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Motor cognition: a new paradigm to study self–other interactions

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Accumulative empirical evidence has been reviewed in support of the notion that the production and perception of action as well as the interpretation of others' actions are functionally connected, and indeed, rely on common distributed neural systems in the premotor and parietal cortices. We suggest that these neural systems sustain shared representations between self and other that are crucial in social interactions. The inferior parietal cortex plays a special role in the sense of agency, which is a fundamental aspect to navigate within this neural network. The role of other brain areas that implement and regulate these shared representations remains to be specified.

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Abbreviations

fMRI functional magnetic resonance imaging

Introduction

Say you have lost your car keys and you are anxious as time passes because you might miss your morning flight. An efficient way to find them is to stop wandering around, then retrace in your mind what you have done the previous evening, where in your house you have been, with whom you have interacted, and so forth. Such a mental simulation reactivates, amongst other things, your motor representations in working memory and hopefully will help you to spot your keys. This everyday example illustrates the intimate and deeply rooted link between motor systems and cognition. The concept of 'motor cognition' grasps the notion that cognition is embodied in action, and that the motor system participates in what is classically considered as high-level mental processing, including those processes involved in our social interactions. The fundamental unit of this paradigm is action, defined as the movements produced to satisfy an intention towards a specific goal, or in reaction to a meaningful event in the physical and social environments. Motor cognition takes into account the preparation and pro-

duction of actions, as well as the processes involved in recognizing, anticipating, predicting and interpreting the actions of others. In this review, we draw on the most recent evidence from several fields of research to illustrate the broad reach of motor cognition and its impact on human social interactions.

Perception-action and shared representations

The continuity between action and cognition is primarily formed on the basis of perception and action cycles, which are the fundamental foundation of the nervous system. These processes are functionally intertwined: perception is a means to action and action is a means to perception. Indeed, the vertebrate brain has evolved for governing motor activity with the basic function of transforming sensory patterns into patterns of motor coordination [1]. Gibson [2] proposed the metaphor of 'affordance' to account for the direct link between perception and action in 1966. Later, Shepard [3] argued that as a result of biological evolution and individual learning, the organism is, at any given moment, tuned to resonate to the incoming patterns that correspond to the invariants that are significant for it. These patterns, according to Shepard, have become deeply internalized (i.e. represented), and even in the complete absence of external information, the system can be excited entirely from within (while imagining, for example). Today, the common coding theory claims parity between perception and action [4]. Its core assumption is that actions are coded in terms of the perceivable effects (i.e. the distal perceptual events) that they should generate [5,6]. This theory also states that perception of an action should activate action representations to the degree that the perceived and the represented action are similar [6]. As such, these representations may be shared between individuals. Indeed, the meaning of a given object, action, or social situation may be common to several people and activate corresponding distributed patterns of neural activation in their respective brains [7]. There is a growing number of behavioral and neurophysiological studies that demonstrate that perception and action have a common coding and that this leads to shared representations between self and others.

Observation–execution matching system

The discovery of 'mirror neurons' provided the first convincing physiological evidence for a direct matching between action perception and action execution. Mirror neurons are found in the ventral premotor cortex of the macaque monkey, and they fire both when it carries out a goal-directed action and when it observes the same action performed by another individual [8]. More recently, it was

found that a subset of these mirror neurons also respond when the final part of an action is hidden and can only be inferred, however when the action is seen in its entirety this part is crucial in triggering the response [9]. Therefore, specific neurons in this region respond to the representation of an action rather than to the action itself. Ongoing work by this laboratory extends this idea by showing that some neurons in the same region display mirror properties between motor sense and other modalities such as audition [10,11**]. This demonstrates that single neurons are concerned with some actions regardless of the modality through which they are inferred, and suggests that it is the consequence of the action that is represented. Such neurons are not restricted to the premotor cortex but have also been identified in other areas of the brain, notably in the posterior parietal cortex in relation to actions performed with objects [12*].

Evidence for a matching system in humans continues to accumulate. For instance, it was found that when subjects observe a block stacking task, the coordination between their gaze and the actor's hand is predictive rather than reactive, and is highly similar to the gaze-hand coordination when they perform the task themselves [13]. These results indicate, in accordance with the common coding theory, that during action observation subjects implement eye motor programs directed by motor representations of manual actions. Consistent with this view, hemodynamic increases have been detected in the premotor cortex, the intraparietal cortex, the parietal operculum and inferior frontal gyrus when subjects observe grasping movements towards an object [14]. These regions were activated to a higher degree during actual execution of the same task. In another domain it has been found that speech listening is associated with an increase of motor-evoked potentials recorded from the listeners' tongue muscles when the presented words strongly involve tongue movements when uttered [15**]. Moreover, a functional magnetic resonance imaging (fMRI) study showed a common functional organization between motor recognition and language production [16].

This matching system offers a parsimonious explanation of how we understand the actions of others: by a direct mapping of the visual representation of the observed action into our motor representation of the same action [17]. This interpretation is also compatible with the simulation theories, which assume that when one observes the actions of others, one covertly simulates the same action (but see update; [18]).

From motor priming to social facilitation

One consequence of the functional equivalence of perception and action is that watching an action performed by another person facilitates the later reproduction of that action in oneself. A series of psychophysics studies have shown that when subjects are asked to produce gestures

on cue, the response is quicker when stimulus and response gestures are matched than when they are incongruent [19]. The response is also faster when subjects are asked to produce the response under imitative cueing rather than under symbolic cueing conditions (e.g. when shown a certain color).

Castiello and co-workers [20] have also explored the nature and specificity of motor priming by examining behavioral responses to actions produced by a robotic arm versus those produced by a human arm. They showed a priming advantage for the latter. Cerebral correlates of this effect seem to involve the right inferior parietal lobule as demonstrated by Perani *et al.* [21], who reported greater activity in this region when subjects observed grasping movements executed by a human hand than when the same actions were performed by a virtual hand. Thus, perception of actions performed by real hands taps into existing action representations, whereas similar conditions involving virtual reality do not access the full motor knowledge available. Subsequent work by Castiello [22**] showed priming effects even when the kinematics (i.e. the movement properties) of a model were not available, and suggested that the motor intention of conspecifics can be inferred from their gaze. A further argument in favor of the common mechanism for observed and executed action is provided by the study of Kilner *et al.* [23*]. Altogether, such findings suggest that the observation of action can prime a similar response in the observer, and that the degree to which the observed action facilitates a similar response depends on the kinematics and visual similarity between the prime and the response. These findings also cast some light onto the phenomenon called 'social facilitation', which accounts for the demonstration that the presence of other people can affect individual performance. An elegant series of experiments on spatial compatibility based on reaction time by Sebanz *et al.* [24] demonstrated that actions at the disposal of another agent are represented and have impact on one's own actions, even when the task at hand does not require taking the actions of another person into account.

Imitation

Imitation involves perception–action coupling but cannot be reduced to a simple motor resonance mechanism, as opposed to motor mimicry. It implicates executive functions and the sense of agency [25], but simple imitation may occur without conscious awareness [26]. Although it is still controversial whether or not non-human primates possess the ability to imitate spontaneously, imitation occurs naturally in human infants [27]. Research shows that young children are capable of rational imitation in the sense that they appear to view human action in terms of the relation between the agent, the means and the goal (physical outcome) of the action [28**]. On the other hand, individuals with autism have often been found to

be impaired at imitation [29]. Recently, Avikainen and co-workers [30] showed that adults with Aspergers syndrome or high-functioning autism were impaired at imitating in a mirror-images manner, a form of imitation that is favored by normal adults.

A neuroimaging study [31] found relative distinct neural instantiation of processing the goal and the means in an imitation paradigm. A new fMRI study demonstrated left versus right hemispheric specificity in the premotor cortex related to the object and the movements that can be performed with the objects [32].

There are other neuroimaging studies of imitation that reported bilateral activation of the inferior frontal gyrus and premotor cortex when subjects imitated finger and hand movements [33,34]. Interestingly, the activity in the inferior frontal gyrus was greater for goal-directed finger movements than it was when movements had no explicit goal. Tanaka and Inui [35] also reported similar activation in the inferior frontal gyrus for imitation of finger configurations, but not for imitation of hand/arm postures. Schubotz and Von Cramon [36] proposed that the lateral premotor cortex transforms into a somatotopic representation not only during observed action but during any kind of sequential perceptual event. The role of the premotor cortex in such a context lies within the representation of the 'pragmatic features', or the potential motor significance of attended sensory events [37,38].

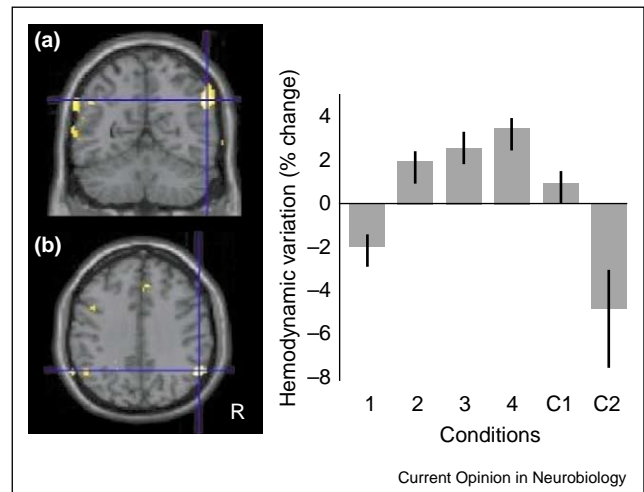
An fMRI study has demonstrated that imitation and observation of emotional facial expressions activate a similar network of brain areas [39]. Comparison of these two actions showed that there was greater activity during imitation in different premotor areas, the superior temporal cortex, insula and amygdala. The authors proposed that the insula is fundamental to the system that uses action representation to understand the emotions of others.

Whereas imitation is useful for learning new skills, the recognition that someone is imitating us plays an important role in communicative exchanges and in the development of intersubjectivity [40,41]. Two neuroimaging studies explored the extent to which being imitated and imitating another individual rely on similar neural mechanisms [42,43]. When the conditions of imitation were contrasted to the control condition in which subjects acted differently from the experimenter, specific activation was found in the inferior parietal lobule, in addition to a common set of cortical areas including the right inferior frontal gyrus, the superior and medial prefrontal cortex. The left inferior parietal lobule was activated more when subjects imitated the other, whereas the right homologous region was associated with being imitated by the other.

The sense of agency and action identity

The research reviewed here strongly supports tight functional coupling between actions produced by the self and actions produced by others. This coupling is underpinned by a distributed pattern of activation in the premotor and parietal cortex that reliably fires in response to both an action internally generated and the perception of the same action produced by another person. However, in normal circumstances there is no confusion between actions produced by the self and actions produced by another. Several models have been proposed to account for the sense of agency (i.e. the sense of being the initiator or source of a movement, action, or thought) including forward models [44]. In fact, there is an asymmetry between observing one's own actions and observing someone else's actions. Individuals are more accurate in recognizing their own actions than the actions performed by another [6]. There is good evidence that the inferior parietal cortex and the insula are crucial components for the sense of agency [42,43,45–49]. In a study designed to investigate the brain correlates of the feeling of being in control of an action, Farrer and co-workers [50] demonstrated an increase in activity in the right inferior parietal lobule as the 'feeling of control' over the manipulation of a virtual hand decreased (Figure 1). Another study found right posterior superior temporal sulcus activation that correlated positively with the temporal delay introduced online between the action of

Figure 1



Parietal cortex and the sense of agency. Right inferior parietal lobule activation ($x = 56, y = -56, z = 36$) superimposed into (a) coronal and (b) sagittal sections of T1-weighted MRI. The histogram shows the relative hemodynamic variations in the right inferior parietal lobule across the experimental conditions. The conditions were; (1) the participant moved a joystick while seeing the exact visual effect on a virtual hand; (2) angular distortions were introduced into the system at various angles from 25°; (3) 50°; or (4) another person moved the joystick. The experiment was also performed in control conditions, in which participants produced random movements (C1) whilst seeing their consequences, and (C2) while they watched the virtual hand moving. Adapted from [50].

the hands and their visual feedback [51]. Thus, distinct networks are involved in perceiving spatial versus temporal features of one's own movements. Finally, an experiment recently demonstrated that the neurodynamic activity starts earlier in several cortical regions involved in motor control when participants made judgements about their own actions versus those of others [52**]. This shows that the dynamics of neural activation within the shared cortical network are an important aspect to distinguish one's own actions from the actions of others.

Conclusions

Motor cognition arises from action/perception cycles that can be mediated by internal representations. This enables us not only to react to our environment but also to anticipate the consequences of our actions. Moreover, these representations not only guide our own behavior but are also used to interpret the behavior of others, because they are shared across individuals [25]. Important questions for future research concern the respective computational role of each brain area that subserves shared representations between self and other, as well as a better description of what precise aspects of an action are actually represented. The temporal distribution of these representations is also likely to shed some light on the various mechanisms that fall under motor cognition.

Update

A recent fMRI experiment has shown that the motor system is engaged when participants use arbitrary visual cues to prepare their own actions, and also when they use the same cues to predict the actions of other people [53**]. However, these two tasks activate separate sub-circuits within the premotor cortex. Forming an explicit representation of another person's intention as an intentional agent necessitates an additional neural/computational mechanism (requiring the participation of the medial prefrontal cortex), beyond the shared representation level.

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