Mirror neurons and motor intentionality

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Summary

Our social life rests to a large extent on our ability to understand the intentions of others. What are the bases of this ability? A very influential view is that we understand the intentions of others because we are able to represent them as having mental states. Without this meta-representational (mind-reading) ability their behavior would be meaningless to us. Over the past few years this view has been challenged by neurophysiological findings and, in particular, by the discovery of mirror neurons. The functional properties of these neurons indicate that intentional understanding is based primarily on a mechanism that directly matches the sensory representation of the observed actions with one’s own motor representation of those same actions. These findings reveal how deeply motor and intentional components of action are intertwined, suggesting that both can be fully comprehended only starting from a motor approach to intentionality.

KEY WORDS: action understanding, mind-reading, mirror neurons, motor intentionality.

Introduction

The actions of conspecifics are among the most important stimuli for many species of animals and for humans. Although the actions of other people very frequently convey information not sent intentionally to the observer, we are nevertheless able to understand what they are doing and why they are doing it.

What mechanism underlies this capacity? How is it that we are able to understand the actions of others not as bodily movements but as intentional actions? A philosophically and psychologically influential view suggests that in order to understand the intentional behavior of others we have to attribute them with “propositional attitudes”, i.e. mental states such as beliefs, desires, intentions etc., that drive that behavior, and make it comprehensible and even predictable. According to this hypothesis, our capacity to understand the actions of others is therefore rooted in our ability to mentalize, or to read their minds, in other words to represent them as having mental states. Without this meta-representational ability, the actions of others could not have any intentional meaning for us and this would prevent us from interacting with our peers and performing adequately in even the simplest social situations.

Over the past few years, however, this view has been challenged by neurophysiological studies on the functional properties of the cortical motor system. These studies and the discovery of a specific class of visuomotor neurons that discharge both during action production and during action observation (mirror neurons) has suggested that our understanding of the actions of others is based primarily on a mechanism that directly matches the visual representation of observed actions with our own motor representation of those same actions. According to this hypothesis, we understand the actions of others by means of our own “motor knowledge”: this knowledge enables us immediately to attribute an intentional meaning to the movements of others. This, of course, does not rule out the possibility that other more complex processes, such as those at the basis of our meta-representational abilities, may be at work and play a role in these functions. It simply underlines that our intentional understanding of the actions of others is not based solely, or primarily, on this mentalizing.

In the present paper we will start by summarizing the basic properties of the mirror system in monkeys and humans. We will then focus on the implications of the mirror mechanism of intentional understanding. Our aim is to show how deeply motor and intentional components of action are intertwined and how they can both be fully understood only by starting from a motor approach to intentionality. This stance goes beyond a mentalistic view of action understanding, which reduces the intentional content of an action to that of the pure (i.e. propositional, non-motor) mental states thought to cause such action, and opposes a hyper-simplified view of motor behavior that relegates the motor content of an action to the mere (i.e. non-intentional) bodily movements needed to execute it.

The mirror system in monkeys and humans

Mirror neurons are a distinct class of visuomotor neurons originally found in the ventral premotor cortex (area F5) of the macaque monkey (1-3). Their defining functional characteristic is that they become active not only when the monkey performs a given motor act (like grasping an object), but also when it observes another individual (monkey or human) performing a similar act. Monkey mirror neurons do not respond to other types of visual stimuli: in fact, they do not become active at the sight of a hand mimicking an action or when meaningless intransitive movements are observed. Similarly,
they do not respond to the mere observation of objects, even when these are of interest to the monkey. Comparison of effective observed actions and effective executed actions indicates that most mirror neurons show congruence between their visual and motor responses. In some neurons this sensory-motor congruence can be extremely strict. In these cases the effective executed action and the effective observed action coincide both in terms of the goal (e.g. grasping) and in terms of how the goal is achieved (e.g. using a precision grip). For most mirror neurons, however, the congruence is broader and it is confined to the goal of the action. For example, a neuron may actually discharge only when the monkey grasps food using a precision grip, but it still responds when the experimenter uses other types of prehension.

F5 is not the only cortical area that responds to the observation of actions performed by others. A recent fMRI study (4) showed that the observation of grasping hand actions activates the region of the superior temporal sulcus (STS), the rostral part of the inferior parietal lobule (IPL) including the cortex within the intraparietal sulcus, some prefrontal areas, as well as different sectors of F5. The neurons of the STS do not appear to have motor properties. While they do code biological actions, including hand-object interactions, their coding appears to be exclusively visual (5,6). The situation is quite different for the rostral part of the IPL, traditionally considered to be an association area. Mountcastle and Hyvärinen’s classic studies (7,8), however, showed that many IPL neurons discharge in association with movements. These findings were confirmed and extended through experiments in which IPL neurons were tested during active monkey behavior and in response to sensory stimulation (9-11). These experiments showed that many IPL neurons are active during the execution of specific motor acts and that many of them also respond to somatosensory and visual stimuli. Among these latter neurons some have mirror properties very similar to those of F5 mirror neurons. The most effective observed actions are grasping, holding, manipulating and bimanual interactions. Thus the monkey mirror system appears to be made up of two main nodes, one located in F5 and the other in the rostral part of the IPL. Electroencephalographic (EEG) and magnetoencephalographic (MEG) investigations, transcranial magnetic stimulation experiments (TMS), and brain imaging studies have provided evidence that, in humans too, the observation of actions performed by others activates cortical areas that are involved in motor activity. In particular, EEG and MEG studies showed that the observation of movements performed by others (e.g. hand opening/closure) desynchronizes the EEG activity of the region located around the central sulcus (12-16). A desynchronization of this region during active movements is a classic finding in EEG literature. Another important piece of evidence that the human motor system possesses mirror neurons came from TMS experiments. Fadiga et al. (17) recorded motor evoked potentials (MEPs), elicited by stimulation of the hand field of the left primary motor cortex, from the right arm and hand muscles of normal volunteers asked to observe an experimenter performing transitive and intransitive hand actions. The observation of both kinds of action produced an increase in the recorded MEPs, which selectively involved the muscles the volunteers used when producing the observed movements. Similar results were found by several other groups (18-21). In particular, Gangitano et al. (19) demonstrated the presence of a strict temporal coupling between changes in cortical excitability and the dynamics of the observed action. MEPs, which were recorded from hand muscles at different time intervals during passive observation of grasping, matched the timing of the kinematics of the observed action.

The use of brain imaging techniques has made it possible to localize the mirror neuron system in humans. These studies showed that observation of actions performed by others activates a complex network comprising the visual occipital and temporal areas and two cortical regions whose function is predominantly or fundamentally motor (22-36). These two latter regions, which form the core of the human mirror neuron system, are the rostral part of the IPL, the lower part of the precentral gyrus, and the posterior part of the inferior frontal gyrus (IFG) that basically corresponds to area 44. Occasionally, the dorsal premotor cortex and the sector of IFG most likely corresponding to area 45 are also found to be active during the observation of actions performed by others.

Taken together, the findings of electrophysiological experiments and brain imaging studies show that the localization of the mirror system in humans is very similar to that found in the monkey. Its functional properties, however, are more sophisticated. Unlike that of the monkey, the human mirror system becomes active also during the observation of *intransitive* and *mimicked* actions and is able to code, in addition to the goal-directedness of an action, the temporal aspects of the movements leading to the goal.

**Motor representation and action understanding**

The idea that the primary function of mirror neurons is to enable the observer to understand the actions performed by others goes back to the studies in which these neurons were first described (1-3,37). The congruence between visual and motor properties of mirror neurons indicates that when we observe an action performed by others, a "potential motor act" is evoked in our brain that is identical (or at least similar) to that which would be spontaneously activated during our own planning and effective execution of that same action. The only difference is that while in the latter case the potential motor act would be translated into an overt series of movements allowing us to achieve the goal, in the former it would remain a motor representation of that goal at its potential stage. The evocation of a potential motor act ensures that the observed movements performed by others immediately take on an intentional meaning for the observer. But what do we really mean when we talk about “action understanding”? What kind of understanding can be associated with the mirror mechanism? What does such a mechanism tell us about the intentional content of an action? If we assume that the mirror mechanism underlies intentional understanding, is there a risk that we are expecting too much of it? In fact, why should a motor activation be needed in order to understand what others are
Mirror neurons and motor intentionality

Doing? Isn’t the purely visual representation of observed movements sufficient? Second, even if the mirror neuron system is needed, what does this understanding tell us about the intentional significance of actions performed by others? Surely intentional understanding requires something more and also quite different, the ability to read the mind of others, to attribute them with those mental states (beliefs, desires, intentions) that drive their actions and render them intentional and understandable as such?

In order to provide answers to these questions, we have to examine the motor properties of mirror neurons, properties that they share with the other F5 neurons. F5 neurons discharge in association with active monkey motor behavior, typically not coding single movements (as do most of the neurons of the primary motor cortex), but rather goal-related motor acts such as grasping, manipulating, or tearing objects (38). For example, many F5 neurons discharge when the monkey performs a motor act such as grasping a piece of food, irrespective of whether it uses its right or left paw or even its mouth to do so. Furthermore, the same neurons that discharge vigorously during finger movements aimed at grasping an object, discharge weakly or not at all during execution of similar finger movements that have another aim such as, for example, scratching.

A recent study showed that the goal-centeredness of the activity of F5 neurons may extend from natural effectors such as the hand to artificial effectors such as tools, even in cases where the (distal) goal of the tool is the opposite of the (proximal) goal of the hand (39). In this study monkeys were trained to grasp objects using two types of pliers (“normal” and “reverse”) requiring different hand movements. When using the “normal” pliers, the object was grasped by opening the hand and then closing it, while with the “reverse” pliers the object was grasped by first closing the hand and then opening it. Recordings of single neuron activity showed that all the F5 neurons studied discharged in relation to the goal-centered motion of the pliers, irrespective of the hand movements.

The motor properties of F5 neurons demonstrate that basic motor acts such as grasping, holding or manipulating have an intentional content, which specifies them as such and does not derive from anything else. Quite apart from being the outcome of some prior and distinct pure mental state (belief, desire, and so on), every basic motor act is defined by its own goal-relatedness, which makes the coherent composition of the various movements possible and enables us to control them while they are being executed. Due to this goal-relatedness a single movement (flexing of the index finger, for example) can assume a number of different intentional meanings as it is part of different motor acts (e.g., scratching vs grasping), just as very different movements (even those which are diametrically opposed, such as the opening and closing of the hand) can have the same intentional meaning, as they are part of the same type of motor act (grasping). Therefore the relation to the goal cannot be interpreted here in abstract mentalistic terms; on the contrary, it presupposes a representation that is both intentional and motor in nature. Intentional, because it is a goal-centered representation characterized by a degree of generality, which although it refers to movement, cannot be reduced to a single sequence of movements; motor, because the goal is represented in motor terms, as the end-point of a motor act, and although this representation can differ with regard to single movements, nonetheless it must have a coherent motor content that enables it to determine a given behavior and to control its execution.

Let us come back now to mirror neurons. As previously mentioned, the distinctive functional characteristic of mirror neurons is that they become active both when an individual executes a motor act and when he/she sees it being executed by others, thus mapping visual representations of the observed actions onto the motor representations of those same actions. The implications of this mapping now appear evident. The motor representation is goal-centered in itself, and individuals code their own movements as motor acts endowed with a specific intentional meaning. The fact that the observation of a motor act performed by others generates a motor representation that is identical to that which the observer himself would activate if planning the same action, shows that the evoked representations possess the same intentional-motor content and that the meaning of a given action, whether observed or performed, depends primarily on this content.

The presence of such motor and intentional content explains the role of mirror neurons in intentional understanding. In fact, mirror neurons map the sensory representations induced by observing the actions of others onto the motor goal-centered representations of those same actions. Without this mapping, at best the sensory representations would be able to provide a description of the various sensory aspects of the observed movements, but they would not be able to pick up their intentional meaning, i.e. what these movements are about, their motor goal, and how they are related to other motor acts (37,40).

Evidence supporting this conclusion has been provided by the “hidden action” experiment (41), in which single neurons were recorded in two different conditions: in the first, the monkey could see the hand of the experimenter grasping an object (“full vision” condition), while in the second, the same act was presented, but the final, crucial part of it (object grasping) was hidden behind a screen (“hidden” condition). The results showed that the majority of the tested mirror neurons responded to the observation of hand grasping even the when final part of this motor act was hidden from view. The fact that the same goal-centered motor representation was elicited both when the monkey watched the entire motor act and when it saw only its initial ambiguous phase, indicates that the monkey was able to understand the intentional meaning of the whole motor act from the partial sequence seen.

Another study provided further evidence to support the hypothesis that mirror neuron discharge reflects understanding of the intentional meaning of the perceived action and does not depend simply upon its visual features. In this experiment F5 mirror neurons were recorded while the monkey was observing the experimenter carrying out a sound-producing motor act and also when it was hearing the sound without seeing the action (42). The results showed that a large number of mirror neurons (also named “audio-visual” mirror neurons) responded selectively and congruently in the different experimental conditions: for example, there were mirror
neurons which responded to peanut breaking both when the action was observed or heard only, and when it was both heard and observed, but which did not respond to the sight and sound of another action, or to non-specific sounds. This means that the motor representation evoked was always the same, while the sensory information could change depending on the situation. The visual aspects of the action appear to be relevant only to the extent that they facilitate comprehension, but if the action can be understood from other factors (such as sound), the mirror neurons are able to code the experimenter’s action even in the absence of visual stimuli.

The “melody” of action and intention understanding

So far, we have focused on isolated motor acts characterized by a specific, restricted, goal-centered representation. In point of fact, however, our actions, just like those of most animals, possess a more complex motor and intentional structure, which cannot be interpreted merely in terms of a simple sequence of motor acts but presupposes the intentional concatenation of the various motor acts involved in a specific goal hierarchy. The same motor act (for example, grasping) may be embedded in different actions leading to different final goals (e.g. grasping-for-eating vs grasping-for-placing); in other words, the goal-centered representation (i.e. motor intentionality) can be part of more complex motor representations centered on final goals that differ one from another.

Fogassi et al. (43) recently studied this motor intentionality organization by recording the activity of parietal motor neurons that discharge in association with hand grasping movements. The experiment had two conditions: in the first, the monkey grasped a piece of food, positioned in front of it, and then put it in its mouth; in the second, the monkey again grasped the food, but this time, instead of putting it in its mouth, put it into a container. The results showed that the majority of the recorded neurons discharged differentially depending on whether the motor act following the grasping of the food consisted of putting the food in the mouth or placing it in the container. A series of controls for grasping force, kinematics of reaching movements, and type of stimuli showed that neuron selectivity was not due to these factors. It may seem bizarre that there are grasping neurons that only code grasping if this act belongs to one type of action and not to another (for example, eating but not placing). However, the selectivity that characterizes these neurons, i.e. the fact that the motor representation they evoke modulates their goal-centeredness with reference to the final goal of a specific action, explains one of the fundamental characteristics of motor organization: the “grasping neurons” are inserted in pre-formed chains that code the entire action, in such a way that each neuron codes the grasping, but is also connected to the subsequent motor act, thereby guaranteeing fluidity of the action. In the same study (43), the authors recorded parietal mirror neurons (parietal neurons that, like F5 mirror neurons, discharge both during active gasping and during grasping observation) under the same two conditions used for studying the motor properties of parietal grasping neurons (grasping-for-eating and grasping-for-placing). The observed actions were performed by one of the experimenters in front of the monkey. The context (presence or absence of the container) or the repetition of the same action by the experimenter (blocked design) provided the monkey with clues as to what action the experimenter was going to perform. The results demonstrated that the majority of tested parietal mirror neurons, which showed a clear congruence between their motor and visual responses, were differently activated when the observed grasping motor act belonged to different actions. It is worth noting that in both cases, when the monkey was effectively executing the action and when it was watching actions performed by the experimenter, mirror neurons became active as soon as the hand (of the monkey or the experimenter) assumed the shape necessary to grip the food or the object. The fact that the visual stimulus activated the same neural pattern – i.e. the same set of motor goal-centered representations that are responsible for the execution of the entire motor chain – shows how the monkey was immediately able to understand the tangible intentional dynamics of the observed action, that is, to understand the experimenter’s complex motor intention and anticipate what would be the outcome of his action, from his very first movements. A recent experiment by Iacoboni et al. (44) indicates that humans also use a similar mechanism in order to understand the intentions of others. In an fMRI experiment, they presented volunteers with three kinds of stimuli: a hand grasping a mug without a context, a context only (scenes containing objects), and a hand grasping a mug in two different contexts. The contexts consisted of two scenes with objects arranged in two different ways: i) as though just about to have tea (“drinking” context) and ii) as though just having finished tea (“clearing away” context). The results showed that hand actions embedded in contexts, compared with the other two conditions, produced a higher activation in the caudal part of the IFG, that is in a region which constitutes the frontal node of the human mirror neuron system. This suggests that this system codes not only the single observed act (in this case, grasping a mug with a particular type of grip), but also the general motor intention with which the single motor act is performed, anticipating possible subsequent acts in the motor chain (for example, grasping-for-drinking or grasping-for-clearing-away). Taken overall, these data corroborate the crucial role of motor knowledge in action understanding, at the same time extending its range and function. This knowledge allows us to recognize the intentional meaning of the motor acts we observe both when they are performed singly and when they are part of motor chains. In this latter case, their meaning is no longer univocally determined by the specific goal-centeredness that differentiates one single act from another. Grasping is no longer just grasping, but grasping for eating or placing: here the goal-centered representation goes further than that of the single motor act, it describes the intentional meaning of the whole action. If our motor representations were not organized in this way, it would be most unlikely that our actions would possess their typical fluidity of movement [Lurija’s “kinetic melodies” (45)]. Moreover, without mirror neurons, we would not be able to grasp in a flash, so to speak, the intention behind those “melodies” when they are executed.
by others. Nor would we be able to anticipate, from the very first movements, both the partial result (e.g. grasping the food with the hand), and, more importantly, the complete outcome (e.g. grasping-for-eating or grasping-for-placing). The clearer the information provided by the context, the more selective the activation of the relative motor goal-centered representations will be. However, even when the sensory stimuli are ambiguous, the activation of one or more intentionally connected motor representations helps us to decipher the intentions of others. We are then able to choose the intention that appears to be most compatible with the context, to the point of identifying the most appropriate one, and it goes without saying that these deciphering and identification processes are bound up with the same motor knowledge that drives and adjusts our own execution of the same chain of motor acts.

**Concluding remarks**

The properties of the motor system and the mirror neuron mechanism show that the actions of others, like our own, possess their own specific intentional content. This content cannot be reduced to that of the “pure” mental states (beliefs, desires, intention, and so on) that might have guided the actions and induced their execution. This is not to say that these “propositional attitudes” do not play a role in determining the intentional meaning of actions. However, whatever the underlying mechanism may be, this meta-representational capacity does not account for the full extent of intentional understanding. If it did, we would have to assume that in the absence of meta-representational activity the actions of others would be basically unintelligible to us, devoid of any intentional meaning whatsoever. But, as the mirror neurons show, this is not the case; the activation of these neurons permits immediate understanding of the intentional meaning of the actions of others without the need for any explicit or deliberate mentalizing. This immediate intentional understanding is entirely different from that traditionally considered as characterizing mind reading. Nonetheless, this does not mean that it is any less important, quite the contrary. In fact, the mirror neuron mechanism captures the motor intentional dimension of action, common to both the agent and the observer, which is not only independent of any mentalization process, but actually makes such a process possible. We would not be able to explain the actions of others in terms of beliefs or desires were we not able to recognize immediately their intentional motor meaning, that is, to understand the goal-centeredness that specifies that a particular movement is part of this or that action. Similarly we would not be able to explain the behavior of others in terms of intentions (in the “propositional” sense of the term) and foresee their possible consequences if we did not possess the motor knowledge that regulates the various goal-centered representations involved in both executing and understanding actions, adjusting them to the intentional direction.

To summarize, motor intentionality appears to be the primary form of intentionality on which both the specification of a motor event as an action and its identification as a given action depend. This holds true both for our own actions and for those performed by others. These latter are immediately recognizable to us because of their motor intentional content. As soon as we see someone doing something, either a single act or a chain of motor acts, his/her movements take on meaning for us, whether he/she likes it or not, and regardless of what he/she has in mind. Obviously, the opposite is also true: our own actions have an immediate value for those who observe them, whether we like it or not, and regardless of what we have in mind. Our motor knowledge and our mirror mechanism allow us to share a common sphere of action with others, within which each motor act and chain of motor acts, be they ours or “theirs”, are immediately detected and intentionally understood before (and independently of) any mentalizing.

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