration of the reuse of planning mechanisms for action observation comes from a study conducted by Flanagan and Johansson (2003). In this study, subjects showed a similar pattern of eye movements while piling up bricks and when observing another subject piling up bricks; in both conditions they made anticipatory saccades to the locations they expected bricks to be placed.

One line of research directly connects mechanisms of action simulation with the mirror neuron system, which discharges during both when (object-directed, hand and mouth) actions are executed and when they are observed (di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992; Gallese & Goldman, 1998; Gallese, Keysers, & Rizzolatti, 2004); by providing a mapping between observed actions and one's own motor structures, mirror neurons could thus support the prediction and understanding of actions executed by others. Extensions of this theory relate not only to strictly motor processes, but more broadly to *embodied simulations* that support also the contagion of emotional and affective states, as in the case of empathy (Gallese, 2005).

Other studies connect action simulation to a wider neuronal network, a so-called "action observation network", whose span is currently not completely known, but might include brain areas typically associated with the perception of biological motion, such as the posterior Superior Temporal Sulcus (pSTS) (Grafton, 2009; Keysers & Perrett, 2004), or wider networks that compose the so called "social brain" (Frith & Frith, 2010; Kilner, 2011). Moreover, processes of motor simulation have been studied in relation to social actions at large, including joint actions (Sebanz, Bekkering, & Knoblich, 2006). The quite literal mapping of one's own and another's behavior into the same neural processing that is stressed in simulative theories has helped to make the case that many of the social skills that form the basis of our collectivities (such as imitation, empathy, behavioral contagion, theory of mind, and communication) could be based on sensorimotor rather than on higher level, amodal processes (although, as we will see, this issue is fiercely debated).

As our brief review illustrates, there is nowadays a proliferation of theories that shift the role of sensorimotor predictions and simulations from the domain of motor control, where they are well studied (Kawato, 1999; Wolpert, Gharamani, & Jordan, 1995), to the broader domain of cognitive phenomena. It has been claimed in various ways that much of cognition is carried out by sensorimotor simulations rather than by recoded symbols and rule-based processes, and that the processes governing the execution of action are not just the output of cognition, but are part and parcel of it (Barsalou, 2003; Grush, 2004; Jeannerod, 2001; Pezzulo, 2011a). Although these theories describe action simulations in somewhat distinct terms, and emphasize their perceptual, motor and predictive elements to different degrees, they all assign simulative processes a prominent role in cognition, and attribute to cognitive skills an embodied and situated nature.

2. Action simulation (AS): twelve questions, and open challenges

Now that a large body of theoretical and empirical literature (too vast to review in detail in this paper) has accumulated over the past decade, we are well positioned to ask whether simulative processes should rightly be considered as central to cognition, or instead the widespread theorizing about "simulations" in the brain is not tenable on empirical grounds.

To motivate the centrality of simulative processes in cognition, in this Section we aim to provide a conceptual clarification of twelve key elements of action simulation (AS) theories, and to discuss currently open and problematic issues.

2.1. What is the conceptual background of AS theories?

Many, though not all, action simulation theories are part of a larger initiative in cognitive science that sees cognition as essentially embodied and dependent on continuous organism–environment coupling.[1] In this conceptual framework, all cognitive operations are realized using representations and mental processes (e.g., simulations) that are grounded in sensorimotor processes, and are re-creations of experienced perceptual and motor processes (Barsalou, 2008, 2009; Jeannerod, 2001, 2006). Within this framework, perception, cognition and action are tightly interwoven; cognition is better described as a continuous dynamic process integrating perception and action than as a "pipeline" of modular subprocesses (Cisek & Kalaska, 2010; Spivey, 2007). Furthermore, there is no place for the recoding of sensorimotor processes into amodal symbols detached from action and perception. The motor system plays an integral role in supporting cognition, rather than being confined to the execution of planned actions; this is why the phrase "motor cognition" has been introduced (Jeannerod, 2006).

The emphasis on grounding, embodiment, and continuity of processing distinguishes action simulation theories from the traditional information-processing accounts of cognition (e.g., Newell & Simon, 1972). At the same time, although they incorporate relevant aspects of dynamicist

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[1] In cognitive and social psychology there are other theories that use the term "simulation" without an explicit link to an embodied framework; see, e.g., Markman, Klein, and Suhr (2009) for a review.

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approaches, action simulation theories are still representational. Rather than de-emphasizing representation, as most dynamicist and ecological approaches do (e.g., Gibson, 1979; Maturana & Varela, 1980; Port & van Gelder, 1995), action simulation theories assign to internally represented intentions and internal models a mediating role between perception and action (Haggard, 2005), and focus on how internal representations of actions, of events and of other persons are grounded in sensorimotor processes.

A second key characteristic of action simulation theories is that they describe the brain as highly proactive and deeply influenced by top-down (mainly predictive) dynamics rather than responding (only) to external stimuli. For this reason, they can be better described using the *predictive coding framework* (Clark, in press; Friston, 2005; Summerfield et al., 2006) or other theories that emphasize predictions, simulations and emulations (e.g., Bar, 2007; Grush, 2004; Hesslow, 2002; Jeannerod, 2006) than the traditional information-processing accounts that describe cognition in terms of a transformation of stimuli into patterns of action through a sequence of stages.

2.2. How is AS implemented computationally?

The concept of AS is particularly connected with theories that emphasize both the re-enactment of past sensorimotor activity and the prediction of future sensorimotor activity. Re-enactment provides a link to embodied phenomena in cognition; prediction indicates that simulative processes do not merely recall past information stored in memory (Glenberg, 1997).

Two major theories have emphasized prediction in the sensorimotor system. The *ideomotor theory* (Greenwald, 1970; Hoffmann, 1993; Hommel, Musseler, Aschersleben, & Prinz, 2001; James, 1890; Prinz, 1990, 1997) sees action-effect codes as fundamental to perception, action and cognition. *Internal modeling theory* emphasizes the learning of predictive models of body and environmental dynamics for motor control and beyond (Frith, Blakemore, & Wolpert, 2000; Wolpert & Flanagan, 2001; Wolpert et al., 1995, 1998). A related but distinct view is the idea of *predictive coding* (and *active inference*) using generative brain structures (Friston, 2008). In the predictive coding framework, higher hierarchical levels send predictions to lower levels to provide them contextual guidance. In turn, lower levels help refining the predictions by providing prediction error signals. In this framework, predictions are typically relative to the present (rather than to future times), but can be extended to generate future-directed predictions so as to support action simulation and planning (Friston, 2008).

Along similar lines, Grush (2004) has established a link between action simulations (more precisely, emulations[2]) and the control-theoretic notion of Kalman filtering (Kalman, 1960), and provided a comprehensive account of how action simulations might work in practice (Grush, 2004). He proposes that living organisms use internal (forward) models to emulate action–outcome relations, so as to enhance their perceptual processing and predict what will be perceived in the near future. Grush (2004) also describes a second kind of emulator (a Kalman emulator) that, by emulating entire external processes (including the parts that are currently unavailable to perception) rather than action–outcome relations, provides perceptual fill-in and could further enhance perceptual processing by giving access to information that is “hidden” (in other words, not present in the stimuli).

Other authors have proposed similar accounts of action simulation based on the idea of internal modeling, which computationally describe the mechanisms underlying action understanding and the mapping of observed actions into the agent’s own motor repertoire (see, e.g., Demiris & Khadhouri, 2005; Dindo, Zambuto, & Pezzulo, 2011; Jeannerod, 2006; Oztop, Wolpert, & Kawato, 2005; Wolpert, Doya, & Kawato, 2003). It has been further argued that when internal modeling loops are used off-line and decoupled from the sensorimotor loop, they provide a substrate for higher cognitive abilities such as planning, choice, and problem solving (Butz, 2008; Hesslow, 2002, 2011; Hurley, 2008; Ito, 2008; Pacherie, 2008; Pezzulo & Castelfranchi, 2007, 2009). For instance, anticipatory processes can be used to select the action plan that better satisfies an organism’s goals; in this sense, simulations can be seen as roughly equivalent to search processes in those model-based systems that implement goal-directed choice by explicitly calculating the rewards associated with possible courses of action (Niv, Joel, & Dayan, 2006).

Most theories of action simulation can be described in terms of internal modeling mechanisms. For instance, as suggested by Wilson and Knoblich (2005), using internal models for emulating and predicting the consequences of another’s actions can enhance perceptual processing if the actor and the perceiver share a similar motor repertoire. A related but distinct use of internal models is proposed by Wolpert et al. (2003), who describe action understanding in terms of which motor primitives in the perceiver’s own motor repertoire could best explain the perceived actions. As this framework is generative (i.e., it can reconstruct the hidden causes beyond observed stimuli), it is capable of more complex computations. It can make the inverse inference from observed movements to actions and even to the long-term intentions that could have led to them, which has been associated with intention understanding (Baker, Saxe, & Tenenbaum, 2009) and mirror neuron function (Kilner, Friston, & Frith, 2007). The same inverse inference can be done in other kinds of generative architectures, which implement action inference and action recognition by suppressing proprioceptive inputs (Friston, Mattout, & Kilner, 2011).

Other proposals describe the simulation of actions as dependent on (chains of) stimulus–stimulus associations rather than action–effect pairs (Hesslow, 2002). One way to implement this idea computationally is via the Dyna (model-based) architecture of reinforcement learning, which uses past experiences to create simulations and planning (Sutton, 1990). It has been variously proposed that short-term predictions, stored in associative memories, can be endogenously re-enacted and chained to produce long-term expectations (Cotterill, 1998; Hesslow, 2002) and

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[2] See (Grush, 2007) for a discussion of the differences between simulations and emulations.

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"simulate" overt behavior. In these theories, anticipatory capabilities allow the re-enactment of the motor programs that are required for situated interaction.

2.3. What are the main areas of application for AS theories in the individual domain?

It is widely assumed that prediction entails numerous advantages in the perception, selection and control of action (Bubic, von Cramon, & Schubotz, 2010; Butz & Pezzulo, 2008). From a computational perspective, systems provided with an internal (forward) model that makes them able to predict the sensory consequences of their actions can overcome delays in feedback and neural processing and are typically better at perceptual processing when their input is corrupted by noise (Desmurget & Grafton, 2000; Shadmehr, Smith, & Krakauer, 2010). By combining sensory stimuli with internal prediction it is possible to compensate for feedback delays, to better estimate the state of the body and the external world, and to better select action based on such estimate (or even without necessarily waiting for sensory inputs). Action simulation mechanisms could reuse predictive abilities, allowing the generation and selection of potential action plans without taking the risk of actual exploration. For instance, Tolman (1948) hypothesized that rats could solve planning and navigation problems using "vicarious trial and error", that is, by mentally simulating possible paths and then comparing their predicted outcomes.

The use of internal predictive and simulative loops has been further related to other abilities, such as the central attenuation or cancellation of self-produced stimuli (reafferences), which in turn permits a focus on external stimuli (exafferences) that have higher relevance for the organism (Blakemore, Wolpert, & Frith, 1998; Crapse & Sommer, 2008; von Holst & Mittelstaedt, 1950; Voss, Ingram, Haggard, & Wolpert, 2005). One intriguing proposal is that this ability is related to the self-other distinction, and dysfunctions in it could be relevant for explaining schizophrenia and other cognitive impairments (Frith et al., 2000).

Another benefit of action simulation might lie in the process of motor preparation and the specification of possible actions to be performed. The idea of automatic, unconscious simulative processes specifying possible actions is put forward by Gallese (2000), who argues that observing objects implies an automatic enactment of the motor programs most appropriate for interacting with them, or a covert simulation of a potential action. In a similar vein, it has been proposed that simulations might help in recognizing currently available affordances and selecting among them (Moller & Schenck, 2008; Pezzulo & Castelfranchi, 2009). The substrate for this process might be canonical neurons (Rizzolatti et al., 1988), a class of visuomotor neurons that are activated when a monkey performs certain actions with an object, and when the object is in its visual field, suggesting that the animal anticipates potential interactions and prepares its body for the object-oriented action. Studies of motor preparation and mental rehearsal of possible action plans suggest that multiple affordances could be encoded in parallel and compete for selection in a "neural race" mechanism (Cisek & Kalaska, 2004; Cisek, 2007). This mechanism could also be proactive and allow preparing in advance the action plans that are more likely to be useful in the future (Pezzulo & Ognibene, 2012).

2.4. What are the main areas of application for AS theories in the social domain?

In the social domain, action simulation was initially studied in relation to action understanding, especially with reference to the mirror neuron system in monkeys and humans (Iacoboni, 2003; Rizzolatti & Craighero, 2004). Alternatively, it has been proposed that mirror neurons are used for emulating observed movements and predicting their consequences, rather than for goal understanding (Prinz, 2006; Springer, de C Hamilton, & Cross, 2012; Wilson & Knoblich, 2005), and are part of a much wider "action observation network". Since then, many studies have studied action simulations in social scenarios of various kinds (observational, collaborative, or competitive), linking them to the prediction and understanding of others' actions, and the selection of complementary actions.

From an evolutionary viewpoint, one may ask what the adaptive advantages might be of simulating actions performed by others, and of mapping their actions into one's own motor repertoire. Considering that observed and executed actions interfere with each other, and that automatic motor contagion leads to automatic imitative behavior (Dijksterhuis & Bargh, 2001), one could draw the paradoxical consequence simulation would actually hinder social interactions, which often require co-actors to perform complementary rather than identical actions. Attempts to solve this problem appeal to generative architectures in which motor contagion (via mirroring) serves to set the prior probabilities of observed actions and to predict them more easily, serving as just the first step in an iterative process of cooperation and selection of complementary actions (Blakemore & Frith, 2005; Pezzulo, 2011b).

As a consequence, the adaptive advantage of action simulation might lie in facilitating action selection (especially in cooperative domains and joint action), not just in guiding action understanding and imitation (see Chersi, 2011; Pezzulo & Dindo, 2011 for related computational ideas). Partial support for this view comes from studies that show (increased) activation of the mirror neuron system in cooperative domains and during the perception of co-actors executing complementary actions (Newman-Norlund, van Schie, van Zuijlen, & Bekkering, 2007, 2008), see also Section 2.9.1. Support also comes from studies showing that the mirror system is sensitive to the placement of to-be-used objects around or outside the person (Caggiano, Fogassi, Rizzolatti, Thier, & Casile, 2009).

2.5. Is AS a (fundamentally) motor process?

Action simulation theories are not restricted to purely motor domains, as the concept of "action" is much wider than that of body movement. Action simulations can involve characteristics of actions that are not purely motoric, including their goals, sensory aspects, semantic knowledge, and various contextual factors; indeed, all these factors can modulate action simulations (see section

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2.9). However, the idea that the motor system plays a key role in action simulation and related tasks is supported by an increasing number of studies. Evidence from neuroimaging, behavioral and neurophysiological studies reveals that motor control systems in the brain are deeply active in a surprising variety of tasks, both individual and social, that were long supposed to exemplify "central" cognitive processing, including planning, hearing music, understanding language, imitation, and understanding others' intentions (Fadiga, Fogassi, Gallese, & Rizzolatti, 2000; Fogassi et al., 2005; Rizzolatti & Craighero, 2004).

As a consequence, the status of the motor system is being reconsidered. Once a peripheral executor of central commands, it is increasingly being regarded as a proper part of cognition (Rosenbaum, 2005). Various proposals have been advanced for an action-based view of cognition with prediction and action simulation at its core (Grafton, 2009; Jeannerod, 2006). A rationale for this idea is that predictions that the motor system normally uses for goal-directed motor control could be reused (on-line and off-line) in other domains, participating in perceptual, cognitive, and social functioning more generally. To probe these theories, many researchers have tried to assess experimentally whether and how the motor system participates in predicting and interpreting observed actions.

A theoretical background to many of the studies that we will mention below is that perception and action share a common code (Prinz, 1990, 1997), leading to ideomotor compatibility effects between perceptual stimuli and motor actions when they share features. Ideomotor compatibility applies bidirectionally. Perception induces modulations of the motor system (Rizzolatti & Craighero, 2004); in turn, action induces modulations of perception (Schuetz-Bosbach & Prinz, 2007).

TMS (transcranial magnetic stimulation) studies have revealed motor facilitation at the muscle level while participants observe congruent actions (arm movements or grasps) executed by an experimenter (Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995). Related research records brain areas active when such actions as pointing or writing are being observed or executed, which reveals a largely shared substrate (Chaminade, Meary, Orliaguet, & Decety, 2001). A widely used paradigm relies on interference between concurrently executed and perceived actions. Numerous studies have manipulated the congruency of perceived and executed tapping movements (Brass, Bekkering, & Prinz, 2001), and of perceived and executed arm movements (Christensen, Ilg, & Giese, 2011; Kilner, Paulignan, & Blakemore, 2003). In all these studies, interference has been found only when perceived and executed actions are incongruent (see also the numerous studies conducted by Prinz and collaborators: Grosjean, Zwickel, & Prinz, 2009; Massen & Prinz, 2007; Schuboe, Prinz, & Aschersleben, 2004; Springer et al., 2011).

In the arena of action-to-perception effects, Witt and Proffit (2008) review evidence indicating that manipulating motor resources and skills (e.g., weights carried by participants) influences perceptual processing (e.g., how subject evaluate distances). Further, performing an action may facilitate (Craighero, Bello, Fadiga, & Rizzolatti, 2002; Wohlschlaeger, 2001) but may also impair (Hamilton, Wolpert, & Frith, 2004; Muesseler & Hommel, 1997) perception of another person's actions.

Other studies have revealed that action observation shares specific properties of motor execution, such as the two-thirds power law relating velocity of a movement and curvature of its trajectory (Kandel, Orliaguet, & Bo, 2000) or Fitts' law (Grosjean, Shiffrar, & Knoblich, 2007). What is relevant in these studies is that the same constraints that apply to overt action execution also apply during movement simulation and perception, suggesting that the same processes might be in play as motor codes are shaped by the structure of the movements to be performed (Graziano & Aflalo, 2007).

Although we have emphasized the importance of motor involvement during action simulations, it is worth noting that not all mental simulations involve the motor system. Kosslyn, Thompson, Wraga, and Alpert (2001) used fMRI to investigate the neural correlates of mental rotation tasks, and found that while motor areas are involved when subjects are asked to imagine rotating objects themselves, but not when they are asked to imagine an electric engine rotating the objects. Moreover, although it has been argued that problem solving and mechanical reasoning could be implemented using mental simulations (Hegarty, 2004), the extent to which they involve motor processes remains an open issue for future research.

2.6. Is motor involvement in AS specific?

Although demonstrations of motor involvement during perception are remarkable per se, some studies leave open the specific nature of the involvement. First, is motor involvement specific (e.g., for the same effectors as those employed in the action when executed) or does it recruit the motor system more broadly? Second, is the motor system involvement at the level of fine-grained movements or at a more abstract level of action specification? Numerous theories describe the motor system as hierarchically organized, with higher levels encoding abstract goal representations and levels descending in the hierarchy specifying kinematic and dynamic details (Hamilton & Grafton, 2007). In theory, then, actions can be specified and also simulated at different levels. Still, it is unclear if action simulation operates preferentially at one or more levels, and if this choice is fixed or depends adaptively on the task (e.g., if the task requires more fine-grained predictions, lower level representations can be used).

Studies mentioned earlier (e.g., Fadiga et al., 1995) already reveal that motor involvement during action perception is specific to the effector that is used for executing the observed actions. Further evidence that representations lower in the motor hierarchy could be involved in perception comes from a study conducted by D'Ausilio et al. (2009). D'Ausilio et al. asked participants to discriminate heard labial speech sounds (/p/and/b/) and dentals (/t/and/d/), whose production involves the lips and the tongue, respectively. Meanwhile, TMS interfered with neural populations controlling their lips and tongue. D'Ausilio et al. found that the interference was selective: inhibiting motor areas controlling the lips impaired performance in discriminating labials, whereas inhibiting motor areas controlling the tongue impaired

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discrimination of dentals. This study reveals a somatotopic organization of speech processing areas, their participation in speech perception, and (most important for us) specificity in their involvement.

Another way to test for specificity of motor involvement compares subjects with different kinds of motor expertise, such as athletes or expert music players, with non-experts in these domains. It becomes possible to determine whether the augmentation of specific motor skills affects the recognition and prediction of skill-related actions. These studies reveal that motor involvement is specific for the observer's skills; what's more, there is an advantage for motor skills over visual skills. For instance, female dancers resonated more with other female dancers (with whom they shared the same motor repertoire) than with male dancers, although they were accustomed to watch males as well as females dancing (Calvo-Merino, Glaser, Grezes, Passingham, & Haggard, 2005, 2006). Similarly, Aglioti, Cesari, Romani, and Urgesi (2008) found that "motor experts" (expert basketball players, in this case) are better at predicting ball movements than "visual but non-motor experts" (basketball coaches). Furthermore, the same study shows increased activity in the cortico-spinal representation of the hand of motor experts (but not other subjects) at the precise time when hand movements are the better cues for the prediction.

Other researchers have studied the effects of expertise by using individuals as "experts" at their own movements. In a series of studies, subjects were found to be better in recognizing self-generated actions rather than actions performed by others (Knoblich & Flach, 2001; Repp & Knoblich, 2004); a plausible interpretation is that this happens because the internal models employed in the recognition process are better tuned to the statistics of one's own actions, again supporting the idea that the motor skills are reused for perceptual tasks.

2.7. *Is AS time-locked?*

As discussed previously, simulations could be performed using mechanisms at quite low levels of the intention-to-action hierarchy (as described by Hamilton & Grafton, 2007), in particular those implied in the online control of action. An implication of this view, which has been studied experimentally, is that those simulations should have the same temporal profile as actual actions. The same issue comes up in relation to a dispute about the basic function of mirror neurons: are they for understanding actions (which is not time-locked) or for predicting them in real time (which is)?

Graf et al. (2007) showed participants videos of biological actions (rendered as point-light action sequences), with occlusions after varying intervals, followed by static test postures. Subjects were asked to judge whether the static test posture was a continuation of the observed video. Subjects were better at this task when the static test postures were presented at the same time that the videos would have shown them, suggesting that a real-time simulation process is involved.

It is worth noting that demonstrations of action prediction whose time profile is compatible with the execution of actual actions do not rule out the possibility of other mechanisms that are not time-locked. In some individual domains, such simulations could support planning systems that do not need to take care of the details of action (e.g., deciding what city to visit), and which can be applied at execution time (Hommel et al., 2001), as well as the prediction of categorical perceptual sequences (Bubic, von Cramon, & Schubotz, 2009). In social domains, those simulations could go beyond immediate resonance with another's mental processes, instantiating more sophisticated forms of sociality, cooperation, and competition (Frith & Frith, 2006).

2.8. *Does AS apply just to movements that one can perform, just to biological motion, or also to nonbiological stimuli?*

Central to action simulation theories is the idea of a simulation network that uses the motor system (for which agents have reliable predictive models) as a generative model for observed actions, so as to facilitate their perceptual processing and understanding. Could the same system be implicated in the prediction of actions that are not part of the agent's motor repertoire (e.g., for a non-athlete, simulating the complex movements of an athlete)? Could it even be implicated in the prediction of non-biological motion or of other external events (e.g., the movements of objects or even the unfolding of melodies)? At present, this is a controversial issue.

Some studies have demonstrated that human ventral premotor cortex (i.e., the region where visuomotor neurons were first described in monkeys, by di Pellegrino et al., 1992) is causally involved in discriminating between observed actions (Urgesi, Candidi, Ionta, & Aglioti, 2007 However, ventral premotor cortex underpins the perceptual function only for actions that do not violate the biological constraints of the different joints in the body (Candidi, Urgesi, Ionta, & Aglioti, 2008). Activity in this area is thought to underlie anticipatory simulation of the motor component of observed actions (Avenanti, Bolognini, Maravita, & Aglioti, 2007; Urgesi, Moro, Candidi, & Aglioti, 2006, 2010).

Evidence has been accumulating that the processing of external events is also anticipatory (Bar, 2009; Zacks, Speer, Swallow, Braver, & Reynolds, 2007). Still, the motor system cannot actually generate these events, so it may not actually be employed in such tasks. One hypothesis is that the motor system is only used to simulate actions that are part of the repertoire of the perceiver, while other actions and events are predicted using alternative mechanisms such as visual extrapolation (Nijhawan, 2008). However, an fMRI study reveals that the same areas of ventral premotor involved in anticipating observed actions is also active during observation of sequences of geometrical figures, suggesting that premotor cortex could provide the basic functionality for representing and predicting sequences of biological and nonbiological events, with different additional areas complementing this common functionality (Schubotz & von Cramon, 2004). Based on this result and others, Schubotz (2007) has suggested that the motor system could be involved in predicting external events at large. According to this theory, the lateral premotor cortex establishes internal models of external, perceived events (e.g., a melody, ocean waves rolling) that can be used to

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predict and simulate them. Like the forward models described above, they employ sensorimotor representations, but these are relative to externally perceived events and lack the interoceptive information normally associated with executed actions. Overall, this theory suggests that the ability to reproduce a movement is not a prerequisite to motor involvement, but influences it. Consistent with this idea, actions that can be (re)produced seem to be easier to discriminate, predict, and map into one's own motor repertoire (Casile & Giese, 2006). At the same time, other external events can also be predicted with the aid of the motor system. For example, the motor system could reuse generative models of biological motion to predict non-biological stimuli having similar characteristics (Grosjean et al., 2009). Furthermore, the motor system could encode invariants that afford (sufficiently) good predictions, such as for instance the sensory consequences resulting from an observed action (even if it cannot be executed) or the relevant parameters that regulate its unfolding in time. In some cases, this could be more efficient than learning sequences of events or percepts, which are necessary for visual extrapolation. From a computational perspective, it is not surprising that the brain adopts all the available means (including forward modeling and visual extrapolations) for generating predictions, and selects among them depending on their success; this implies that when the motor system is a reliable source of predictions, it should be plausibly recruited. Consistent with this idea, Neal and Kilner (2010) have shown that the brain can adaptively consider the accuracy of the motor system while calculating the uncertainty of the prediction.

2.9. Is AS encapsulated, or permeable by other motor and cognitive phenomena?

One way to study the impact of other cognitive processes on motor simulation has been to measure an index of AS (some kind of behavior or brain activity) and test whether this index varies with perceptuo-motor or cognitive demands. Some studies have focused on changes in the AS contributions to the perception and execution under varying motor-related and attentional task requirements. Others have studied the impact of socio-cultural and higher-level individual psychological factors on AS. Below we shortly review three lines of research that collectively point toward the idea that action simulation flexibly adapts to constraints and tasks, rather than behaving like an encapsulated process.

2.9.1. Influences of task requirements (individual, joint, collaborative, competitive)

Evidence that movement execution may be impaired by concurrent observation of incongruent movements (Kilner et al., 2003) and that, conversely, movement training may improve perception of biological movement (Casile & Giese, 2006) indicates that action execution and perception are functionally linked and shape each other bidirectionally (Wilson & Knoblich, 2005).

Crucially, however, the compatibility effects found when executing individual actions (Prinz, 1990) fade away when individuals are acting jointly and need to perform complementary actions to achieve a shared goal (van Schie, van Waterschoot, & Bekkering, 2008). Such effects point to the flexible nature of AS, which is thought to be critical not only for individual action-related processes, but also in ecological, interactive contexts. Indeed, if two individuals must synchronously perform two complementary actions to achieve a common goal, the brain needs to turn the perception of the other person's movement into information that will help in executing one's own action (Sebanz et al., 2006).

Synchronous complementary movements are thought to be coordinated through shared representations and through predictive and monitoring mechanisms, among which some “coordination smoothers” play essential roles for sensorimotor coordination (Vesper, Butterfill, Knoblich, & Sebanz, 2010). The notion that AS may be time-locked (see Section 2.7 above) makes joint actions, especially complementary joint actions (when two co-actors need to perform complementary actions to achieve a shared goal), useful for studying both predictive and monitoring features of AS.

Studies have shown that carrying out complementary joint actions activate the same fronto-parietal network that is associated with individual AS – indeed, to a greater extent. Furthermore, the induced activation is not confined to the AS network but spreads to temporo-parietal regions such as the posterior superior temporal sulcus and temporal–parietal junction (Kokal, Gazzola, & Keysers, 2009; Newman-Norlund, Bosga, Meulenbroek, & Bekkering, 2008). These latter regions are thought to be crucial for thinking about the beliefs of others (Saxe & Kanwisher, 2003) as well as for determining agency in situations in which one must distinguish one's own actions from those of another agent (Chaminade & Decety, 2002).

By studying the behavior and the neural correlates of joint actions it is therefore possible to dissociate the role of AS in predicting and monitoring imitative and non-imitative behavior. Joint actions are a good way of testing the role played by bimodal visuomotor frontal and parietal neurons (di Pellegrino et al., 1992; Fogassi et al., 2005), which are thought to be essential for imitative AS. Single-cell recording studies have described strictly congruent, broadly congruent and non-congruent neurons in monkeys' premotor cortex, showing different degrees of representation of action movement and goals (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996). These may be particularly important in complementary joint actions where, instead of imitating their interactive partner, individuals must execute incongruent movements in order to achieve the goal.

Another critical factor modulating action simulations is attention (Tipper, 2010). Classical behavioral compatibility effects during action observation are found only when the observer's attention is directed to the body part performing the action (Bach, Peatfield, & Tipper, 2007). Although action perception induces increased neural activity in the sensorimotor system even when the perceived action is task-irrelevant (Schuch, Bayliss, Klein, & Tipper, 2010), neural responses in brain regions associated with AS (e.g., the inferior frontal gyrus) are reduced when action observation competes with another attention-demanding task (Chong, Williams, Cunnington, & Mattingley, 2008). Attention

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thus appears to guide AS by either enhancing or suppressing the processing of the action.

Different forms of AS may take place depending on the format of the action-related triggering stimulus: direct action observation, linguistic reference to action, or derivative knowledge about actions inferred from the individual's identity. Based on a growing body of experimental evidence, it has been proposed that linguistic representation of actions triggers AS (Buccino et al., 2005; Pulvermuller, 2005), even though the specific role played by the sensorimotor system in language comprehension is fiercely debated (Mahon & Caramazza, 2008).

Even higher-order action representations are mapped onto the agent's sensorimotor system through AS. Observing famous athletes known for their excellent motor skills, for example, induces contrast effects during a recognition task when individuals respond with the same limb associated with the athlete's sport (hand for tennis, foot for soccer; see Bach & Tipper, 2006). This form of derivative AS is reflected in a reduction of cortico-spinal excitability: direct action observation generally induces specific facilitatory action simulation at the cortico-spinal level, but derived action simulation may trigger inhibitory processes instead (Candidi, Vicario, Abreu, & Aglioti, 2010).

2.9.2. *Influences of social factors (affinity with the performer agent)*

AS also provides the opportunity to test hypotheses concerning the effects of high-level psychological and sociocultural factors on the representation of other people's actions. Although individual movement performance may be designed to be social even before birth – as demonstrated by the kinematics of intra-pair contact for twin fetuses (Castiello et al., 2010) –communicative action performance and understanding during postnatal development are greatly shaped by sociocultural variables. AS may be refined by higher-order psychological, emotional cultural and social factors (Molnar-Szakacs, Wu, Robles, & Iacoboni, 2007).

Evidence is accumulating that other simulative processes are shaped by personality and socio-cultural biases. For example, somatomotor resonance while observing a painful stimulation being delivered to the hand of a model is reflected in a selective reduction of motor reactivity of the same muscles in the observer (somatomotor empathic contagion), according to the personality of the observer, specifically to his ability to adopt the model's perspective (Avenanti, Minio-Paluello, Bufalari, & Aglioti, 2009; Minio-Paluello, Baron-Cohen, Avenanti, Walsh, & Aglioti, 2009). This sensorimotor contagion is absent when observing a model from a racial out-group and correlates with implicit measures of the observer's racial bias (Avenanti, Sirigu, & Aglioti, 2010). But the physiological somatomotor contagion reappears when observing an unfamiliar out-group individual toward whom the observer has no negative bias.

A seminal neurophysiological study reported reduced AS during the observation of communicative gestures from out-group members, showing for the first time that simulative motor mapping may be shaped by social and cultural membership (Molnar-Szakacs et al., 2007). The authors proposed that unconscious motor resonance mechanisms are modulated by interacting biological and cultural factors.

AS may also in turn enhance interpersonal connectedness and perceived psychological similarity between partners. For example, observing an action triggers AS which in turn induces the attribution of personality traits. For instance, observers tend to attribute sporty or academic psychological traits to individuals whom they have seen performing athletic or typewriting actions respectively (Bach & Tipper, 2006).

Furthermore, imitative actions facilitate group living and promote affiliative behavior, possibly because they trigger simulations of others' actions. For example, monkeys prefer to interact with individuals who imitate their behavior (Paukner, Suomi, Visalberghi, & Ferrari, 2009). AS and imitation may at some level promote prosocial behavior and facilitate affiliation. It is not just that the interindividual sharing of representations may change the ability to simulate the observed action, but that overtly imitating other's behavior may induce individuals to perceive each other as more familiar.

A recent study has demonstrated that frontal brain regions are more strongly activated in human beings when a person has to anticipate the action of another individual with whom he/she has already interacted than when anticipating the same action by a person he/she did not interact with (Kourtis, Sebanz, & Knoblich, 2010). Thus, previous social interactions shape and strengthen the ability to predictively simulate the behavior of other persons.

The link between movement observation, AS and interpersonal bonds is further supported by the literature on nonconscious mimicry, which has demonstrated links between affiliation and the tendency to mimic other people's actions and mannerisms (Lakin & Chartrand, 2003). The relation between motor interaction and perceived interpersonal bond has also been studied in the domain of joint actions (Hommel, Colzato, & van den Wildenberg, 2009; Iani, Anelli, Nicoletti, Arcuri, & Rubichi, 2011). The specific role played by cooperation and competition in AS and shared representations, as well as the specific role played by the interpersonal relationship, still need to be clarified; see also Ruys and Aarts (2010) on competition and shared representations.

Based on this evidence a recent framework has been put forward which reverses the functional relationship between social cognition and the motor processes involved in joint action, possibly also in AS mechanisms. Marsh, Richardson, and Schmidt (2009) suggest that the motor ability to cope with other individuals (e.g., through AS) provided the neurobiological basis for social cognition to emerge.

2.9.3. *Influences of action semantics and action goals: AS is modulated by action words and AS changes the perception of goal-object*

A number of behavioral, neuroimaging, neurophysiological studies as well as studies on brain damaged patients converge in showing that AS is triggered by different formats of action-related stimuli (see above), among which particular attention has been given to action words (Jirak,

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Menz, Buccino, Borghi, & Binkofski, 2010). This is particularly relevant as humans may have developed language in order to unchain their communication from time contingencies, which in turn may have resulted in the bootstrapping of other cognitive functions. Strong theories of embodied language representation place AS at the core of language comprehension (Glenberg & Kaschak, 2002).

It has to be noted, however, that AS triggered by action verbs partially results in different behavioral patterns and neural responses from AS that has been induced by direct action observation (see, for example, Candidi, Leone-Fernandez, Barber, Carreiras, & Aglioti, 2010; Liuzza, Candidi, & Aglioti, 2011). These differences may reflect the complex representation of individuals' motor repertoire in the sensorimotor cortex (Graziano & Aflalo, 2007), which is more than a rigid somatotopic representation of the body (Fernandino & Iacoboni, 2010).

Further, these different forms of AS interact. AS triggered in order to solve a perceptual action-related task may interact with the semantics conveyed by action verbs. Individuals' ability to solve an occluded action prediction task (Graf et al., 2007) was greatly impaired when they were primed with verbs that implied motion. Behavioral performance showed the expected gradient of discrimination impairment depending on the temporal mismatch between occlusion and postural-change time; crucially, it also showed that AS triggered by the motion implied by the priming verbs biased performance. Verbs that implied fast or moderate motion induced more errors than verbs implying slow motion and non action-related words (Springer & Prinz, 2010).

Other studies have tried to isolate the impact of an action's goal from the impact of action kinematics on AS. These two features of actions seem to be coded by partially different neural substrates and may therefore play different roles in AS (Bouquet, Shipley, Capa, & Marshall, 2011). The distinction is crucial to defining transitive and intransitive actions for which mirroring phenomena are consistent in humans and absent in monkeys (Blakemore & Frith, 2005; Gallese et al., 1996).

As mentioned above, variance in movement execution may be increased by observing incongruent movements being executed (Kilner et al., 2003), which is thought to be an index of interference between AS and action performance. Bouquet et al. (2011) have demonstrated that observing the very same movement (i.e., moving the arm up and down) may impair action execution even further if the movement is transformed into a form of transitive action. Including a start and an end target (i.e., moving the arm up and down between two target dots) increased the amount of interference with the concurrent execution of an incongruent movement, showing that goal-directed action may be more strongly rooted in sensorimotor simulation and may be more effective in triggering AS (Bouquet et al., 2011).

Action goals may not merely improve AS, they may also change the perception of end goal objects. The effect of the goal on AS and the resulting change in the perception of the goal object of the action may be regarded as a specific instantiation of "emulator theories" (Wilson & Knoblich, 2005). It has been also shown that visual processing of objects is biased (there is an accentuation effect) when these are the goal objects for an action (Witt & Proffitt, 2005). Witt and Proffitt asked softball players who had just finished playing to choose from among eight circles depicted on a poster the one they thought best matched the size of a softball. They found that size of circle chosen was positively correlated with the players' batting average (i.e., players with higher ratios of hits to at-bats tended to select larger circles). Crucially, this effect is abolished when the same object, although the target of an action, does not represent the end goal of a sequence of movement (Caal-Bruland & van der Kamp, 2009).

Finally, it is plausible that reward information associated with actions and goals modulates action simulation, as it does for various kinds of perceptual and decision processes (Platt & Glimcher, 1999; Serences, 2008); however, studying this topic deserves further investigations.

2.10. *What characteristics of events are typically simulated?*

Not only action simulation mechanisms are modulated by tasks demands, but they also afford flexibility as to which aspects of external events should be simulated. For example, depending on the task at hand, it could be more useful to predict the sensory consequences of actions, their timing, or the rewards they will produce.

Theories of motor control tend to link action simulation to the prediction of *sensory and proprioceptive information* (Miall & Wolpert, 1996), using for instance Kalman filters (Grush, 2004) or Smith predictors (Miall, Weir, Wolpert, & Stein, 1993). However, there is evidence that more *abstract perceptual characteristics* of actions and events can also be predicted (Bubic et al., 2010). In the social domain, simulation can be applied at different levels of action representation, ranging from immediate sensory consequences to distal intentions, although it is still debated if these simulations are realized by the same brain mechanisms (see section 2.4).

Numerous studies have focused on predicting the *timing* of external events (Nobre, Correa, & Coull, 2007). Simulating timing is useful in social and joint-action domains. A kinematic study reveals that two subjects instructed to jump different distances but to land at the same time can simulate the other person's landing time successfully and use this information to carry out the task, even without seeing the other person jumping (Vesper, van der Wel, Knoblich, & Sebanz, 2013).

In decision-making tasks, action simulations can be used to predict reward and utility information. In neuroscience, the substrate for reward prediction has been widely investigated, and numerous studies suggest that the dopamine system could encode reward prediction errors as is done in Temporal Difference (TD) methods of reinforcement learning (Schultz, Dayan, & Montague, 1997). However, it is plausible that this mechanism does not depend on simulations but uses "cached" values of actions instead; this mechanism, which is fast but inflexible, has been linked to *habitual* forms of choice. To implement the more flexible *goal-directed* forms of choice, the brain could use a second mechanism based on simulations (Balleine & Dickinson, 1998; Niv et al., 2006). This mechanism could allow predicting the outcome of multiple courses of action,

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and them evaluating and choosing among them depending on their expected utility and costs (Solway & Botvinick, 2012; Pezzulo & Rigoli, 2011). The impairment of this mechanism could prevent adaptive decision-making (Damasio, 1994).

Furthermore, numerous studies have suggested neural mechanisms that allow *anticipation of goals* of others. Some (particularly those involving mirror neurons) have, as we have noted, been associated with action simulations (Gallese, 2005). Other studies, particularly with children, have been also related to non-simulative mechanisms of teleological reasoning (Csibra & Gergely, 2007; see also Bekkering, Wohlschlager, & Gattis, 2000; Meltzoff & Decety, 2003). Although the links between motor simulation and goal understanding remain a matter of debate, it is worth noting that some studies (Gredebaeck & Melinder, 2010; Sommerville & Woodward, 2005) have reported that the ability to form motor plans (e.g., for solving puzzles) and to understand other people's goals in the same domain develop at the same time; thus, further studies are necessary to assess whether the plans are used for action simulation (as was reported for action perception by Flanagan & Johansson, 2003).

2.11. Is AS confined to the sensorimotor domain or does it also play a role in higher cognition?

In recent years, many researchers have proposed that neural circuits for prediction and internal modeling are reused to implement cognitive operations, such as reasoning and cognitive control (Cotterill, 1998; Hesslow, 2002, 2011; Ito, 2008; Pezzulo, 2011a), social interaction (Decety & Grèzes, 2006; Wolpert et al., 2003), categorization (Barsalou, 1999), tool use (Imamizu & Kawato, 2009, 2012), and language processing (Glenberg & Gallese, 2011). In parallel, the idea of a *proactive brain* that continuously generates and evaluates internal simulations of future events is challenging the traditional view of a passive brain that transforms sensory stimulations into behavioral outputs (Bar, 2007).

Although these proposals are primarily theoretical at the present time, they are all contributing to an emerging view of cognitive processing whose ambition is explaining higher cognition in continuity with the processes that govern sensorimotor action and prediction. In this view, cognition and thought as an "internalized" form of action, supported by the same kind of predictive and simulative mechanisms as those permitting the execution (and observation) of overt goal-directed actions. A comprehensive framework has been developed over the years by Jeannerod (2001, 2006), who proposed that action simulation is the key ingredient of (motor) cognition, linking it to planning, motor imagery, imitation, and social cooperation. A large body of evidence, reviewed extensively by Jeannerod (2006), supports this framework. Grush (2004) proposed a related framework that links emulation mechanisms to representation and higher cognition (see also Clark & Grush, 1999; for a discussion of the importance of this theory for cognitive robotics). Furthermore, it has been proposed that cognitive skills could be grounded in sensorimotor anticipation, and could ultimately be characterized as internalized sensorimotor actions, retaining vestigial aspects of their original motor functions. In this view, prediction and action simulations mechanisms originally developed for the on-line execution of action were successively exapted during evolution to support increasingly more complex forms of off-line cognition and thought, thus provide a link between sensorimotor and cognitive processes (Pezzulo & Castelfranchi, 2007, 2009).

Still, to allow a reuse of predictive abilities across cognitive abilities at large, the brain must bridge the gap between sensorimotor skills and the forms of representation that, according to most cognitive theories, allow flexible reasoning, problem solving, and deliberation. One hypothesis is that simulations could give access to tacit knowledge incorporated in the internal models used for motor control, and allows reusing it for other purposes, as in linguistic, memory and reasoning tasks (Pezzulo, 2011a). Supporting this theory is evidence positively correlating motor expertise and action simulation abilities with higher cognitive skills. For instance, a recent study of expert climbers engaged in a memory task suggests that they might employ simulation strategies to remind themselves of a sequence of holds on a climbing route, but only if they are able to climb it (Pezzulo, Barca, Bocconi, & Borghi, 2010).

Another intriguing suggestion is that the brain networks implementing prospection and "mentalizing" (i.e., the ability to imagine oneself in the future) overlap to a significant extent (Mitchell, 2009); both require the reuse of episodic memories to run imaginary scenarios, whether centered on the self or on another actor. Along similar lines, it has been proposed that (beyond the simpler simulation mechanisms) human beings can project their episodic memories into the future, so as to form mental simulations imbued with episodic information, much as they can self-project into the past; the same self-projection mechanisms could also underlie the ability to assume another person's perspective (Buckner & Carroll, 2007; Suddendorf & Corballis, 2007). This line of research links to the foundational idea in embodied theories of cognition that memory supports future thinking instead of reconstructing the past (Glenberg, 1997).

In sum, several lines of research within grounded, embodied and motor theories of cognition point toward a key role of action simulation and related mechanisms in higher cognition; but despite such initial attempts, further studies are necessary to assess how, and how much, sensorimotor and simulative processes are reused for cognitive tasks.

2.12. What can neuropsychology tell about AS?

In addition to behavioral studies and research on brain substrates for action simulation, more can be learned about the links between internally simulated and overtly executed actions by looking at populations with specific impairments. Schwoebel, Boronat, and Coslett (2002) studied a patient with bilateral parietal lesions who was unable to refrain from executing imagined hand movements, and was unaware of these movements. Such observations suggest that the representation of actions

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formed during simulations would be sufficient to elicit overt action if the inhibition mechanisms are dysfunctional. A related piece of evidence comes from the studies of Lhermitte (1983), who first described utilization behavior in frontal lobe patients; i.e., the failure to inhibit prepotent action processes (such as grasping) that are elicited by seen objects. In this case, the simulative process of motor preparation could elicit overt action in the absence of functioning inhibitory mechanisms.

Compelling evidence has come from studies addressing motor imagery strategies in impaired populations. When patients with locked-in syndrome (i.e., with total damage to descending motor pathways) were asked to decide whether a hand stimulus represents a left hand or a right hand, their performance was affected by the spatial orientation of the hand stimulus but (differently from normal subjects, see Costantini et al., 2005) not by biomechanical constraints (e.g., awkward rotations such as 270° for the left hand), suggesting that they can access an internal representation of the hand but could not activate a motor rotation strategy to judge hand laterality (Conson, Pistoia, Sar, Grossi, & Trojano, 2010). Similar dissociations have been reported in stroke patients with selective damage to the left or right hemisphere (Daprati, Nico, Duval, & Lacquaniti, 2010). A relation between compromised motor planning and impaired motor imagery has been reported in young adults with cerebral palsy (Craj et al., 2010).

A causal link between the production and recognition of actions has been reported by Pazzaglia, Pizzamiglio, Pes, and Aglioti (2008), who found that patients with limb and/or buccofacial apraxia were selectively unable to recognize the sound of actions they were not able to produce (i.e., the sound of actions performed with hand or mouth). This result is consistent with the idea that the internal models used for action control are also used to emulate the same actions during perceptual processing (Grush, 2004; Wilson & Knoblich, 2005).

Other studies have reported a mixture of normal and altered body- and action-related processing in patients who have lost the senses of cutaneous touch and proprioception (Bosbach, Cole, Prinz, & Knoblich, 2005, 2006). This evidence points to a complex relationship between AS and the interplay of multimodal body- and action-representations in the brain.

Neurodevelopmental research suggests that early damage to brain structures involved in movement control detracts from building internal representations of movements and actions. Paradigmatic in this regard is the clinical condition known as Developmental Coordination Disorder (DCD), wherein performance in daily activities that require motor coordination is substantially below average for the person's chronological age and measured intelligence, and is not caused by either a general medical condition (e.g., cerebral palsy, hemiplegia, muscular dystrophy) or by mental retardation. Despite variability in the degree of motor impairment, overall children with DCD present deficits in a variety of motor imagery tasks, suggesting the presence of a core deficit in the ability to utilize internal models of motor control (Williams, Thomas, Maruff, & Wilson, 2008; Wilson, Maruff, Ives, & Currie, 2001). This line of research has mainly been driven by neurorehabilitation issues; it characterizes an effective training intervention as including motor imagery and action observation as tools for rehabilitation.

A final relevant issue concerns the relations between episodic memory systems, which we have previously linked with self-projection into the future (a particularly sophisticated kind of internal simulation). Hassabis, Kumaran, Vann, and Maguire (2007) report that patients with hippocampal amnesia cannot imagine future events, suggesting that the ability to process memories appropriately is a precondition for this kind of self-projection.

2.13. Open challenges and major objections to AS theories

As action simulation theories have become widespread, it is not surprising that they have received many criticisms.

From a computational perspective, one could ask whether simulation processes depend on the intrinsic dynamics of neural representations (e.g., on the dynamics of populations of neurons in the motor cortex), similar to the representational momentum (Freyd, 1987) and visual extrapolation (Nijhawan, 2008), or whether motor simulation adopts a forward model and efferent copies of issued (or simulated) motor commands. As we noted above, many researchers favor the latter hypothesis. However, the "forward search" used by internal models to implement simulations is computationally expensive and does not scale up well with the size of the problem space.

This problem can be alleviated in many ways. One possibility is using approximate inference methods (e.g., sampling methods) that implement action simulations with bounded resources at the expenses of accuracy (Dindo et al., 2011). Alternatively, or in addition, the brain could overcome the combinatorial problems of forward search by pruning or biasing the search space. Recent successes with machine learning algorithms in solving games suggest that properly guided forward search can be very efficient (Gelly & Silver, 2008). Still, it is unclear whether the brain is able to bias and guide forward search, or how it would do this. In neuroscience, it has been proposed that as-if simulations could be linked to valuation mechanisms that prune the search (Damasio, 1994). Also, expectations of reward could bias the search, by directing overt and covert attention exclusively to the region within the space that is expected to lead to reward (see Baldassi & Simoncini, 2011; Serences, 2008 for evidence that rewards modulate sensory processing by biasing spatially selective visual areas, and Gershman & Wilson, 2010 for related computational ideas).

Another way simulations could be more efficiently performed is by optimizing internal representations to afford good predictions; for instance, via methods that consider prediction as an objective function for learning (Weiller, Märtin, Dähne, Engel, & König, 2010). Finally, the brain could "cache" the results of partially executed simulations to reuse them in similar circumstances, or use "black-box" simulators rather than explicit problem representations (Silver & Veness, 2010). To what extent these methods might make action simulations practical and feasible is an open objective for future research.

Beyond the computational challenges for action simulation theories in general, there have been a multitude of

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interpretations of the process of action simulation and of the underlying neural representations. Many accounts of action simulation have been proposed that describe it differently, from both functional and neural viewpoints (see, e.g., Gallese, 2005; Grush, 2004; Hesslow, 2002; see also Bubic et al., 2010; Colder, 2011; for recent reviews). For example, action simulations have been described in terms of Kalman filtering (Grush, 2004), generative schemes (Kilner et al., 2007), or associative mechanisms (Hesslow, 2002). Jeannerod (1994) links motor imagery directly to completed premotor plans, whereas Johnson (2000) links it to the process of constructing a plan (see also Johnson, Corballis, & Gazzaniga, 2001). Further research, empirical and theoretical, is therefore needed to assess the specific computations and the neural substrates associated with the manifold simulative processes that we have reviewed so far.

The application of action simulation theories to the social domain has also been disputed in various ways, especially after the discovery of mirror neurons in the macaque brain (Gallese et al., 1996; Rizzolatti & Craighero, 2004), which has revitalized the simulation theory of mindreading. Still, even among those who assign a functional role to mirror systems in action prediction and understanding,[3] there are various hypotheses as to the computations they realize. “Mirrorists” (Rizzolatti & Craighero, 2004) argue that goals are recognized first, then this information is used to steer action predictions. “Estimators” (Kilner et al., 2007; Wolpert et al., 2003) argue instead that success in predicting actions leads to goal understanding, and cast this process as a Bayesian inference. Finally, “simulationists” (or “emulationists”) (Prinz, 2006; Wilson & Knoblich, 2005) see action simulation as time-locked and useful for enhancing perceptual processing, rather than for goal inference (see Csibra, 2005; Jacob, 2008; for related ideas on simulation). According to simulationism, goal recognition is better linked to contextual factors than to action simulation.

Attempts have been made to integrate these views, by treating action simulation as a flexible process that can be influenced by various sources of information (acting as Bayesian priors in the simulation process). This can be perceptual, contextual or goal information, depending on which is available. In an integrated model, the same process of action simulation that serves primarily for enhancing perceptual processing, generates as a by-product hypotheses concerning which goal could have produced the perceived actions, as these are mapped into the perceiver’s motor repertoire (see Dindo et al., 2011).

In addition, there is an ongoing dispute whether mechanisms of motor resonance and action simulation really explain action understanding, whether it is based on non-simulative mechanisms that implement teleological reasoning, or the two co-exist in a “social brain” network (Frith & Frith, 2006; Keysers & Gazzola, 2007; Kilner, 2011). According to Csibra and Gergely (2007), humans predict and understand others’ actions by assuming that they follow principles of efficiency and rationality, and that they are constrained by goals and various kinds of environmental constraints (e.g., the presence of a barrier might constrain which action is more efficient). This theory is often assumed to be alternative to the idea of action simulation; however, the simulation of the action kinematics could provide an additional source of evidence that improves prediction and understanding. Kilner et al. (2007) proposed that mechanisms of action simulation, goal inference, and context recognition might co-exist and combine in a Bayesian way.

It is also disputed whether action simulations can access the underlying intention of the observed action. Along these lines, Jacob and Jeannerod (2005) have maintained that action simulations cannot readily distinguish the opposed intentions (curing vs. killing) of Dr. Jekyll and Mr. Hyde, when they both execute the same motor action (cutting into a person) – see also Saxe (2005). Attempts to solve this problem point to generative (Bayesian) architectures in which underlying beliefs (relative to the context in which action takes place) provide priors for interpreting the intentions behind intended actions (Kilner et al., 2007). Furthermore, evidence is accumulating that the way proximal actions are executed is not really independent of the opposed distal intentions; rather, subtle changes at the level of proximal action kinematics could allow distinguishing between distal intentions (Becchio, Manera, Sartori, Cavallo, & Castiello, 2012).

Finally, from a computational perspective, another open issue is whether the observed and executed movements interact because the two share a single dynamic representation (de Vignemont & Haggard, 2008; Wolpert et al., 2003), or there are two dynamic representations that interact (Erlhagen, Mukovskiy, & Bicho, 2006). Such theories make different predictions concerning how permeable action simulations are to concurrent brain processes (see Section 2.9).

From this less than exhaustive review, it emerges that, despite the considerable evidence accumulated to date in favor of the widespread use of simulative processes, many open issues remain concerning how the brain implements such simulations, and to what extent they are used in individual and social cognitive tasks. Advancing our understanding of the functional and neural aspects of action simulation remains an important objective for future research.

With that aim in mind, in the rest of the article we will now offer a neuro-computational perspective on action simulation. We present an integrative model that links neural evidence (as revealed in neuroimaging studies of action simulation) to the computational-level constructs of internal modeling, action monitoring, and inhibition that we have discussed so far.

3. Action simulation: a neuro-computational perspective

A large body of evidence indicates that the neural underpinnings of action simulation involve a wide neuronal

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[3] Several researchers have disputed the leading interpretation of mirror neurons as related to action understanding and prediction. Heyes (2010) proposes a sensorimotor theory of mirror neurons as a byproduct of associative learning during social interaction (see also Keysers & Perrett, 2004), challenging the idea that they are an adaptation for action understanding. Hickok, Houde, and Rong (2011) argue that mirror neurons support action selection, not understanding.

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network. This is not surprising if we hypothesize that running action simulations can be considered a "mode" of processing that recruits the same parts of the brain normally used to chose and execute actions, rather than a modularized function. It has even been proposed that the "simulation mode" defines the brain's so-called default network (Buckner, Andrews-Hanna, & Schacter, 2008; Schacter, Addis, & Buckner, 2007).

A considerable amount of evidence has accumulated on the involvement of various brain areas in simulations of different kinds (principally, but not only, in relation to motor involvement during actions, objects and events perception). To organize this large body of evidence coming from many different lines of research, here we follow a computational approach, taking the idea of internal modeling as the starting point. We assume that, to generate simulations, the brain reuses the same neuronal networks implied in the online planning and control of goal-directed actions. Consequently, the simulation network needs to perform at least four operations (see Fig. 1). These are (1) defining the goal of the simulation to be performed (either self-generated or imitated) and establishing an internal model for realizing it; (2) running the internal model to generate the simulation; (3) steering and controlling the simulation and inhibiting overt execution; and (4) guiding sensory processing.

3.1. Defining the goal of the simulation and establishing an internal model

According to Jeannerod (2006), fronto-parietal mirror neurons (MN) and posterior parietal cortex (pPAR) collaborate to encode the goal and to establish an internal model of the action to be simulated (i.e., deciding what are its inputs and outputs, or what has to be simulated); see also Roth et al. (1996) for evidence of involvement of parietal cortex during mental imagery. The goal can either be self-generated or imitated from another person's action. In the self-generated case, the simulation can be initiated by an external stimulus, or by an internal representation not associated with any available sensory stimulus (see Mushiake, Inase, & Tanji, 1991; for a study that distinguishes visually triggered from internally triggered actions). These two conditions rely primarily on the activity of motor and prefrontal areas, respectively (see below). In the imitative case, the internal model can receive input from brain areas devoted to the processing of biological stimuli, such as the pSTS (posterior superior temporal sulcus). The pSTS becomes active during the perception and even the imagination of biological motion; to a lesser degree also in response to the stylized representation of biological motion with point-light displays (Grèzes & Decety, 2001; Grossman & Blake, 2001).

3.2. Running the internal model to generate the simulation

Once the goal is selected and the internal model is established, the model can mimic motor control and prediction functionalities as if the action was being overtly performed. The internal model does this by connecting to areas responsible for the overt control of movements: M1 (primary motor cortex), PM (the premotor area), and SMA (supplementary motor areas). These areas can be taken to implement a hierarchy in which movements and actions are specified at the lowest level (in M1), then at the level of specific goal-directed actions and sequences (in PM), with SMA involved in the formulation of (nonroutine) plans. Rather than operating sequentially, these areas act in concert through feedforward and feedback connections; see Shadmehr and Krakauer (2008) for a recent computationally oriented framework describing the neurobiology of motor control, and Hamilton & Grafton, 2007 for a discussion of intention-to-action hierarchies.

Further, motor areas in the cortex interconnect with the cerebellum (which also receives feedback information from the spinal cord). The cerebellum has been associated with the timing and temporal control of actions, and the specification of predictive components of internal models more generally (Miall & Wolpert, 1996; Wolpert, Miall, & Kawato, 1998). Finally, Broca's area has been indicated as a candidate for processing the "grammatical" aspects of action (as well as of language and music; see Fadiga, Craighero, & D'Ausilio, 2009).

Simulative theories based on the idea of internal modeling suggest that the same M1-PM-SMA network could produce action simulations, because the internal models internally recreate sensorimotor loops analogous to those used to carry the actions out. Numerous studies have suggested that populations of neurons in the monkey motor cortex could support motor plans and simulations (Georgopoulos, Kalaska, Caminiti, & Massey, 1983). For instance, the population vector code could be used in visuomotor tasks as well as in purely visual tasks and possibly in visual extrapolations, given that motor control requires predictions (Georgopoulos & Massey, 1987; Pellizzer & Georgopoulos, 1993). In related research, Tkach, Reimer, and Hatsopoulos (2007) found a similar activation in motor areas of monkeys executing and observing a self-produced action, provided that the visual target was evident, and Cisek and Kalaska (2004) found that dorsal premotor cortex is active during mental rehearsal. Studies using PET and fMRI have found significant overlap of neural activation in premotor cortex and supplementary motor area during performed and imagined movements (Decety et al., 1994; Rao et al., 1993).[4]

Although many studies have focused on the cortical motor areas, in our model these are just a part of the wider brain networks that generate the simulations. Consistent with the general idea that action simulation reuses the same brain networks as those involved in overt sensorimotor engagement, we expect that useful brain areas can be flexibly recruited depending on the kind of simulation to be performed. For example, it has been reported that simulations involving spatial processing recruit hippocampal

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[4] Note that these areas normally guide goal-directed action by continuously receiving (and producing) interoceptive and exteroceptive information, some of which is missing when the action is being simulated (because of inhibition; see below). The absence of proprioceptive information normally available during overt actions could be one way to distinguish perceived and imagined actions from those actually performed.

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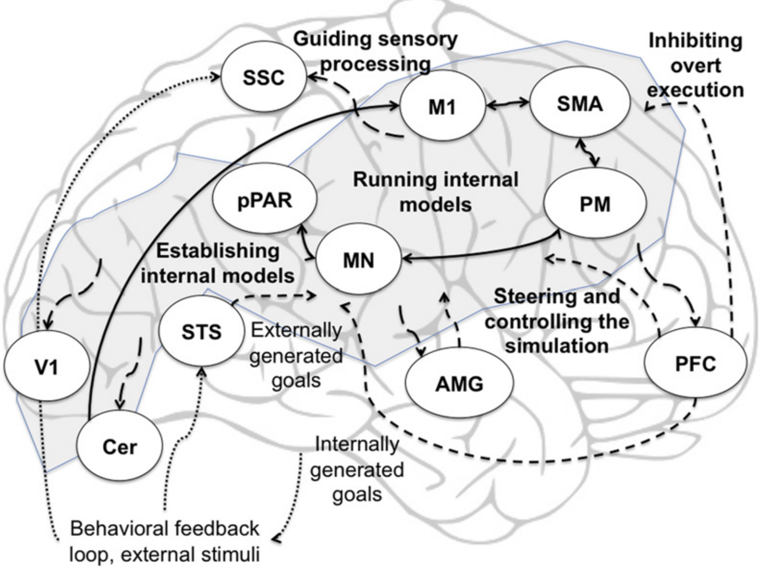

Fig. 1. Sketch of the neuro-computational model. Cer = Cerebellum; V1 = Primary visual cortex; STS = Superior Temporal Sulcus; AMG = Amygdalae; PFC = Pre Frontal Cortex; MN = Mirror Neurons; pPAR = posterior Parietal; P = PreMotor; M1 = Primary motor cortex; SMA = Supplementary Motor Area; SSC = Somato Sensory Cortex. Neuroanatomical labels are indicated only for descriptive purposes, and the figure includes many simplifications concerning localization and connectivity of brain areas. Solid edges and the filled areas represent the main action simulation loops. Dashed edges represent additional elements influencing simulations, and reentrant loops originating from the action simulation process. Dotted edges represent the external loop (through the environment). See main text for explanation.

place cells so as to represent projected future locations (Diba & Buzski, 2007; Johnson & Redish, 2007); see also Gerlach, Spreng, Gilmore, and Schacter (2011) and Schacter et al. (2007) for the idea that the medial temporal lobe could afford self-projection into future situations. Slotnick, Thompson, and Kosslyn (2005) report the activation of early visual cortex during visual imagery. Although they are less studied in this context, subcortical areas could contribute to action simulations, too. In this vein, Middleton and Strick (1994) describe subcortical loops between the cerebellum and basal ganglia that could implement a simulative circuit adaptable for higher cognitive tasks (see also Ito, 2008).

Overall, it is plausible that action simulation is a flexible resource that can recruit different brain areas depending on the task demands. Because simulations are permeable by many factors (e.g., knowledge of action goals and their associated rewards, the individual or social context of operation, and the identity of the co-actor; see Sec. 2.9), brain areas that encode such information are likely to participate in the simulation and influence its unfolding in time. The fact that action simulations typically incorporate the most salient and contextually relevant factors (e.g., to generate successful predictions) suggests the presence of mechanisms of covert attention modulation (or similar) that help selecting these factors. At the same time, this flexibility also entails that information irrelevant to the task (elicited for instance by automatic bottom–up processes) can influence the results of a simulation process and provoke “intrusion errors”. For this, it is required that simulations are actively controlled and monitored.

3.3. *Steering and controlling the simulation, and inhibiting overt execution*

Although simulations can be automatic or influenced by external stimuli, they can also be endogenously activated and strategically controlled, in the sense of being directed toward certain goals (this is what happens when we are asked to mentally rotate an object; see also Pezzulo & Castelfranchi, 2009). The endogenous activation of simulations plausibly involves motivational and affective areas, such as the amygdala (AMG, see below), plus the internal generation of goals that are used as inputs to the internal models. The internal generation and maintenance of goals, along with the control and inhibition of simulations, are plausibly linked to PFC (prefrontal cortex), which is associated with cognitive control, conflict monitoring and the planning and maintenance of action sequences that lead to distal goals; thus, it is particularly important for executing internally triggered actions and avoiding slips (Botvinick, Braver, Barch, Carter, & Cohen, 2001; Koechlin & Summerfield, 2007; Miller & Cohen, 2001; Mushiake, Saito, Sakamoto, Itoyama, & Tanji, 2006). Prefrontal cortical areas could exert control on simulations by sending inhibitory signals that prevent commands from being sent to motor neurons and thus executed overtly (Decety et al., 1994). A recent study further pointed to the ventral premotor cortex (i.e., the region where visuomotor mirror neurons were first described by di Pellegrino et al., 1992) as playing a role in the inhibition of self-movement during action observation (Kraskov, Dancause, Quallo, Shepherd, & Lemon, 2009). Further areas such as ACC (anterior cingulate cortex) could participate in resolving conflicts that arise, for

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example, when the perceived and to-be-executed actions differ, as is the case in many experimental paradigms. Finally, prefrontal areas could be involved in selecting stimuli from internal (simulated) or external (perceptual) sources, and consequently in the “switch” between simulations and actions, as suggested in the gateway model of rostral prefrontal cortex (Burgess, Dumontheil, & Gilbert, 2007; see also Pezzulo & Castelfranchi, 2009). Whether or not these mechanisms permit the passage from on-line action simulations to more complex ones that supports off-line thinking remains an important issue for future research.

3.4. *Guiding perceptual (sensory, interoceptive, and affective) processing*

Simulations not only entail the inhibition, but also the guidance of sensory processing, for instance during imagery or the perception of actions executed by others.[5] Within a generative framework (Friston, 2005; Wolpert et al., 2003), such guidance can be realized through top-down modulations: higher-level expected sensory consequences of actions (possibly represented in association areas, parietal and temporal) could guide the generation of increasingly low-level and detailed sensory representations, possibly in somatosensory (SSC) and higher and primary sensory areas (e.g., primary visual cortex V1) (Avenanti, Annella, Candidi, Urgesi, & Aglioti, 2013), which in turn guide perceptual processing. In turn, errors in the perceptual processing are propagated back to higher areas, leading to a revision of the initial hypotheses. Simulations can thus be associated to preparatory processes that preactivate relevant brain areas in anticipation of stimuli, such as for instance gustatory cortices in anticipation of foods (Simmons, Martin, & Barsalou, 2005) or somatosensory cortex in anticipation of tickling (Carlsson, Petrovic, Skare, Petersson, & Ingvar, 2000).

Although we have emphasized sensory processing, simulations can also involve interoceptive and affective information, which plausibly link future scenarios to considerations of their value for the organism (Freedberg & Gallese, 2007; Wilson-Mendenhall, Barrett, Simmons, & Barsalou, 2011). For example, the processing of biological movements in pSTS is affected by their emotional content, probably on account of its connection with subcortico-cortical structures (in particular, the amygdala). The dissociation of emotional and neutral movements in this area is demonstrated through evidence that while inhibiting pSTS activity impairs the detection of neutral body movements it may facilitate the detection of emotional (i.e., socially salient) body movements, as these may rely on other affective nodes of the network (Candidi, Stienen, Aglioti, & de Gelder, 2011). This evidence is consistent with the notion that the amygdalae modulate visual sensory processing (Phelps & LeDoux, 2005) and facilitate reactive behavior to emotional visual stimuli via their connections with area in the prefrontal cortex (Adolphs, 2002; Kawasaki et al., 2001) that may provide a neural underpinning to the motivation to move.

3.5. *A systemic perspective on action simulation*

In sum, we have described the essential functional processes that produce and control simulations. Our model assumes a systemic perspective, in which these processes are not isolated but form a coherent “processing mode” of the brain: an *action simulation* mode. Consistent with the evidence that we have reviewed in section 2, there is a core action simulation network, but depending on the task at hand many more brain areas can participate and influence the action simulation. In turn, the ongoing simulation can influence these areas through reentrant processes.

For illustrative purposes, we have focused on how action simulations map onto the essential components of internal modeling mechanisms. This computationally oriented analysis permits to better understand how different parts of the brain act in concert to realize action simulations and to generate hypotheses on which parts should be recruited depending on the task at hand. Although the internal modeling framework we adopted is intuitively better suited to explain on-line action control (and action simulations), there have been several attempts to link it to higher cognition and off-line thinking (Grush, 2004; Jeannerod, 2006; Pezzulo, 2011). Thus, in principle our computationally oriented analysis could help understanding how action simulations realize increasingly more complex cognitive functions; this remains, however, as an open objective for future research.

In our discussion we have mainly emphasized sensorimotor brain structures and motor control tasks, which are by far the most studied topics in the action simulation literature. At the same time, it is worth reminding that the concept of action simulation that we introduced is far wider than the idea of body movement, and involves all (including the non-motor) characteristics of actions, such as their goals and intentions, affective states, as well as more abstract information related to mean–ends relations, contextual knowledge, and distal events, etc.

4. Conclusions

Over the last decade, many researchers have argued that action simulation mechanisms in the brain play a fundamental role in individual tasks such as planning, decision-making, and reasoning, and in social tasks such as action prediction, understanding and imitation. Moving from isolated studies to integrative approaches, a “simulation network” in the brain has been proposed as a putative common substrate for all these abilities, which are taken to be intimately intertwined. Most of these theories rely on motor involvement: The general idea is that the motor system is reused across all of the tasks mentioned earlier for its predictive abilities. Within this prediction-based framework,

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[5] Although we have emphasized the similarities between the mechanisms for simulating self-movements and for simulating actions performed by others, they recruit partially distinct neuronal networks (see Ruby & Decety, 2001). In control-theoretic terms, the explanation could be that internal models are not used in the same way to simulate self-generated actions and action observation (see Sec. 2.2). The parietal cortex and insula could be involved in comparing one's own intention with another person's (Blakemore & Decety, 2001).

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action simulation could be conceived as a natural extension of short-term into long-term predictions. In turn, this could explain how this component of primitive mechanisms of sensorimotor control developed to become a fundamental "mode" of mental processing (see also Colder, 2011; Schacter et al., 2007), which is now widely present in perceptual, motor and cognitive tasks. Ultimately, this hypothesis links the mechanisms of selection of guidance of actions to the mechanisms of thinking and cognition, and give action simulation a role that extends well beyond the realm of body movements.

Theories of action simulation have produced a large body of evidence, which we have partially reviewed. They have also generated consistent debate among the proponents of theories that emphasize distinct aspects of action simulations, and among proponents of simulative vs. non-simulative views of cognition. Although these disputes are not settled, simulative, predictive and motor processes are being considered more and more in the current cognitive (neuro)science literature, even in cognitive robotics (see, e.g., Pezzulo, Butz, & Castelfranchi, 2008).

It emerges from our review that (at least during the tasks that have received more attention, such as the prediction of others' actions) action simulation is real-time process that can be modulated by numerous contextual, affective, cognitive and social factors, and that involves the motor system (along with other brain structures flexibly recruited depending on the task demands). In the realms of grounded, embodied and motor cognition, many theories have been advanced that give action simulation a role in sophisticated forms of higher cognition and thinking, too. Although preliminary supporting evidence exists, more research is needed to further test these theories, and to clarify the relations between different kinds of action simulation and their neural substrate.

A major implication of action simulation theories (from both theoretical and empirical viewpoints) is that all cognitive processes are essentially predictive, not part of a chain of reactions to stimuli. Empirically, many studies have reported essentially anticipatory coding of action representations (Pezzulo, 2008; Urgesi et al., 2010) and of perception (Bar, 2007; Friston, 2005; Summerfield et al., 2006). From theoretical and computational perspectives, this kind of evidence suggests that the basic control loop of cognitive processing could be better described in terms of proactive generation and testing of expectations, rather than stimulus–response processes that continuously transform perceptual inputs into motor outputs through feedforward projections, as is still (explicitly or implicitly) assumed in current psychology and neuroscience methods.

Progress along these lines can be accelerated by the realization of good mechanistic models of this anticipatory, simulative and proactive view of the brain. Already a long time ago the proponents of the ideomotor theory claimed that the trigger to a goal-directed action is an anticipatory representation of the desired effect (James, 1890), and that anticipations serve as reference signals for the control of voluntary acts (Adams, 1971). The modern incarnations of this view, using the formal notions of *internal modeling*, *ideomotor codes*, and *predictive coding*, could help developing better process models of cognition that explain how predictions and simulations are continuously generated, how they guide perception, cognition and action, and what mechanisms ensure that progress is being made toward a goal. The model we have presented represents a first, certainly incomplete, step in this direction.

In addition, assessing the idea the brain as essentially anticipatory and proactive may also require novel empirical methodologies, because the methods in current use were developed to measure transformations from sensory to cognitive to motor elements, not anticipations. New experimental paradigms could be required to study and measure the continuous dynamics of a predictive mind, to assess how the brain encodes predictions, and test how such predictions guide cognitive processing (see Engel, Fries, & Singer, 2001; for considerations on predictive brain dynamics and Spivey, 2007 for a discussion of methods of studying continuous brain processes).

Furthermore, theories of action simulation carry theoretical and epistemological implications for the study of brain and cognition. The pervasiveness of predictive and motoric processes entail an action-centric understanding of the external world, and of other actors, and gives prominence to the pragmatic dimension of meaning ("what I can or should do in the world, or with/against others", and "what I expect"), rather than its categorical dimension ("what is out there" and "what its properties are"). Many theorists in grounded cognition (Barsalou, 2008) and developmental studies (Thelen & Smith, 1994; von Hofsten, 2004) have described higher cognitive abilities as contiguous to situated actions; still, further studies are necessary to fully understand if pragmatic representations can explain complex cognitive operations and abstract concepts.

Finally, the idea that many cognitive processes can be implemented using internal simulations is also important for cognitive robotics. It provides a link between a robot's sensorimotor skills and its higher cognitive abilities, indicating how to ground the latter in the former (Clark & Grush, 1999; Pezzulo et al., 2011, 2013).

For all these reasons, despite still being incomplete and partial, action simulation theories form a significant milestone in our developing understanding of cognitive phenomena and their implementation in the brain, and – we believe – they will continue to exert a significant impact on many scientific domains in the years to come.

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