

Understanding motor resonance

Sebo Uithol, Iris van Rooij, Harold Bekkering, and Pim Haselager

Donders Institute for Brain, Cognition and Behaviour, Radboud University Nijmegen, Nijmegen, The Netherlands

The discovery of mirror neurons in monkeys, and the finding of motor activity during action observation in humans are generally regarded to support motor theories of action understanding. These theories take motor resonance to be essential in the understanding of observed actions and the inference of action goals. However, the notions of “resonance,” “action understanding,” and “action goal” appear to be used ambiguously in the literature. A survey of the literature on mirror neurons and motor resonance yields two different interpretations of the term “resonance,” three different interpretations of action understanding, and again three different interpretations of what the goal of an action is. This entails that, unless it is specified what interpretation is used, the meaning of any statement about the relation between these concepts can differ to a great extent. By discussing an experiment we will show that more precise definitions and use of the concepts will allow for better assessments of motor theories of action understanding and hence a more fruitful scientific debate. Lastly, we will provide an example of how the discussed experimental setup could be adapted to test other interpretations of the concepts.

Keywords: Mirror neurons; Motor resonance; Action understanding; Goals.

The discovery of mirror neurons in macaque monkeys (Di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996) has generally been greeted as support for the idea that motor areas play an essential role in understanding observed actions and the inference of the pursued goals of these actions, as these neurons fire upon both observing and executing actions, leading to the idea that the observer simulates the observed action (Gallese & Goldman, 1998). This suggestion was further backed up by the finding that the human motor system becomes activated during action observation (Buccino et al., 2001; Buccino, Binkofski, & Riggio, 2004; Fadiga, Craighero, & Olivier, 2005; Rizzolatti & Craighero, 2004). Due to the supposedly direct and non-inferential character of this process, this phenomenon is often referred to as “motor resonance.”

Ever since the discovery of mirror neurons, many fascinating findings have been reported. However, the explanatory power of mirror neurons regarding action understanding has fallen out of step with the continuing stream of experiments and accompanying findings. Theories on the mirror-neuron system (MNS) and motor resonance have recently received criticism (Dinstein, Thomas, Behrmann, & Heeger, 2008; Hickok, 2009; Jacob, 2008). The general purport of this criticism is that mirror neurons cannot account for certain experimental findings (Hickok, 2009; Saxe, 2005a, 2009), or that the generalization from monkey data to the human MNS is not warranted (Dinstein et al., 2008; Lingnau, Gesierich, & Caramazza, 2009). Theoretical concerns about the limitation of action understanding by means of direct-matching have also been raised (Csibra, 2007; Jacob & Jeannerod, 2005; Uithol, van Rooij, Bekkering, & Haselager, in press).

Correspondence should be addressed to: S. Uithol, Donders Institute for Brain, Cognition and Behaviour, Spinoza Building, B01.03, PO Box 9104, 6500 HE Nijmegen, Netherlands. E-mail: Uithol@donders.ru.nl

The present study was supported by a Donders internal graduation grant to the second and last authors, and the EU-Project Joint Action Science and Technology (IST-FP6-003747) grant and an NWO-VICI grant to the last author. The authors wish to thank Janny Stapel for commenting on an earlier draft of this paper.

It is not the purpose of this paper to review the extensive body of research on mirror neurons and to argue for a specific framework in which the experimental findings are best explained. To a large extent, we will remain neutral on these matters. Instead, we will show that the ongoing discussion of the function of motor resonance often makes use of imprecise terminology. Due to the use of ambiguous concepts on both sides, the discussion between proponents and critics of motor resonance-based theories of action understanding advances only with great difficulty. By means of a careful analysis of the concepts of “motor resonance,” “action understanding,” and “action goals,” we aim to clarify the troubled debate on motor theories of action understanding and the role mirror neurons play.

The notion “motor resonance” appears to be used ambiguously in the literature on the MNS. At least two fundamentally different interpretations of the notion of resonance are used in neurocognitive explanations of the MNS, which we will call *intrapersonal* and *interpersonal resonance*. Each interpretation has different elements taking part in the resonance process. Next we will show that three qualitatively different interpretations can be found of what the goal of an action is: the goal as a more abstract action, the goal as a graspable object, and the goal as a desired world state. We will discuss these three interpretations. Finally, we will show that the notion of action understanding can describe three different cognitive functions, which we will label *action recognition*, *goal recognition*, and *action anticipation*. An overview of the different interpretations and our terminology is shown in Table 1. The interpretations will be discussed in detail below.

It is important to note that none of these interpretations is in itself right or wrong, or better than another one. As long as it is specified what is precisely meant by a notion, any of the interpretations is valid and could fulfill a role in theories on action understanding.

A consequence of this variability in interpretations is that the exact meaning of any claim about motor resonance, action goals, and action understanding that does not specify which of the interpretations of these notions is used can vary to a great extent. A careful analysis of these claims allows better interpretation of theories about underlying neurocognitive matching mechanisms of action observation and action execution, and can help guide the design of future experiments. We will discuss an existing experiment from the literature, Umiltà et al.’s (2001) mirror-neuron paper, as a case study and illustrate how the experimental data and the interpretation of them have diverged as a result of the above-mentioned indeterminacy of terminology. As an indication of the empirical applicability of the distinctions we propose, we will finish by presenting a concrete suggestion of how this study could be adapted so that other interpretations of the concepts presented in Table 1 can be tested.

RESONANCE

In the literature on the MNS, the notion of resonance is used to describe the activation of the motor system during action observation. The notion is adopted from physics and is used to describe the phenomenon that one (part of a) system oscillates at the same frequency and in the same phase as another (part of

TABLE 1
The possible interpretations of resonance, action goal, and action understanding, as found in the literature

<i>Notion</i>	<i>Interpretation</i>	<i>Explanation</i>	<i>Example</i>
Resonance	Intrapersonal	Resonance between visual and motor areas	Visual representation of grip type is propagated to motor areas
	Interpersonal	Resonance between observer and executor of action	Both observer and executor have representation of grasp action in motor areas
Action goal	Action	Action of higher abstraction than observed action	Drinking
	Object	Object at which the action is directed	Cup
	World state	Desired world state that can be achieved by action	A full cup of coffee
Action understanding	Action recognition	Recognition of observed action	Recognize action as grasping
	Goal recognition	Recognition of goal of an action	Recognize grasping action as serving drinking
	Action anticipation	Generation of response to observed action	Prepare grasping action when offered a cup.

the) system. In the neurocognitive domain, it is not claimed that the motor system is literally resonating in the sense that premotor neurons are firing in the same frequency and phase as neurons in other areas (we will come to the question of what areas soon). These claims should thus not be read as claims about *neural synchrony* (Damasio, 1989; Ward, 2003) or *neural oscillation* (Fries, 2005). Instead, a more liberal sense of the notion is usually adopted. Rizzolatti et al. (2001, p. 661) write, “We understand actions when we map the visual representation of the observed action onto our motor representation of the same action.” Elsewhere (Rizzolatti & Craighero, 2004, p. 172), it is explained: “The proposed mechanism is rather simple. Each time an individual sees an action done by another individual, neurons that represent that action are activated in the observer’s premotor cortex.... the motor ‘resonance’ translates the visual experience into an internal ‘personal knowledge.’” This process is often characterized as a form of simulation, in which the observer simulates the observed motor act in order to understand it (Decety & Grezes, 2006; Gallese & Goldman, 1998).

When we examine the literature on mirror neurons and action understanding, two different meanings or interpretations of the notion can be discovered, each having different elements participate in the resonance process. We will call these two interpretations *intrapersonal resonance* and *interpersonal resonance*.

In the intrapersonal interpretation of resonance, it is claimed that the motor system of the observer of an action resonates with her own perceptual system, so both brain areas taking part in the resonance process lie within the same person. Examples of this kind of use can be found in, for example, Rizzolatti, Fogassi, and Gallese (2001), Rizzolatti and Craighero (2004), and Buccino et al. (2004).

The idea is that the observation of an event leads to a representation in the perceptual system of the observer. This perceptual representation is thereupon propagated to the motor system. When the perceived event is an action and a matching motor representation is available, the motor system resonates like a tuning fork that starts to resonate when a note of the right pitch is played nearby (Jacob, 2009; Saxe, 2005b). As the resonance of the tuning fork provides information about the pitch of the note played, the resonance of the motor system provides information about the action that is perceived. This is possible, according to the theory, because the resonance is specific for different actions. For example, at the observation of a certain grasping action, such as a precision grip, a motor representation corresponding with that specific grasping action is activated in the motor system. The observer

“recognizes” the activity in her motor system as being a representation of the specific grasping action, and she thereby recognizes the observed precision grip action. As the coupling of a perceptual representation to a motor representation happens unmediated by higher cognitive processes, this theory is also known as the *direct-matching hypothesis* (Iacoboni et al., 1999; Rizzolatti et al., 2001; Rizzolatti & Sinigaglia, 2010).

Figure 1 depicts the causal chain from a motor plan in the executor to an action representation in the observer, and the place where intrapersonal resonance occurs.¹

The strongest evidence for this theory comes from single-cell recordings in macaque monkeys. Neurons in the inferior premotor areas were shown to fire selectively for different actions and action means, such as precision and power grips, both performed and observed (Di Pellegrino et al., 1992; Gallese et al., 1996; Rizzolatti et al., 1996). This has led to the conclusion that these areas are involved in the recognition (and understanding) of actions. These monkey data were backed up by imaging data that showed that the human motor system is activated differently upon observations of different actions (Buccino et al., 2001, 2004; Fadiga et al., 2005; Rizzolatti & Craighero, 2004).

This theory can elegantly account for the finding that mirror neurons do not fire when the observed event is not an action (Gallese et al., 1996), or when the action is carried out by a non-biological effector (e.g., a robot arm) (Kilner, Friston, & Frith, 2007; Tai, Scherfner, Brooks, Sawamoto, & Castiello, 2004). Resonance occurs when a matching motor representation is available, so when the perceived event is not an action or an action that is carried out by a non-biological effector, there is no matching motor representation and the motor system remains silent.²

In a second interpretation, the notion of resonance is used to denote functional correspondence between the states in the motor system of the observer and that of the executor of an action. This view is present in the work of, for instance, Decety and Grezes (2006), de Vignemond and Haggard (2008), Fadiga et al.

¹ It is still debated whether the final action representation—provided that such a representation exists—resides in motor areas (as embodied approaches to cognition argue) or whether there are disembodied representations of actions. Here we choose not to take a side in this debate.

² There are experiments, such as those of Fogassi et al. (2005) and Umiltà et al. (2008), that show mirror-neuron response to tool-based actions, but this was only after extensive training with tools. A possible explanation is that, through training with tools, the monkey creates a motor representation of these actions.

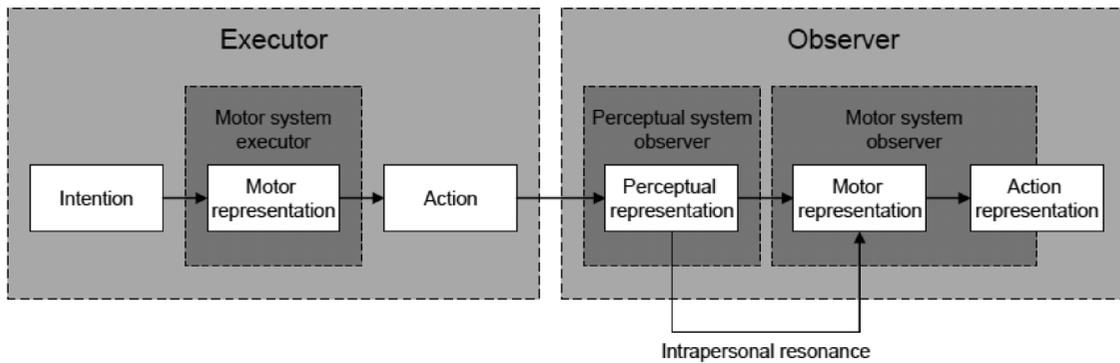


Figure 1. The causal path from action plan in the executor to action representation in the observer and the location of intrapersonal resonance.

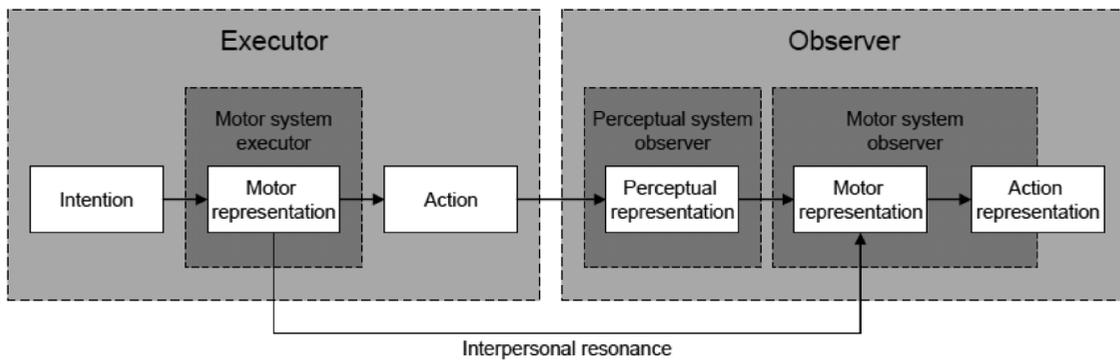


Figure 2. The causal path from action plan in the executor to action representation in the observer as presumed in motor theories of action understanding, and the two parts of the system that take part in interpersonal resonance.

(2005), Gallese (2001), Jacob (2008), and Wilson and Knoblich (2005). As the two systems taking part in the resonance process are situated in two different persons, we will call this form of resonance *interpersonal resonance*.

In the interpersonal interpretation of resonance, the notion is used in an even more metaphorical sense. It is assumed that there is a semantic or functional resemblance between the motor representation in the observer of an action and the motor representation of the executor of the action (e.g., both motor systems represent a grasping action at the same time). In a sense, the observer and the executor of an action share a representation (de Vignemont & Haggard, 2008). It is therefore stated that the observer's motor system resonates with that of the executor (Gallese, 2001; Gallese & Goldman, 1998; Goldman, 2009; Jacob, 2008; Wilson & Knoblich, 2005) or, in shorter form, that the observer resonates with the executor (Fadiga et al., 2005). Figure 2 shows the presumed causal sequence from an action plan in the executor to a representation of that action in the observer. The two elements that take part in the interpersonal resonance are marked with an arrow.

Resonance in the interpersonal meaning is a higher-level description of the result of various processes from a motor representation in the executor to an activated motor system in the observer. It describes a resemblance between the two motor systems, and it can be established without making claims about the underlying mechanism. This is evident from Figure 2: The resonance process covers multiple causal steps that can be accomplished by various underlying mechanisms. This interpretation of resonance is not committed to specific mechanisms bringing about these steps. Usually, a form of intrapersonal resonance is presumed to establish interpersonal resonance, but this is not necessarily the only option: An inferential process could also result in interpersonal resonance.

SETTING GOALS

It is often claimed that motor resonance allows the recognition of not only the action as such, but also of the goal that is served by the action (Iacoboni et al., 2005; Rizzolatti et al., 2001; Rizzolatti & Sinigaglia, 2010). Yet, like the notion of motor resonance, the

notion of goal allows for various interpretations. A survey of the literature on mirror neurons yields three qualitatively different interpretations of the goal of an action.

First, the goal of an action is often interpreted as another, less specific action that is abstracted from execution specifics. For example, Gallese et al. (1996) classify mirror neurons as broadly congruent when the neurons appear to be activated by the goal of the observed action, regardless of how it was achieved. An example of such a goal could be “grasping,” and grasping with a precision grip, grasping with a full-hand grip, and grasping with the mouth all serve the goal of grasping. The goal-as-an-action interpretation is also present in the work of Ferrari, Rozzi, & Fogassi (2005), Fogassi et al. (2005), and Iacoboni (2005), and it predominates in the early papers on mirror neurons (Gallese et al., 1996; Rizzolatti et al., 1996).

The fact that the goal of an action is itself another action is potentially problematic, as nearly every action itself can be said to serve a new, higher goal. To illustrate, the action “grasping a cup,” can serve the goal, “drinking.” Thus conceived, drinking is an action goal. “Drinking,” however, can also be considered an action, having “quenching thirst” or “engaging in social activity” as a goal. Quenching thirst serves the goal “maintaining homeostasis,” which serves the goal “survival,” and so on. There thus exists a continuum from concrete, readily observable events (the use of a precision grip) to highly abstract events (survival).³ Although individual preferences may be possible, there seems to be no a priori level at which actions are located and a level at which action goals are located.

Umiltà et al. (2008) provide a clear example of goals and actions lying on the same continuum. Macaque monkeys were trained to use normal and reverse pliers to grasp objects. The researchers found that the same motor neurons that under normal conditions fire when an object is grasped, also fire when the object is grasped with reversed pliers, which means that the hand needs to be opened to grasp the object. This suggests that these motor neurons respond to the act of grasping (an action higher in the continuum)

³ Besides actions and action goals, two more related notions can be found in the literature. An “action means” is a particular way of performing an action. Action means also lie on the same continuum as actions and goals, and can therefore, upon different interpretations, also be actions themselves. The notion “movement” is often used to denote a movement that does not serve a goal—see, for instance, Gallese and Goldman (1998) or Hommel (2003). Action thus conceived is a subclass of movements; that is, those movements that serve a goal.

and not the motor act of closing the hand (an action lower in the continuum). Although not discussed in the paper, it is not difficult to see how the grasping with pliers serves actions of even higher abstraction, such as eating. Fogassi and his colleagues, for instance, found different responses in mirror neurons, depending on whether the grasping action was part of an eating action or a placing action (Fogassi et al., 2005). In all, because interpretations on all levels are possible, a clear indication of the level at which the analysis takes place can be helpful in interpreting the findings correctly.

A second interpretation of the goal of an action is a target object. It is this interpretation that has given us the term “goal-directed action,” meaning a transitive or object-directed action.⁴ This interpretation can be found in, for instance, Umiltà et al. (2001, p. 161), who state that “mirror neurons have to infer and represent the occluded specific action in addition to the inferred object, which is the goal of the action.”⁵ This interpretation of goals is also often present in the early mirror-neuron papers (Gallese et al., 1996; Rizzolatti et al., 1996), but also later (Hamilton & Grafton, 2006). Similar to this is the interpretation of a goal as a point in space, such as a cross on the desk (Wohlschläger & Bekkering, 2002) or the end location of an action (Bekkering, Wohlschläger, & Gattis, 2000). At other places, the goal as an object is contrasted with the goal as a location (Hamilton & Grafton, 2006).

A third interpretation of goal is a desired state of the world. A possible state could be “a full cup of coffee” and several actions—picking up the coffee pot, transferring it to the cup, tilting the coffee pot, etc.—are needed in succession to reach that state. This interpretation can be found in, for example, Csibra and Gergeley (2007), Grafton and Hamilton (2007), or Sebanz, Bekkering, and Knoblich (2006).

These interpretations do not necessarily exclude each other. For example, “taking possession of an object” seems to have aspects of all three interpretations. First, taking possession can be viewed as an

⁴ As we said in footnote 3, the difference between a movement and an action is often taken to be that the latter serves a goal and the former does not. This would entail that every action serves a goal, making the term “goal-directed action” a pleonasm for other interpretations of “goal”, as non-goal-directed actions cannot exist—just non-goal-directed movements.

⁵ This statement illustrates how terminology can cause confusion. Apart from the personal/subpersonal violation, the claim that “mirror neurons infer” also departs from the initial claims that mirror neurons engage in direct reflection and no inferential processes are needed. See Uithol et al. (submitted) for a more detailed discussion on direct reflection versus inferential processing with respect to mirror neurons.

action that can be executed in different ways (grasping, ordering, buying). Second and obviously, this action is directed toward an object. Third, taking possession of an object can be viewed as reaching a world state in which a certain object is in my possession (in my hands, my mouth, my stomach). In general, the difference between the interpretation of goal as another action and goal as a desired world state seems to be a matter of emphasis. Sometimes one of the interpretations is more natural or evident; sometimes the other. For example, when one or two persons are carrying a table out of the room (Sebanz et al., 2006), it is generally not the action that one is interested in; it is a state of the world in which the table is located outside the room. In other cases, such as eating and drinking, it is not so much the world state that a person is interested in, but the action itself: The person enjoys the action of eating or drinking. Of course eating serves a purpose and is a mechanism by which a species acquires necessary nutrients. So in a way one could say that having the food in one's stomach is a desired world state albeit often an unconscious one, but this seems a rather awkward way of phrasing a goal.

Notwithstanding the possible overlap, the differences can be crucial. The meaning of the claim that mirror neurons respond selectively to goals can differ to a great extent in the three different interpretations of "goal." For example, recognizing that an action is directed toward a cup and recognizing that this cup-grasping contributes to getting a clean table are two quite different capacities that require different experiments for testing the nature of motor activation. As a consequence, experimental results that support a certain neuroscientific hypothesis (e.g., about neural mechanisms underlying goal understanding) under one interpretation of goal understanding do not automatically support that same hypothesis under other interpretations of goal understanding. Fogassi et al.'s (2005) study on parietal mirror neurons provides a clear example of an experimental setup where precise terminology is crucial. The researchers found mirror neurons in the monkey's inferior parietal lobule that responded selectively for different intentions underlying the same actions. Monkeys were trained to grasp a piece of food and either place it in a container on their shoulder or eat it. Some neurons responded differently for these two intentions. Importantly, in some neurons, this difference in firing was preserved when the monkeys observed the experimenters perform the same actions. Because Fogassi and his colleagues use the unambiguous notions "object" and "intention" to denote the different interpretations of goal (although the latter is sometimes also referred to as "goal"), there is no confusion or conflation of the notion "goal"

here. However, if Fogassi and his colleagues had used the notion "goal" in both the meaning of object and intention—as can be found elsewhere in literature, as shown above—then the finding that the recognition of an object can cause the recognition of the intention of the actor would result in a circular statement about goal recognition causing goal recognition.

Hamilton and Grafton (2007) provide an illustration of all three uses of this notion. In their introduction, they discuss goals as being a desired world state (e.g., getting refreshment), and they refer to goal-dependent mirror neuron firing in the meaning of a more abstract action, while their experiments are based on the object interpretation of goals. The authors themselves seem to be aware of the differences in interpretation when they write, "It is also important to note that the goals we have studied were defined by the identity of the object taken by the actor, contrasting between a 'take wine bottle' goal and a 'take dumbbell goal.' It remains to be seen if the same parietal regions encode other types of goal, for example manipulating the same object in different ways." Yet, the discussion of these other interpretations in the introduction, and the fact that the authors do not further specify their interpretation of goal throughout the paper could easily entice other researchers into applying the results to the other interpretations as well. In the section entitled "Diverging concepts," we will discuss a case in which, upon systematic conceptual analysis, the original experimental setup no longer matches subsequent interpretations by other authors.

UNDERSTANDING ACTION

What is meant by "action understanding" differs from paper to paper. The difficulty with the notion is that it consists of two elements, *action* and *understanding*, and the meaning of these elements is interdependent and open to different interpretations. To start with actions: We have seen that action means, actions, and action goals can be placed on a continuum from specific, readily observable events (e.g., the use of a precision grip) to highly abstract events (maintaining homeostasis), and there seems to be no a priori way to make a clear-cut and objective contrast between action means, actions, and action goals.

Despite the lack of a priori considerations for contrasting actions with goals in this interpretation of goals, it seems that the capacity to understand grip types differs to such an extent from the capacity to understand homeostasis that differentiation is necessary. With the mirror-neuron literature in mind, we will limit the use of the notion "action" to movements that

exist in the here and now and that serve a goal, such as grasps. We use the label “goals” for more abstract actions than the observed one, in the sense that they either are nonvisible (like maintaining homeostasis or keeping to one’s diet) or involve future actions (grasping *in order to clean up the table*; cleaning up the table might be a visible action, but it is not yet observed at the time of picking up a cup).

The fact that actions can be found along a broad continuum of increasing abstraction has consequences for the interpretation of “understanding.” Understanding can mean recognition (i.e., a form of classification: “That’s a precision grip”), but also recognizing the goal that is served by an action (“That’s grasping *to eat*”). However, as we have just seen, what is considered to be an action and what is the goal of an action, are liable to interpretation. This makes the difference between recognizing an action and recognizing the goal of an action also a matter of interpretation. To stick with the drinking example, when “grasping a cup” is interpreted as an action, the goal of the action can be “to drink.” So the action can be recognized (“that’s grasping”), or its goal can be recognized (“that’s drinking”). When, however, we see drinking as an action, and quenching thirst as the goal of an action, then “that’s drinking” is a matter of action recognition, and “that’s quenching thirst” is understanding the goal of the action.

Many authors seem to pitch their interpretation of action understanding somewhere along this continuum, but very few delimit or make their interpretation explicit. This makes it difficult to assess the exact claims that are made. For example, Rizzolatti and Craighero (2004, p. 172) state, “This automatically induced, motor representation of the observed action corresponds to that which is spontaneously generated during active action and whose *outcome* is known to the acting individual” (our italics). Without specification, this “outcome” can mean anything from a precision grip to maintaining homeostasis. However, the claim that the MNS detects grip types is quite different from (and more modest than) the claim that the MNS is capable of detecting long-term goals or intentions. The two claims presume different capacities of the system and demand different tests to verify them.

Beside recognizing the action and recognizing the goal an action serves, a third interpretation is that understanding an action is “knowing how to respond appropriately to an observed action” (Gallese et al., 1996; Rizzolatti et al., 2001). For example, Rizzolatti et al. (2001, p. 661) write: “By action understanding, we mean the capacity to achieve the internal description of an action and *to use it to organize appropriate future behavior*” (our italics). So in addition to

“the capacity to achieve the internal description of an action,” which is in line with the first interpretation, this definition adds that it should be used to generate an appropriate response.

Again, the different interpretations of action understanding refer to capacities that can differ to a large extent, so we will have to disentangle them. We will use the term “action recognition” when we mean the classification of an action and the ability to differentiate it from other actions. By “goal recognition,” we mean classification of the goal of an action. This goal can be an action more abstract than the movement that takes place in the here and now, as discussed above, or another interpretation of goal, as discussed in the previous paragraph. Knowing how to respond appropriately to an action we will call “action response.” Table 1 presents an overview of these different interpretations.

To illustrate the empirical relevance of our conceptual discussion and terminological distinctions, we will analyze a well-known mirror-neuron study by Umiltà et al. (2001) that produced fascinating results. We will show that a univocal interpretation of the experimental data is troubled by the use of indefinite terms. As a result, their data is often interpreted as supporting mirror neurons involvement in forms of goal understanding, while, in our terminology, only action recognition is demonstrated.

DIVERGING CONCEPTS

Umiltà and her colleagues (2001) had monkeys watch grasping actions with the object to be grasped occluded from the monkey’s sight. By means of single-cell recordings, they showed that the monkey’s mirror neurons that normally respond to the observation of a certain action also respond when the final, crucial part of that action was hidden. This shows that the build-up to the action (e.g., the opening of the hand and the reaching toward an object) is enough to trigger the mirror-neuron response, and that observation of the actual action (the grasping of an object) is not necessary. The authors conclude that these findings support the idea that the goal of an action can be recognized, even when the monkey is provided with an incomplete perception of an action, provided that the monkey knew that there was an object behind the occluder. They subsequently conclude that their findings “further corroborate the previously suggested hypothesis that the mirror neurons’ matching mechanism could underpin action understanding” (p. 161); a conclusion that is subsequently adopted by others (e.g., Ferrari et al., 2005; Rizzolatti & Sinigaglia, 2010).

However, interpretation of these findings is not straightforward. We have shown that three different interpretations of both the notions “action understanding” and “action goal” circulate (let alone the range of abstraction on which actions and goals can be formulated). Umiltà and colleagues showed that certain mirror neurons that fire upon observing a certain action also fire when the final part of the action was occluded. As the neuron exclusively fires upon viewing actions of this type, this is a form of what we would call action recognition: the recognition and classification of an action. Their interpretation of “goal” is that of “object,” as becomes clear in phrases like “the inferred object, which is the goal of the action” (p. 161).

So, when we rephrase their findings in our systematic terminology (see Table 1), this experiment shows that the *recognition* of an action depends on knowledge of the presence of a graspable object. This suggests that the monkey understands that the observed movement is grasping only when it knows that it is directed toward an object. This finding is in line with early mirror-neuron studies (e.g., Gallese et al., 1996; Rizzolatti et al., 1996) that also found that mirror neurons did not respond to mimed actions (i.e., actions not directed toward an object). These studies show that mirroring in order to recognize actions involves more than mirroring the kinematic features, as these features in mimed actions are identical to object-directed actions but do not evoke mirror-neuron response.

However, the findings of this experiment cannot be used to draw conclusions regarding goal understanding, that is, inferring the goal that is served by a certain action from observation of that action alone, as the data show that the presence of a goal in the object sense is a prerequisite for the recognition of the action.

So the tenability of the claim that these findings “further corroborate the previously suggested hypothesis that the mirror neurons’ matching mechanism could underpin action understanding” depends on what is meant by both the “previously suggested hypothesis” and “action understanding.” Regarding the first, support for the direct-matching hypothesis (Rizzolatti et al., 2001) is problematic. This hypothesis states that the visual representation of the observed action (i.e., the kinematic features of the movement) is mapped onto the motor representation of the same action, and when a matching motor representation exists, resonance occurs and the action is recognized. According to this hypothesis, action recognition thereby enables goal inference, as the observer of the action knows, from his own experience, which goal is (usually) served by the recognized action.

When we try to explain Umiltà et al.’s data within the framework of the direct-matching hypothesis, we seem to run into some circularity: Goal recognition is a prerequisite for action recognition, yet, according to the direct-matching hypothesis, action recognition is a prerequisite for goal inference.

In their 2010 paper, Rizzolatti and Sinigaglia have reformulated the direct-matching hypothesis. In this formulation, action mirroring is rendered as a dual-route process, with one route directly matching movements and the other mapping the goal of the observed motor act onto the observer’s own motor repertoire. When these routes are genuinely parallel, action recognition no longer is a prerequisite for goal recognition, but these two processes take place simultaneously and independently.

However, support for this revised direct-matching hypothesis is also problematic, and now what is meant by action understanding becomes crucial. When action understanding is taken to mean action recognition, then these data can only provide support for half the reformulated hypothesis. Umiltà et al. found neurons that respond selectively to different actions, and this can only support the already well-established part of the revised direct-matching hypothesis: the direct matching of actions. No evidence is provided for the second route: the direct matching of goals.

When action understanding is taken to mean goal recognition, the findings cannot support the direct-matching hypothesis, as only action recognition is established, and according to the revised formulation of the hypothesis, action recognition does not underpin goal recognition, but goal recognition takes place independently along a different route.

In all, these findings seem more in line with competing hypotheses, such as Csibra’s (2007) or Jacob’s (2008), that state that action understanding is modulated by non-mirroring processes, such as processing of the presence of an object.

Based on proper distinctions of terms, as done in Table 1, we have been able to reveal difficulties in the interpretation of data in the literature. We have given an example of how our conceptual work can help analyze existing data, allowing for a more precise match between empirical results and conceptual interpretations. Next we will show that this conceptual analysis can also help guide the design of new experiments in such a way that conceptual confusion can be prevented. As an illustration of one such possible experiment, we will discuss how Umiltà et al.’s (2001) experiment can be modified in a way to test a different interpretation of the concepts in Table 1.

Let us interpret “action understanding” as “goal recognition,” and let us stick to the interpretation of

goal as object. In that case, “goal recognition” means “recognizing what object an action is directed at.” One way to test mirror neurons’ contribution to goal recognition in this sense is to identify mirror neurons that fire differently upon grasping actions toward different objects. This could be done by placing two objects instead of one behind the occluder, each demanding a different grip type (say, an apple and a peanut, demanding a full hand grip and a precision grip respectively). When the monkey knows that only one of the objects is placed behind the occluder, and this object is approached with the wrong grip type, mirror neurons that fire for that grip type should remain silent, as this action cannot have the object behind the occluder as its goal. For example, the monkey knows that there is only an apple, but observes a grasping action with precision grip toward the occluder. When mirror neurons that respond only to actions performed with a precision grip remain silent (as they should when they fire selectively for different objects and there is no appropriate object behind the occluder), it could be considered further evidence that mirror neurons’ firing characteristics are dependent on the object that an action is directed at. Failure to demonstrate the ability of mirror neurons to “recognize” the wrong grip for the object behind the occluder could be considered evidence against the idea that mirror neurons contribute to goal recognition when the goal is interpreted as the target object of an action.

In all, different interpretations of the concepts used in theories on action understanding demand different experimental setups. We have given an example of how Umiltà et al.’s (2001) experiment can be modified in such ways that other interpretation of the concept of action understanding could be tested. Other interpretations of action understanding and goal will each require a different setup tuned specifically to the conceptualization and hypothesis that one intends to test.

CONCLUSION

The exact meaning of any statement involving action understanding, goal recognition, and motor resonance can vary to a great extent, depending on the interpretation of the concepts used. In the cognitive neuroscience literature, it is often not explicated which of the multitude of possible interpretations are used. As a result, different sets of experimental data can be taken in mutual support of neuroscientific hypotheses, even though interpretations might diverge in ways that make the result in fact incompatible.

By means of a careful conceptual analysis, we aimed to disentangle the different possible

interpretations of “action understanding”, “action goals,” and “motor resonance.” The fine-grained distinctions we have proposed, exemplified in Table 1, allow better interpretations of experimental data and more adequate design of experiments. We have shown that our proposed systematic labeling scheme is empirically relevant in interpreting research data, by showing how the use of the scheme leads to a reinterpretation of existing experimental results in the cognitive neuroscience literature. Moreover, we have illustrated how our scheme can guide the design of experimental setups aimed to test different interpretations of action understanding.

The systematic use of well-defined concepts is an important aspect of the constructive and fruitful analysis of experimental data. In this paper, we performed a conceptual analysis to arrive at more precise and unequivocal definitions of the terms “action understanding,” “action goal,” and “motor resonance,” terms that are central to the cognitive neuroscientific study of action and perception. We hope to have shown that the types of conceptual analyses that we performed in this paper are not mere theoretical exercises, but a constructive contribution to the empirical cognitive neuroscience.

Original manuscript received 2 September 2010

Revised manuscript accepted 24 January 2011

First published online day/month/year

REFERENCES

- Bekkering, H., Wohlschläger, A., & Gattis, M. (2000). Imitation of gestures in children is goal-directed. *Quarterly Journal of Experimental Psychology. A, Human Experimental Psychology*, *53*(1), 153–164.
- Buccino, G., Binkofski, F., Fink, G. R., Fadiga, L., Fogassi, L., Gallese, V., et al. (2001). Action observation activates premotor and parietal areas in a somatotopic manner: An fMRI study. *European Journal of Neuroscience*, *13*(2), 400–404.
- Buccino, G., Binkofski, F., & Riggio, L. (2004). The mirror neuron system and action recognition. *Brain and Language*, *89*(2), 370–376.
- Csibra, G. (2007). Action mirroring and action interpretation: An alternative account. In P. Haggard, Y. Rosetti, & M. Kawato (Eds.), *Sensorimotor foundations of higher cognition. Attention and performance XXII* (pp. 427–451). Oxford, UK: Oxford University Press.
- Csibra, G., & Gergely, G. (2007). ‘Obsessed with goals’: Functions and mechanisms of teleological interpretation of actions in humans. *Acta Psychologica*, *124*(1), 60–78.
- Damasio, A. R. (1989). Time-locked multiregional retroactivation: A systems-level proposal for the neural substrates of recall and recognition. *Cognition*, *33*, 25–62.
- Decety, J., & Grezes, J. (2006). The power of simulation: Imagining one’s own and others’ behavior. *Brain Research*, *1079*, 4–14.

- de Vignemont, F., & Haggard, P. (2008). Action observation and execution: What is shared? *Social Neuroscience*, 3(3), 421–433.
- Dinstein, I., Thomas, C., Behrmann, M., & Heeger, D. J. (2008). A mirror up to nature. *Current Biology*, 18(3), R13–R18.
- Di Pellegrino, G., Fadiga, L., Fogassi, L., Gallese, V., & Rizzolatti, G. (1992). Understanding motor events: A neurophysiological study. *Experimental Brain Research*, 91(1), 176–180.
- Fadiga, L., Craighero, L., & Olivier, E. (2005). Human motor cortex excitability during the perception of others' action. *Current Opinion in Neurobiology*, 15(2), 213–218.
- Ferrari, P. F., Rozzi, S., & Fogassi, L. (2005). Mirror neurons responding to observation of actions made with tools in monkey ventral premotor cortex. *Journal of Cognitive Neuroscience*, 17(2), 212–226.
- Fogassi, L., Ferrari, P. F., Gesierich, B., Rozzi, S., Chersi, F., & Rizzolatti, G. (2005). Parietal lobe: From action organization to intention understanding. *Science*, 308(5722), 662–666.
- Fries, P. (2005). A mechanism for cognitive dynamics: Neuronal communication through neuronal coherence. *Trends in Cognitive Sciences*, 9(10), 474–480.
- Gallese, V. (2001). The 'shared manifold' hypothesis: From mirror neurons to empathy. *Journal of Consciousness Studies*, 8(5–7), 33–50.
- Gallese, V., Fadiga, L., Fogassi, L., & Rizzolatti, G. (1996). Action recognition in the premotor cortex. *Brain*, 119(2), 593–610.
- Gallese, V., & Goldman, A. (1998). Mirror neurons and the simulation theory of mind-reading. *Trends in Cognitive Sciences*, 2(12), 493–501.
- Goldman, A. I. (2009). Mirroring, simulating and mindreading. *Mind & Language*, 24(2), 235–252.
- Grafton, S. T., & Hamilton, A. F. D. (2007). Evidence for a distributed hierarchy of action representation in the brain. *Human Movement Science*, 26(4), 590–616.
- Hamilton, A. F. d. C., & Grafton, S. T. (2006). Goal representation in human anterior intraparietal sulcus. *Journal of Neuroscience*, 26(4), 1133–1137.
- Hickok, G. (2009). Eight problems for the mirror neuron theory of action understanding in monkeys and humans. *Journal of Cognitive Neuroscience*, 21(7), 1229–1243.
- Hommel, B. (2003). Planning and representing intentional action. *Scientific World*, 3, 593–608.
- Hommel, B., Müsseler, J., Aschersleben, G., & Prinz, W. (2001). The theory of event coding (TEC): A framework for perception and action planning. *Behavioral and Brain Sciences*, 24(5), 849–877.
- Iacoboni, M. (2005). Neural mechanisms of imitation. *Current Opinion in Neurobiology*, 15(6), 632–637.
- Iacoboni, M., Molnar-Szakacs, I., Gallese, V., Buccino, G., Mazziotta, J., & Rizzolatti, G. (2005). Grasping the intentions of others with one's own mirror neuron system. *PLoS Biology*, 3(3), e79.
- Iacoboni, M., Woods, R. P., Brass, M., Bekkering, H., Mazziotta, J. C., & Rizzolatti, G. (1999). Cortical mechanisms of human imitation. *Science*, 286(5449), 2526–2528.
- Jacob, P. (2008). What do mirror neurons contribute to human social cognition? *Mind & Language*, 23(2), 190–223.
- Jacob, P. (2009). A philosopher's reflections on the discovery of mirror neurons. *Topics in Cognitive Science*, 1(3), 570–595.
- Jacob, P., & Jeannerod, M. (2005). The motor theory of social cognition: A critique. *Trends in Cognitive Sciences*, 9(1), 21–25.
- Kilner, J. M., Friston, K. J., & Frith, C. D. (2007). Predictive coding: An account of the mirror neuron system. *Cognitive Processing*, 8, 159–166.
- Lingnau, A., Gesierich, B., & Caramazza, A. (2009). Asymmetric fMRI adaptation reveals no evidence for mirror neurons in humans. *Proceedings of the National Academy of Sciences of the United States of America*, 106(24), 9925–9930.
- Rizzolatti, G., & Craighero, L. (2004). The mirror-neuron system. *Annual Review of Neuroscience*, 27, 169–192.
- Rizzolatti, G., Fadiga, L., Gallese, V., & Fogassi, L. (1996). Premotor cortex and the recognition of motor actions. *Cognitive Brain Research*, 3(2), 131–142.
- Rizzolatti, G., Fogassi, L., & Gallese, V. (2001). Neurophysiological mechanisms underlying the understanding and imitation of action. *Nature Reviews Neuroscience*, 2, 661–670.
- Rizzolatti, G., & Sinigaglia, C. (2010). The functional role of the parieto-frontal mirror circuit: Interpretations and misinterpretations. *Nature Reviews Neuroscience*, 11(4), 264–274.
- Saxe, R. (2005a). Against simulation: The argument from error. *Trends in Cognitive Sciences*, 9(4), 174–179.
- Saxe, R. (2005b). Tuning forks in the mind. *Trends in Cognitive Sciences*, 9(7), 321.
- Saxe, R. (2009). The neural evidence for simulation is weaker than I think you think it is. *Philosophical Studies*, 144(3), 447–456.
- Sebanz, N., Bekkering, H., & Knoblich, G. (2006). Joint action: Bodies and minds moving together. *Trends in Cognitive Sciences*, 10(2), 70–76.
- Tai, Y. F., Scherfler, C., Brooks, D. J., Sawamoto, N., & Castiello, U. (2004). The human premotor cortex is 'mirror' only for biological actions. *Current Biology*, 14(2), 117–120.
- Uithol, S., van Rooij, I., Bekkering, H., & Haselager, W. F. G. (in press). What do mirror neurons mirror? *Philosophical Psychology*.
- Umiltà, M. A., Escola, L., Intskirveli, I., Grammont, F., Rochat, M., Caruana, F., et al. (2008). When pliers become fingers in the monkey motor system. *Proceedings of the National Academy of Sciences of the United States of America*, 105(6), 2209–2213.
- Umiltà, M. A., Kohler, E., Gallese, V., Fogassi, L., Fadiga, L., Keysers, C., et al. (2001). I know what you are doing – a neurophysiological study. *Neuron*, 31(1), 155–165.
- Ward, L. M. (2003). Synchronous neural oscillations and cognitive processes. *Trends in Cognitive Sciences*, 7(12), 553–559.
- Wilson, M., & Knoblich, G. (2005). The case for motor involvement in perceiving conspecifics. *Psychological Bulletin*, 131(3), 460–473.
- Wohlschläger, A., & Bekkering, H. (2002). Is human imitation based on a mirror-neuron system? Some behavioural evidence. *Experimental Brain Research*, 143(3), 335–341.