Opinion

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What is so special about embodied simulation?

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Simulation theories of social cognition abound in the literature, but it is often unclear what simulation means and how it works. The discovery of mirror neurons, responding both to action execution and observation, suggested an embodied approach to mental simulation. Over the past few years this approach has been hotly debated and alternative accounts have been proposed. We discuss these accounts and argue that they fail to capture the uniqueness of embodied simulation (ES). ES theory provides a unitary account of basic social cognition, demonstrating that people reuse their own mental states or processes represented with a bodily format in functionally attributing them to others.

Embodied cognition and simulation

A delightfully provocative paper recently warned that a spectre is haunting the laboratories of cognitive science: the spectre of embodied cognition [1]. In the same vein, one could point out that another spectre is haunting the laboratories of cognitive science as well as the departments of philosophy: the spectre of simulation. Indeed, embodied cognition and simulation (see Glossary) seem to suffer a similar fate. Their advocates have opposed, albeit in different ways and for different reasons, the reigning paradigms of classic cognitive science and philosophy of mind. Nevertheless, how embodied cognition and simulation should be understood is still matter of controversy because they mean different things to different theorists [2–6].

The discovery of mirror neurons in the macaque monkey brain and evidence for the existence of a mirror mechanism (MM) in humans [7] (see Box 1) have fueled debate about the nature of embodiment and simulation, their applications and their possible connections. Mirror neurons not only stimulated a renewed interest in simulation theories [5,8–11] but also suggested an embodied approach to simulation [12–15].

Embodied simulation (ES) mainly aimed to account for basic social interactions by means of a neurobiologically plausible and theoretically unitary framework [12,13]. ES and its role in mind-reading have been criticized, however, not only by those who do not endorse any kind of embodiment or simulation [16–19] but also by scholars championing embodiment [20,21] and simulation [22].

In this article, we tackle these criticisms and argue that they fail to capture the uniqueness of ES. We first examine candidate notions of mental simulation and embodiment in terms of their fit with the functional properties of the MM given the current state of knowledge. We then argue that ES might play a constitutive role in mind-reading.

The mirror mechanism and simulation

The first attempt to account for the MM in terms of Simulation Theory (ST) was provided by Gallese and Goldman [8]. ST claims that understanding the behavior of others usually involves pretense. People first create in themselves pretend desires, preferences and beliefs of the sort they assume others to have. These are then fed into their own decision-making mechanism, which outputs pretend decisions that they use to predict the decisions of others. Simulation can also be used to retrodict mental states, that is, to identify which mental states led another individual to perform a given action. Gallese and Goldman suggested that mirror neuron discharge "serves the purpose of retrodicting the target mental states, moving backwards from the observed action" ([8], p. 497), thus representing "a primitive version, or possibly a precursor in phylogeny, of a simulation heuristic that might underlie mind-reading" ([8], p. 498).

Glossary

Embodied cognition: according to its advocates in philosophy of mind and cognitive neuroscience, this notion usually means that many features of cognition are causally or even constitutively related to the physical body and the bodily actions of an agent. It is still controversial whether and to what extent embodied cognition exploits mental representations.
Mind-reading: mind-reading is usually conceived of as the attribution or ascription of a mental state to self or other. The nature of this attribution or ascription is a matter of debate. Similarly debated is whether the representations involved should be propositional only or could instead allow other formats, such as a bodily one.
Mirror mechanism: this mechanism, given the present state of knowledge, maps the sensory representation of the action, emotion or sensation of another onto the perceiver's own motor, viscero-motor or somatosensory representation of that action, emotion or sensation. This mapping enables one to perceive the action, emotion or sensation of another as if she were performing that action or experiencing that emotion or sensation herself.
Simulation: the notion of simulation is employed in many different domains, often with different, non-overlapping meanings. Simulation is a functional process that possesses a certain representational content, typically focusing on possible states of its target object. Motor control theory characterizes simulation as the mechanism employed by forward models to predict the sensory consequences of impending actions. In philosophy of mind the notion of simulation has been used to characterize the production of pretend mental states that match the mental states of others as closely as possible to enable mind-reading.

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Two questions, at least, remained open to further research [5,9,12,13,23,24] and discussion [16–19]. First, what kind of simulation heuristic is involved in the MM? Second, what kind of mind-reading is rooted in the MM?

ES theory was introduced to answer both of these questions [12,13]. In what follows, we discuss its distinctive features and explain how these features enable us to account not only for variety in the range of the domains of the MM (actions, emotions, and sensations) but also for its actual contribution to mind-reading.

Mental simulation: looking for a suitable candidate

How should mental simulation be understood? Its core meaning has been discussed by emphasizing two different but not mutually exclusive features: resemblance and reuse. On the one hand, mental simulation has been essentially conceived of as a form of inter-personal similarity: a subject's mental state or process simulates another's mental state or process just in case it resembles the second state or process in some significant respect and in doing so fulfills one of its functions or aims [5,23,24]. On the other hand, it has been proposed that reuse rather than resemblance captures the core meaning of mental simulation: inter-personal similarity between a simulator's and a target's mental state or process does not qualify as mental simulation unless it arises from intra-personal reuse of the simulator's own mental state or process [11,25].

ES does not aim to provide a general theory of mental simulation covering all kinds of simulational mind-reading. Rather, it aims to explain the MM and related phenomena (see Box 2). Given this aim, ES theory endorses the emphasis on reuse as the core notion of mental simulation and posits that the MM implements mental simulation primarily because brain and cognitive resources typically used for one purpose are reused for another purpose. For instance, the activation of parieto-premotor cortical networks, which typically serve the purpose of representing and accomplishing a single motor goal (such as grasping something) [7,26] or a hierarchy of motor goals (such as grasping something for bringing it to the mouth or for placing it at a specific location) [27–29], might also serve the purpose of attributing that motor goal [30] or motor intention [27–29] to others. The same holds for emotions and sensations. Within the anterior insula, the same neuronal populations typically underpinning the subjective experience of disgust are also activated when attributing disgust to others [31,32].

Certainly, this does not amount to denying resemblance any relevance for the MM. From the very beginning, the MM has been interpreted as mapping the sensory representation of another's action, emotion or sensation onto the observer's own motor, viscero-motor or somato-sensory representation of that action, emotion and sensation, respectively [33,34]. Notably, however, the mapping here is intra-personal, pertaining to the mental states or processes the same individual undergoes both when planning actions or experiencing emotions and sensations and when observing someone else's actions, emotions and sensations. The MM mapping may also allow for inter-personal similarity of mental states or processes, but the latter would be dependent upon the inter-personal sharing of the same kind of neural and cognitive resources. When this sharing is limited (or even missing), people are not fully able (or are not able at all) to map the mental states or processes of others because they do not have suitable mental states or processes to reuse [7,35].

Embodiment: a matter of format

The notion of reuse, however, is not sufficient to explain the MM. Indeed, a distinctive feature of the MM is that the simulational reuse of mental states and processes is constitutively embodied [12,13].

'Embodied' usually means that body parts, bodily actions, or body representations play a crucial role in cognition. Goldman and de Vignemont [1] recently shed new light into this issue, by emphasizing the crucial role of body representations, characterized as a distinctive class of mental representations by virtue of their format rather than their content. They argued that the bodily format of body representations should be considered as "the most promising for promoting an embodied approach to social cognition" ([1], p. 155).

We subscribe to this view of embodiment, according to which mental states or processes are embodied primarily because of their bodily format. In a nutshell, the idea is that, just as a map and a series of sentences might represent the same route with a different format, so mental representations might have partly overlapping contents (e.g., a motor goal, an emotion or sensation) while differing from one another in their format (e.g., bodily instead of propositional).

We propose that the format of a mental representation constrains what a mental representation can represent. For instance, in planning and executing a motor act such as grasping a cup, bodily factors (e.g., bio-mechanical, dynamical and postural) constrain what can be represented. This representational format constrains the body representation of a single goal (e.g., grasping something) or of a hierarchy of goals (e.g., grasping something for eating it) making it different from a propositional representation of

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Box 1. Mirror neurons and their functional properties

Mirror neurons are a specific class of neurons discharging both during the execution and the observation of a given behavior. They have been found in various brain areas of birds [47,48], monkeys [7] and humans [7,49]. As these areas are anatomically and functionally different, mirror neurons have been argued to subserve different cognitive functions, ranging from song and action recognition in birds [47,48] and monkeys [33] to empathy in humans [34].

Single cell recordings from the ventral premotor cortex of macaque monkeys (area F5) showed that mirror neurons encode goal-related motor acts regardless of the effector (hand or pliers) and the sequence of movements (opening or closing the fingers) required to accomplish the goal [30] (see Figure I). Interestingly, F5 mirror neurons have also been demonstrated to respond differentially when the observed action occured either in the peri- or in the extra-personal space of the monkey [50]. Furthermore, it has been shown that there are neurons in the posterior parietal area LIP involved in oculomotor control that fire both when the monkey looks in a given direction and when it observes another monkey looking in the same direction [51]. It has

been suggested that LIP mirror neurons for gaze might contribute to the sharing of attention. Another recent study [52] showed the presence of neurons with mirror properties in the ventral intraparietal area (VIP). Body-centered visuo-tactile bimodal neurons exhibited visual responses to stimuli presented within the peri-personal space of equivalent body parts of the experimenter facing the monkey. Neurons with mirror properties have been also described in dorsal premotor and primary motor cortex [53].

Several studies in humans demonstrated that observing someone else performing a given motor act recruits the same parieto-premotor areas involved in executing that act [7]. A similar functional property was also evident in congenitally blind patients [54]. Recent neuro-physiological evidence both in monkeys [55] and humans [56]

showed that mirror neurons can be activated during action execution, while being inhibited during the observation of the same actions done by others.

Finally, brain imaging experiments showed that witnessing someone else expressing a given emotion (e.g., disgust, pain, etc.) or undergoing a given sensation (e.g., touch) recruits some of the viscero-motor (e.g., anterior insula) and sensori-motor (e.g. SII, ventral premotor cortex) brain areas activated when one experiences the same emotion [31,32,34,49] or sensation [57]. Other cortical regions, though, are exclusively recruited for one's own and not for others' emotions [32], or are activated for one's own tactile sensation, but are actually deactivated when observing someone else being touched [58] (see Figure II).
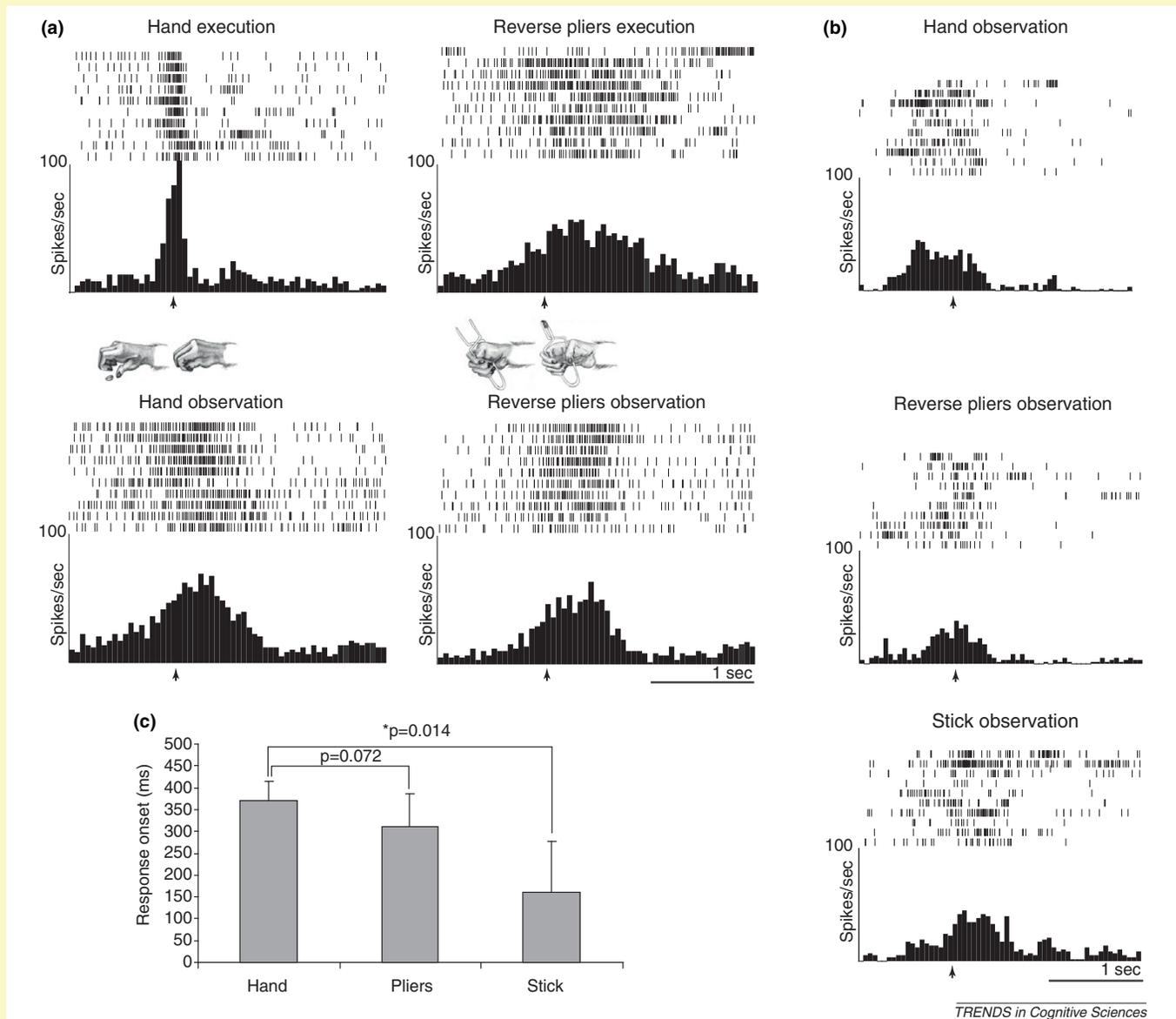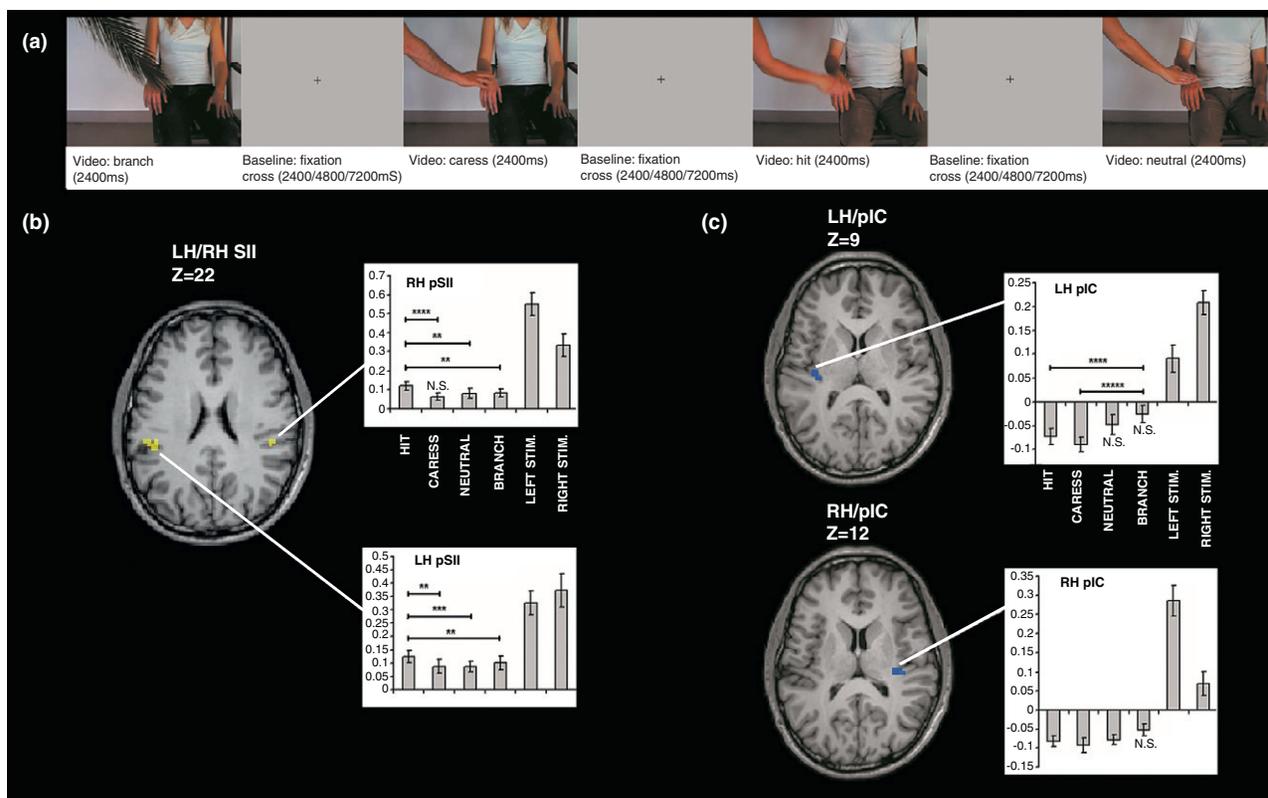

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Figure I. ES, mirror neurons and goal-relatedness. **(a)** Response of one hand-grasping mirror neuron during the execution and observation of hand and reverse pliers grasping. Upper panels show rasters and histograms of ten trials recorded during grasping execution with hand (left) and reverse pliers (right). Lower panels illustrate the neuron's responses during the observation of hand (left) and reverse pliers (right) grasping performed by an experimenter. With reverse pliers the monkey and the experimenter had to first close the hand in order to open the pliers tips and then to open the hand in order to close the pliers tips over the object. All rasters and histograms are aligned (arrows) with the moment in which contact occurred between the object and the hand or the reverse pliers tips. **(b)** Response of one mirror neuron during the observation of grasping with hand, reverse pliers and the observation of stick spearing. All three rasters and histograms are aligned (arrows) with the moment in which contact occurred between the object and the hand, the reverse pliers tips, and the stick, respectively. **(c)** Onset of the mirror neurons response relative to the contact of the effectors with the food. Response onset of the population of neurons shows a clear pattern: the earliest onset occurred during hand grasping observation, followed by that during the observation of pliers, while the latest discharge onset occurred during stick spearing observation. Adapted from [30].

Figure II. ES and touch observation. **(a)** Examples of the time course of stimulus presentation during an fMRI study in which participants observed 4 types of randomly presented touch conditions (i.e., neutral inanimate touch ''BRANCH,'' positive social affective touch ''CARESS,'' negative social affective touch ''HIT,'' neutral social touch ''NEUTRAL''). At the end of the visual runs a tactile localizer run was performed, during which participants kept their eyes closed while one of the experimenters stimulated the back of either their right or left hand by means of soft stroking with a washing glove. Brushing frequency was approximately 1 Hz. **(b)** Group statistical maps with brain regions showing overlapping (yellow) activation patterns for the experience and observation of touch, and graphics showing % signal change for the different observation (HIT, CARESS, NEUTRAL, BRANCH) and experience of touch conditions. **(c)** Group statistical maps with brain regions showing opposite (blue) activation patterns for the experience (activation) and observation of touch (deactivation), and graphics showing % signal change for the different observation (HIT, CARESS, NEUTRAL, BRANCH) and experience of touch conditions. Adapted from [58].

that goal or that hierarchy of goals. The same holds for emotions and sensations: representing in a bodily format an emotion, such as disgust or pain, or a sensation, such as being touched, is different from representing them in a propositional format.

A core claim of ES theory is that similar constraints apply both to those representations of one's own actions, emotions or sensations involved in actually acting and experiencing and also to the corresponding representations involved in observing someone else performing a given action or experiencing a given emotion or sensation; and that the constraints are similar precisely because the representations have a common (bodily) format.

In sum, ES is the reuse of mental states and processes involving representations that have a bodily format. The nature and range of what can be achieved with ES is constrained by the bodily format of the representations involved. At the same time, we shall argue, the bodily format determines how ES contributes to mind-reading.

Embodied Simulation and mind-reading
ES and its role in mind-reading have recently been discussed [5,17,18] and challenged by criticisms and alternative accounts [20,23,24,36]. The discussion and challenges pivot on two main topics: (i) putative problems for ES

theory arising from the simulation account of the MM and (ii) the actual contribution of ES to action and emotion understanding.

ES trouble? Not at all
Three different arguments have been raised against the simulation account of the MM provided by ES theory. According to the first argument (the so-called phenomenological argument) [20,36], this account, similarly to the standard Simulation Theory, is at risk of assuming a view of one's making sense of others as a step-wise process beginning with perception and ending with inferential reasoning. People first would see, for instance, an action; they then would simulate it in their motor system; finally, they would attribute agency for the action and infer something about the other's experience. However, there is no evidence, at the phenomenological level, for such a step-wise process because people directly perceive the meaning of the actions of others, without having to simulate them.

A second argument (the pretense argument) against ES is that its account of the MM fails to meet the two conditions that any kind of mental simulation must meet [20,36]. According to this argument, for a process to qualify as mental simulation it should be deliberately adopted and

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Box 2. Language in a bodily format

Language is a crucial feature of human social cognition. Viewing social cognition as an embodied enterprise offers the possibility of a new neuroscientific approach to language. Accumulating evidence shows that humans may process language by recruiting brain areas typically involved in the motor representation of action. Such involvement occurs at three different levels. The first level pertains to phono-articulatory aspects of language. The second level concerns the semantic content of a word, verb, or sentence. The third level concerns syntax. All three levels share the same reuse notion and bodily format characterizing ES as we defined it here. When processing action-related linguistic expressions, listeners or readers reuse their own action representations in bodily format.

The activation of motor representations in the brain of the reader or listener has been demonstrated at the phono-articulatory level, as well as during the processing of action-related linguistic expressions (words and sentences) and of morpho-syntactical aspects of language (for review, see [59–61]).

Brain imaging studies revealed a somatotopic organization and an overlap between motor areas activated during observation of actions and motor areas activated during the comprehension of sentences describing those actions. It is worth noting that right- and

left-handers, who perform actions differently, use correspondingly different areas of the brain (left and right premotor cortex, respectively) for representing action verb meanings [62].

Let us finally briefly turn to the abstract and non-literal uses of language. A recent study showed that motor behavior shares with linguistic syntax an abstract representation, namely, a means-end parse independent of specific actions and goals [63]. Aziz-Zadeh and Damasio [64] proposed that the verb 'to kick' (literal) and 'kick off the year' (idiomatic) imply the same 'kick' motor representation. TMS evidence supports this view. Glenberg et al. [65] showed that abstract transfer sentences (e.g., give the news) activate the motor system exactly as concrete transfer sentences do (e.g., give the pizza). A remarkable feature of ES in the linguistic domain is also its timing. The activation of motor representations during language processing occurs very early in time so that it is highly implausible that ES might occur as a late motor imagery following comprehension, supposedly occurring outside the motor system.

In sum, these results, although preliminary and widely debated [19,66], suggest causal contributions of ES to language processing and understanding. This view also offers the possibility to apply ES to the study of narratology from an embodied perspective [67].

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controlled; in addition, it should involve pretense. However, MM activation and its construal in terms of ES requires neither deliberation nor pretense.

Finally, it has been argued that ES can be actually considered an argument against ST (the redundancy argument) [20,36]. If the understanding of others were in fact mediated by ES, people would have little or even no need for the explicit mental simulation defended by advocates of ST. Indeed, to the extent that ES explains the phenomenological scarcity of explicit mental simulation, it would seem to support the phenomenological argument against ST as a default mode of social cognition [20,36].

With respect to the phenomenological argument, there is no need for ES to be construed as a step-wise process. Indeed, the reuse of neural and cognitive resources is a constitutive part of observing and making sense of others. On the other hand, the appeal to any sort of direct perception of the mental states of others [20,21,36] does not take into account the fact that one's ability to make sense of the actions, emotions and sensations of others can be modulated by one's ability to act [7] and to experience emotions and sensations [37,38]. Of course, this does not imply that ES should always grant successful making sense of others, especially when high-level socio-cultural features are involved. Our proposal is that ES provides us with a primary way of making sense of others that is particularly reliable at the basic level.

Concerning the pretense argument, as previously argued, there is no need for a core notion of mental simulation to meet the pretense and the control conditions [5,12,13,24]. In particular, ES theory can endorse a simulation account of the MM without necessarily involving any kind of pretense or deliberation.

Finally, the redundancy argument can be easily overridden by acknowledging that ES *per se* does not constitute an argument either in favour or against ST. Indeed, there is no reason to postulate that people should adopt just one kind of mental simulation heuristic in making sense of others. Biology as well as phenomenology tell us that redundancy is often better than homogeneity.

Simulation or emulation?

Critics of ES theory have focused not only on its account of the MM, but also and primarily on the role ES and the MM supposedly play in mind-reading. In particular, it has been argued that ES does not essentially contribute to understanding the actions of others [17–19]. Despite admitting that when observing actions people recruit motor representations as if they were themselves acting, some authors [17,18] have argued that such recruitment falls short of grasping the goals and intentions of others. The recruitment of their own motor representations would only provide observers with an 'emulation' of the motor commands suitable for achieving the goals and intentions of agents. The representations of these goals and intentions would have to be generated elsewhere [17].

Two sets of replies are in order. First, ES consists in the reuse of mental representations that are bodily in format. In the action domain, there is no reason to assume that ES deals only with single motor commands and no reason to assume that goal and intention representations cannot be specified in bodily format. There is substantial evidence that the MM is selective for motor goals and motor intentions, regardless of the body effectors and kinematic features enabling their accomplishments (see Box 1). Similar selectivity can hardly be provided by purely sensory mechanisms, even high-order ones, such as those characterizing extrastriate cortices such as the superior temporal sulcus (STS) [7]. Indeed, sensory mechanisms do not generalize motor goals to body effectors as different as hand and foot, while the MM does [39]. Furthermore, there is no evidence to date that sensory mechanisms can encode the motor intentions of others in a manner similar to the MM [27–29]. Finally, the goal and intention selectivity of the MM does not seem to be fully explained by appealing to other highly cognitive kinds of goal and intention encoding because such upstream coding would be hardly compatible with the activation pattern of the MM and its early timing [40].

Note that dissociations between damage to cortical motor representations and deficits in action recognition do not pose serious problems for ES theory. The ventral

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Box 3. ES beyond the MM: motor imagery and object perception

ES theory aims at providing an account not only of the MM in a variety of domains but also of other processes that are functionally related to the MM. There are, at least, two processes meeting this condition in the action domain: mental motor imagery and object perception.

Like the MM, mental motor imagery is an example of ES as we define it here. Imagining doing something consists of reusing neuronal resources typically employed when planning and executing action. Indeed, mental motor imagery recruits cortical (dorsal and ventral premotor cortex, primary motor cortex, SMA) and sub-cortical (cerebellum, basal ganglia) motor regions (for a review, see [68]). Interestingly enough, the vividness of mental motor imagery is parametrically correlated with activation of sensorimotor areas [69]. In addition, many temporal and spatial constraints characteristics of executed actions are also present when those actions are simply imagined (for a review, see [70]).

Differently from the MM, however, mental motor imagery appears to be essentially similar to preparation to act [22,68]. As a consequence, the type of motor representations being reused in this case may be the one most closely matching the actual execution of the same action. In contrast, the MM mainly relies upon motor representations with a higher degree of generalization, hence favoring their reuse for attributing them to others [7,22,33]. In this regard, it has been shown that imagining using reverse pliers to grasp objects activates the cortical representation of the hand movements required to use this peculiar tool. In contrast, the observation of reverse pliers grasping actions activates the cortical representation of the observed motor goal, irrespective of the individual movements and the order of movements required to achieve it [71].

Object perception provides another example of ES in the action domain. Seeing a manipulable object selectively recruits the same motor resources typically employed during the planning and execution of actions targeting the same objects. Several single neuron recording studies in monkeys and electrophysiological and brain imaging studies in humans demonstrated that the same neuronal populations in the premotor and posterior parietal cortex selectively activate both when grasping an object and merely perceiving it (for a review, see [72]).

It is worth noting that during object perception, the recruitment of grasping motor representations can be affected by the same spatial constraints that govern the execution of grasping actions. The ability of an object, such as a handled mug, to afford a suitable grip (e.g., a precision grip) has been shown to depend on its actual reachability, even when people do not act upon it, nor intend to do it [73,74]. Strikingly, spatial constraints affect one's reuse of her own action representations even when observing someone else who is about to act upon the object [75].

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premotor cortex and the inferior parietal lobule contain a large number of purely motor neurons that have motor properties identical to those of mirror neurons but are not reused during action observation. Claiming that motor syndromes damaging premotor or parietal motor areas must be accompanied by deficits in action recognition [19] amounts to presupposing a one-to-one correspondence between motor and mirror neurons. This assumption is neither true nor necessary for ES. What is crucial for ES is that specific action recognition deficits can (but do not necessarily) occur following damage to premotor or parietal motor areas. Several neuropsychological studies and TMS-induced inactivation studies (for review, see [41]) did show that this is the case, thus indicating that the recruitment of motor resources cannot be explained in terms of mere motor emulation.

Moreover, the 'emulation' argument does not seem to apply naturally to emotion or sensation. If emulation itself does not constitute a form of understanding but is generated by a prior understanding of emotions or sensations, what is this understanding? If, alternatively, emotion recognition occurs independently from ES, why do we emulate emotions?

Clinical neuropsychology shows that deficits in representing emotions in a bodily format affect both emotion experience and emotion recognition [37,38]. This does not amount to claiming that ES might cover any kind of mind-reading, of course. On the contrary, ES contributes to mind-reading to the extent that the bodily format of representations enables their reuse for making sense of others.

ES in mind-reading: causal or constitutive role?
In relation to the contribution of ES to mind-reading, it has been suggested that the activation of the MM "might relate to mind-reading in one of two ways": first, "it may *constitute* an instance of mind-reading"; second, "it might *cause* (or causally contribute to) a distinct neural event or set of events that constitute an attribution of a mental state to the target" ([23], pp. 236-237). The main argument in favor

of a causal role of the MM in mind-reading is that mental simulation might be just a part of the mind-reading process, which in order to be fully accomplished requires the simulated mental state or process to be attributed to the target. According to the same argument, the MM does not qualify for such attribution [5,23,24].

Attribution can be understood in two ways [42]. Representationally, an attribution is a representation of a relation between an agent and a goal, intention or belief. Functionally, an attribution is a representation of a goal, intention or belief which plays some role in enabling one to deal with an agent by virtue of its being appropriately related to that agent's goal, intention or belief. This appropriateness is higher the more the attributor and the target share the same kind of neural structures and cognitive resources. A claim of ES theory is that the MM implies a functional (but not a representational) attribution of mental states and processes that are bodily in format.

In the action domain, the MM is not the only case of ES, as the recruitment of motor resources is also crucial for motor imagery and object perception (see Box 3). The comparison between the MM and motor imagery can be instructive here. In both cases, motor representations typically used for planning and executing actions are reused for representing those actions even when they are not overtly produced. However, the type of reuse is different. Indeed, in motor imagery the motor representation is reused in order to enable one to imagine performing an action by virtue of its being appropriately related to that action's goal. By contrast, in the MM the motor representation is reused in order to enable one to understand or interact with another agent by virtue of its being appropriately related to that agent's goal.

ES theory maintains that the MM can be constitutive of (one form of) mind-reading because it involves functional attribution of mental states or processes (such as a motor goal or a motor intention, but also an emotion and a sensation) having a bodily format. This does not amount to maintaining that the MM plays a constitutive role in any

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Box 4. Questions for future research

• Although ES has been so far studied in the domains of action, emotion and sensation separately, it is likely that a given mental state or process (e.g., disgust) can be simulated in parallel across several of these domains (e.g., at the sensory-motor and viscero-motor level). How can these domains be integrated?

• To what extent might the MM involve the reuse of mental representations such as beliefs or desires that do not have a bodily format, thus going beyond ES?

• Can the theoretical framework provided by ES theory shed new light on psychopathology (e.g., schizophrenia)?

• Can ES theory provide a new approach to aesthetic experience by emphasizing the crucial role played by the bodily format of mental representations?

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form of mind-reading, however. MM-driven ES can have a causal but not a constitutive role when mind-reading needs representational attribution, that is, when attribution concerns propositional attitudes such as beliefs and desires that can be construed as putative reasons for action [7,12]. Indeed, fMRI studies have demonstrated that the observation of the actions of others recruits brain regions activated by, among others, representational attribution tasks [43], such as the mesial frontal cortex, the anterior cingulate cortex, and the temporo-parietal junction, when participants are required to judge the reasons behind the observed actions because of their unusual nature or their implausible context [44–46]. The same fMRI studies have showed, however, that the MM was active without requiring "a distinct neural event or set of events that constitute an attribution of a mental state to the target" ([23], pp. 236-237) in all conditions in which the motor goals and motor intentions of others could be directly understood and attributed.

Concluding remarks

To sum up, what is distinctive about the MM-driven ES is that people reuse their own mental states or processes in functionally attributing them to others, where the extent and reliability of such reuse and functional attribution depend on the simulator's bodily resources and their being shared with the target's bodily resources.

Future research (see also Box 4) should focus on the integration of the various kinds of ES across the different domains discussed in the present paper, given the common bodily format shared by them. A further crucial aspect that needs to be empirically and theoretically addressed is the relationship between the functional attribution of mental representations in bodily format and the representational attribution of mental representations in propositional format.

References

1 Goldman, A. and de Vignemont, F. (2009) Is social cognition embodied? *Trends Cogn. Sci.* 13, 154–159

2 Wilson, M. (2002) Six views of embodied cognition. *Psychon. Bull. Rev.* 9, 625–636

3 Nichols, S. and Stich, S. (2003) *Mindreading: an integrated account of pretence, self-awareness, and understanding of other minds*, Oxford University Press

4 Shapiro, L. (2011) *Embodied cognition*, Routledge

5 Goldman, A.I. (2006) *Simulating minds: the philosophy, psychology, and neuroscience of mindreading*, Oxford University Press

6 Clark, A. (2008) Pressing the flesh: A tension in the study of the embodied, embedded mind. *Philos. Phenomenol. Res.* LXXVI, 37–59

7 Rizzolatti, G. and Sinigaglia, C. (2010) The functional role of the parieto-frontal mirror circuit: interpretations and misinterpretations. *Nat. Rev. Neurosci.* 11, 264–274

8 Gallese, V. and Goldman, A.I. (1998) Mirror neurons and the simulation theory of mind-reading. *Trends Cogn. Sci.* 2, 493–551

9 Gallese, V. (2001) The 'Shared Manifold' Hypothesis: from mirror neurons to empathy. *J. Conscious. Stud.* 8, 33–50

10 Jeannerod, M. (2001) Neural simulation of action: A unifying mechanism for motor cognition. *Neuroimage* 14, S103–S109

11 Hurley, S. (2008) Understanding simulation. *Philos. Phenomenol. Res.* 77, 755–774

12 Gallese, V. (2003) The manifold nature of interpersonal relations: the quest for a common mechanism. *Philos. Trans. R. Soc. Lond. B* 358, 517–528

13 Gallese, V. (2005) Embodied simulation: from neurons to phenomenal experience. *Phenomenol. Cogn. Sci.* 4, 23–48

14 Yeh, W. and Barsalou, L.W. (2006) The situated nature of concepts. *Am. J. Psychol.* 119, 349–384

15 Niedenthal, P.M. *et al.* (2010) The simulation of smiles (SIMS) model: embodied simulation and the meaning of facial expression. *Behav. Brain Sci.* 33, 417–433

16 Saxe, R. (2005) Against simulation: the argument from error. *Trends Cogn. Sci.* 9, 174–179

17 Csibra, G. (2007) Action mirroring and action understanding: an alternative account. In *Sensorimotor foundations of higher cognition. Attention and Performance* (Vol. XII) Haggard, P., Rosetti, Y. and Kawato, M.,eds In pp. 453–459, Oxford University Press

18 Jacob, P. (2009) The tuning-fork model of human social cognition: a critique. *Conscious. Cogn.* 18, 229–243

19 Hickok, G. (2009) Eight problems for the mirror neuron theory of action understanding in monkeys and humans. *J. Cogn. Neurosci.* 21, 1229–1243

20 Gallagher, S. (2007) Simulation trouble. *Social Neurosci.* 2, 353–365

21 De Jaegher, H. and Di Paolo, E. (2007) Participatory sense-making. An enactive approach to social cognition. *Phenomenol. Cogn. Sci.* 6, 485–507

22 Jeannerod, M. (2006) *Motor Cognition: what Actions tell the self*, Oxford University Press

23 Goldman, A.I. (2008) Mirroring, mindreading, and simulation. In *Mirror neuron systems: the role of mirroring processes in social cognition* (Pineda, J., ed.), Humana Press

24 Goldman, A.I. (2009) Mirroring, simulating, and mindreading. *Mind Lang.* 24, 235–252

25 Gallese, V. (2011) Neuroscience and Phenomenology. *Phenomenol. Mind* 1, 33–48

26 Umiltà, M.A. *et al.* (2008) How pliers become fingers in the monkey motor system. *Proc. Natl. Acad. Sci. U.S.A.* 105, 2209–2213

27 Fogassi, L. *et al.* (2005) Parietal lobe: from action organization to intention understanding. *Science* 302, 662–667

28 Cattaneo, L. *et al.* (2007) Impairment of actions chains in autism and its possible role in intention understanding. *Proc. Natl. Acad. Sci. U.S.A.* 104, 17825–17830

29 Bonini, L. *et al.* (2010) Ventral premotor and inferior parietal cortices make distinct contribution to action organization and intention understanding. *Cereb. Cortex* 20, 1372–1385

30 Rochat, M.J. *et al.* (2010) Responses of mirror neurons in area F5 to hand and tool grasping observation. *Exp. Brain Res.* 204, 605–616

31 Wicker, B. *et al.* (2003) Both of us disgusted in my insula: The common neural basis of seeing and feeling disgust. *Neuron* 40, 655–664

32 Jabbi, M. *et al.* (2008) A common anterior insula representation of disgust observation, experience and imagination shows divergent functional connectivity pathways. *PLoS ONE* 13, e2939

33 Rizzolatti, G. *et al.* (2001) Neurophysiological mechanisms underlying the understanding and imitation of action. *Nat. Rev. Neurosci.* 2, 661–670

34 Gallese, V. *et al.* (2004) A unifying view of the basis of social cognition. *Trends Cogn. Sci.* 8, 396–403

35 Gallese, V. *et al.* (2009) Motor cognition and its role in the phylogeny and ontogeny of action understanding. *Dev. Psychol.* 45, 103–113

36 Gallagher, S. and Zahavi, D. (2008) *The phenomenological mind. an introduction to philosophy of mind and cognitive science*, Routledge

37 Calder, A.J. *et al.* (2000) Impaired recognition and experience of disgust following brain injury. *Nat. Neurosci.* 3, 1077–1078

38 Adolphs, R. *et al.* (2003) Dissociable neural systems for recognizing emotions. *Brain Cogn.* 52, 61–69

39 Cattaneo, L. *et al.* (2010) State-dependent TMS reveals a hierarchical representation of observed acts in the temporal, parietal, and premotor cortices. *Cereb. Cortex* 20, 2252–2258

40 Ortigue, S. *et al.* (2010) Understanding actions of others: the electrodynamics of the left and right hemispheres. A high-density EEG neuroimaging study. *PLoS ONE* 5, e12160

41 Gallese, V. *et al.* (2011) Mirror neuron Forum. *Persp. Psychol. Sci.* 6, 369–407

42 Dienes, Z. and Perner, J. (1999) A theory of implicit and explicit knowledge. *Behav. Brain Sci.* 22, 735–808

43 Saxe, R. and Kanwisher, N. (2003) People thinking about thinking people: fMRI investigations of theory of mind. *Neuroimage* 9, 1835–1842

44 Brass, M. *et al.* (2007) Investigating action understanding: inferential processes versus action simulation. *Curr. Biol.* 17, 2117–2121

45 de Lange, F.P. *et al.* (2008) Complementary systems for understanding action intentions. *Curr. Biol.* 18, 454–457

46 Liepelt, R. *et al.* (2008) How do we infer other's goals from non stereotypic actions? The outcome of context-sensitive inferential processing in right inferior parietal and posterior temporal cortex. *Neuroimage* 43, 784–792

47 Prather, J.F. *et al.* (2008) Precise auditory-vocal mirroring in neurons for learned vocal communication. *Nature* 451, 249–250

48 Keller, G.B. and Hahnloser, R.H. (2009) Neural processing of auditory feedback during vocal practice in a songbird. *Nature* 457, 187–190

49 Keysers, C. *et al.* (2010) Somatosensation in social perception. *Nat. Rev. Neurosci.* 11, 417–428

50 Caggiano, V. *et al.* (2009) Mirror neurons differentially encode the peripersonal and extrapersonal space of monkeys. *Science* 324, 403–406

51 Shepherd, S.V. *et al.* (2009) Mirroring of attention by neurons in macaque parietal cortex. *Proc. Natl. Acad. Sci. U.S.A.* 106, 9489–9494

52 Ishida, H. *et al.* (2010) Shared mapping of own and others' bodies in visuotactile bimodal area of monkey parietal cortex. *J. Cogn. Neurosci.* 22, 83–96

53 Tkach, D. *et al.* (2007) Congruent activity during action and action observation in motor cortex. *J. Neurosci.* 27, 13241–13250

54 Ricciardi, E. *et al.* (2009) Do we really need vision? How blind people "see" the actions of others. *J. Neurosci.* 29, 9719–9724

55 Kraskov, A. *et al.* (2010) Corticospinal neurons in macaque ventral premotor cortex with mirror properties: a potential mechanism for action suppression? *Neuron* 64, 922–930

56 Mukamel, R. *et al.* (2010) Single-neuron responses in humans during execution and observation of actions. *Curr. Biol.* 20, 750–756

57 Ebisch, S.J. *et al.* (2008) The sense of touch: embodied simulation in a visuo-tactile mirroring mechanism for the sight of any touch. *J. Cogn. Neurosci.* 20, 1611–1623

58 Ebisch, S.J.H. *et al.* (2010) Differential involvement of somatosensory and interoceptive cortices during the observation of affective touch. *J. Cogn. Neurosci.* 23, 1808–1822

59 Pulvermüller, F. and Fadiga, L. (2010) Active perception: sensorimotor circuits as a cortical basis for language. *Nat. Rev. Neurosci.* 11, 351–360

60 Jirak, D. *et al.* (2010) Grasping language – a short story on embodiment. *Conscious. Cogn.* 19, 711–720

61 Glenberg, A. and Gallese, V. (2011 Apr 27) Action-based language: A theory of language acquisition production and comprehension. *Cortex* [Epub ahead of print]

62 Willems, R.M. *et al.* (2010) Body-specific representations of action verbs: neural evidence from right- and left-handers. *Psychol. Sci.* 21, 67–74

63 Allen, K. *et al.* (2010) Abstract structural representations of goal-directed behavior. *Psychol. Sci.* 21, 1518–1524

64 Aziz-Zadeh, L. and Damasio, A. (2008) Embodied semantics for actions: Findings from functional brain imaging. *J. Physiol. Paris* 102, 35–39

65 Glenberg, A.M. *et al.* (2008) Processing abstract language modulates motor system activity. *Q. J. Exp. Psychol.* 61, 905–919

66 Tettamanti, M. and Moro, A. (2011 Jun 1) Can syntax appear in a (mirror) system? *Cortex* [Epub ahead of print]

67 Wojciehowski, H.C., and Gallese, V. (in press) How stories make us feel. Toward an embodied narratology. *California Ital. Stud.*

68 Jeannerod, M. (2001) Neural simulation of action: a unifying mechanism for motor cognition. *Neuroimage* 14, S103–S109

69 Lorey, B. *et al.* (2011) Activation of the parieto-premotor network is associated with vivid motor imagery–A parametric fMRI study. *PLoS ONE* 6, e20368

70 Munzert, J. *et al.* (2009) Cognitive motor processes: The role of motor imagery in the study of motor representations. *Brain Res. Rev.* 60, 306–326

71 Cattaneo, L. *et al.* (2009) Representation of goal and movements without overt motor behavior in the human motor cortex: a transcranial magnetic stimulation study. *J. Neurosci.* 29, 11134–11138

72 Gallese V. and Sinigaglia C. (in press) Cognition in action. A new look at the cortical motor system. In *Joint Attention and Agency* (Metcalfe, J. and Terrace, H., eds.), Oxford University Press

73 Costantini, M. *et al.* (2010) Where does an object trigger an action? An investigation about affordances in space. *Exp. Brain Res.* 207, 95–103

74 Cardellicchio, P. *et al.* (2011) The space of affordances: A TMS study. *Neuropsychologia* 49, 1369–1372

75 Costantini, M. *et al.* (2011) Ready both to your and my hands: mapping the action space of others. *PLoS ONE* 6, e19723