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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

[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.