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Conceptualizing and testing action understanding

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ABSTRACT

The term 'action understanding' has been defined in several ways since it was first proposed to describe the psychological process subserved by mirror neurons. Here we outline and critique these definitions of 'action understanding' in order to evaluate the claim that mirror neurons perform such a process. We delineate three distinct definitions of 'action understanding', each involving a distinct psychological process. *Action identification* comprises using the specific configurations of body parts in observed actions to identify those actions, whereas *goal identification* and *intention identification* involve generalising across different observed actions to identify the immediate goal of, or the hidden mental state motivating, the actions. This paper discusses the benefits and drawbacks of using these definitions to describe the process purportedly performed by mirror neurons. We then examine each definition in relation to the mirror neuron literature. We conclude that although there is some evidence consistent with the suggestion that mirror neurons contribute to action identification, there is little evidence to support the claim that they contribute to goal or intention identification.

1. Introduction

In order to communicate and interact successfully, we need to be able to identify the actions of others, infer the goal of their actions and extract the underlying intention behind them. These abilities – often grouped together under the umbrella term 'action understanding' (Gallese et al., 1996) – have been claimed to be involved in processes including recognition of the emotional states of others, action prediction, and the coordination of joint actions (Hamilton and Grafton, 1993; Sebanz and Knoblich, 2009). In turn, these processes are thought to be important for a range of social abilities, such as imitation (Iacoboni, 2009), empathy (Decety and Jackson, 2004; Nummenmaa et al., 2008) and theory of mind (Baron-Cohen et al., 1985); abilities which are considered crucial for human survival and success (Blakemore and Frith, 2004). Furthermore, impairments in these social abilities have been associated with a range of psychiatric conditions, including autism (Baron-Cohen et al., 1985; Huang et al., 2016; Trimmer et al., 2016; Williams et al., 2004; although see Leighton et al., 2008; Press et al., 2010) and schizophrenia (Frith and Corcoran, 1996; Lee et al., 2011; Matthews et al., 2013). Therefore, investigating the mechanisms involved in processing others' actions is essential for our understanding of a range of social abilities and may contribute to our understanding of psychiatric conditions. However, at present, research in this area is hampered by lack of consensus as to what is meant by the term 'action understanding', making it difficult to design tasks assessing this ability and hindering understanding of the neurocognitive mechanisms underlying it.

Until the mid 1990s, the processing of others' actions was treated as a purely perceptual process, known as biological motion perception, and evidence accumulated demonstrating that this function was performed in the superior temporal sulcus (STS). Using single-cell recording in the macaque, Perrett et al. (1985) found that the majority of cells in the STS responded to observed actions and were selective for type of observed action, with cells responding specifically to actions such as head turning, arm movements, and hand-object interactions including reaching, manipulating, tearing, and holding (Perrett et al., 1990). The perception of biological motion, therefore, was considered a separate function to that of action execution, which relies on motor networks. However, around this time, Rizzolatti et al. (1988) found that although neurons in premotor area F5 respond primarily during the execution of motor acts such as grasping, holding and tearing, a proportion of the neurons in this area also respond to sensory stimuli, including passive somatosensory or visual stimulation, in the absence of action. The investigation of the sensory properties of these motor cells led to the discovery of 'mirror' neurons in this area (di Pellegrino et al., 1992), and subsequently the consideration of motor involvement in the

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processing of others' actions.

Mirror neurons, found originally in frontal area F5 of the macaque monkey, are cells which fire to both the observation and execution of actions (di Pellegrino et al., 1992). The specificity of the relationship between the observed and executed action required for these neurons to fire differs across cells. Across the original studies of these neurons, between 15% and 61% of all sensorimotor neurons were 'broadly congruent', firing to observed and executed actions which shared only one general aspect of the movement (such as action type or grip type) and differed on other aspects (such as effector), while around 32% were 'strictly congruent', firing to the observation and execution of the same actions executed in a particular way (di Pellegrino et al., 1992; Gallese et al., 1996). A further subset of sensorimotor neurons (around 28%; di Pellegrino et al., 1992) responded to different actions when observed and executed. Such 'logically-related mirror neurons' have been investigated to a much lesser extent than congruent mirror neurons, and are largely absent from discussions relating to action understanding. Indeed, their existence has been argued to be problematic for claims that mirror neurons contribute to action understanding (Cook and Bird, 2013). Therefore, this paper will focus on broadly and strictly congruent mirror neurons and their potential relationship to action understanding.

Neurons with 'mirror' properties (that is, firing during both observation and execution of actions) have subsequently been found in the anterior intraparietal area, inferior parietal lobule, intraparietal sulcus, lateral intraparietal cortex, medial frontal cortex, ventral premotor cortex, dorsal premotor cortex, primary motor cortex, and ventral intraparietal area (Cisek and Kalaska, 2004; Fogassi et al., 2005; Fujii et al., 2007; Ishida et al., 2010; Pani et al., 2014; Shepherd et al., 2009; Tkach et al., 2007; Yoshida et al., 2011). Although direct recordings in humans are rare, one study provides direct evidence of mirror neurons in the human brain (Mukamel et al., 2010), and indirect evidence has been provided by a variety of neuroscientific techniques (Fadiga et al., 1995; Iacoboni et al., 1999; Kilner et al., 2009). The firing of these cells (or, in the human brain, the specificity of neural responses), to both the observation and execution of actions, suggests that an observed action may be mapped onto the same motor program that is used to execute that action in the observer. This pattern of neural responses makes plausible the suggestion that the processing of others' actions is not just perceptual, but has a motor aspect too.

The realisation that action processing might have a motor component led to the description of a new psychological process: 'action understanding', which was believed to be distinct from the processes involved in perceiving actions (Rizzolatti and Fadiga, 1998; Rizzolatti et al., 1996). However, the term 'action understanding' has generated considerable controversy (Cook et al., 2014; Hickok, 2009), with a range of definitions proposed (Gallese et al., 1996; Kilner, 2011; Rizzolatti and Craighero, 2004; Rizzolatti and Sinigaglia, 2010). This situation is particularly problematic because studies of the contribution of mirror neurons (or, in the human brain, areas with mirror responses) to action understanding that have used different definitions of action understanding (e.g. Spunt and Adolphs, 2014; Umiltà et al., 2001) have reached contradictory conclusions, hampering progress in determining whether mirror neurons are required for action understanding.

This article outlines the different ways in which the term 'action understanding' has been conceptualised, discussing the advantages and disadvantages of each. It then explores how these concepts should be taken into account in order to design tasks that measure action understanding. Finally, it will discuss, based on the evidence so far, whether any of the proposed action understanding processes are subserved by mirror neurons.

2. Definitions

2.1. Action understanding involves determining the identity of the action

Action understanding was first defined as "the capacity to recognize that an individual is performing an action, to differentiate this action from others analogous to it, and to use this information in order to act appropriately" (Gallese et al., 1996, p. 606). Since then, it has also been conceptualised as 'how' an action is performed (Spunt et al., 2011). For example, when observing an individual grasping a cup, this definition would suggest that action understanding involves the identification of the type of grip used: precision or whole-hand. Thus, key to this definition of action understanding is the notion that an individual identifies an observed action by using the configural relationships between body parts to distinguish one action from another. This definition will be referred to as *action identification*.

The term 'action identification' rather than 'configural body posture identification' is chosen in part for simplicity, but also to align with similar uses in the literature (e.g. Uithol et al., 2011a, page 610: "we will speak of actions in relation to the level of grips or simple actions"). We have also decided not to use a term relating to movement kinematics, because although kinematic information can be a useful source of information about an observed action, it is not an absolute requirement for action identification (e.g. in the studies by Spunt and colleagues (Spunt and Adolphs, 2014; Spunt et al., 2011), single images without any kinematic information are sufficient to identify actions).

2.2. Action understanding involves determining the goal of the action

Action understanding has also been defined as the ability "to understand directly the goal of the actions of others without needing inferential processing" (Rizzolatti and Sinigaglia, 2010, p.268). However, the word 'goal' has been used to refer to a range of different concepts, which has led to further confusion in the literature (see Cook and Bird, 2013, for review). Here we use an intermediate conceptualisation of goal; where the goal of an action is more general than a particular action (many actions can be used to achieve the same goal), but less general than the hidden mental state (intention) underlying an action (an intention can be achieved via any one of a number of goals). In the example above, when observing an individual grasping a cup, whether with a precision or whole-hand grip, the goal would be 'to grasp the cup'. Crucially, this definition suggests that action understanding involves generalising across different observed actions (as regardless of the type of grip used, the goal of the action is to grasp the cup) in order to identify the goal of the observed action. This definition will be referred to as *goal identification*.

2.3. Action understanding involves determining the actor's underlying intention

A third definition of action understanding involves "understanding the intention of others" (Fogassi et al., 2005, p. 665) or determining 'why' an action is being performed (Spunt et al., 2011). Whereas a goal is an immediate end-point of a current action, an intention is the underlying, hidden, mental state: the actor's motivation for performing the action (Kilner, 2011). In regard to the example mentioned, this definition implies that action understanding involves determining the motivation behind grasping the cup, for example 'to quench thirst'. This may involve incorporating contextual cues, such as how much liquid is in the cup, as well as the current mental state of the individual performing the action (for example, whether they are thirsty), or their enduring traits (for example, whether they enjoy the taste of coffee). This definition implies that action understanding involves generalizing across different configurations of body parts (the intention to quench thirst can be implemented using different grips), and across different immediate action goals (the intention to quench thirst can be

accomplished by inserting a straw into a cup or by grasping it), in order to identify the underlying motives of the actor. Therefore, this definition will be referred to as *intention identification*.

What is meant by the term 'intention' has not always been explicitly stated in the mirror neuron literature. For example, some studies define intentions as superordinate action goals such as 'to eat' versus 'to place' (e.g. Fogassi et al., 2005; see section 4.1.1). The problem with defining intentions as superordinate action goals is that it is unclear whether any particular goal should be classified as a goal or as an intention: in an action hierarchy such as 'form whole-hand grip' – 'grasp cup' – 'place in dishwasher' – 'tidy table', the terms 'to place' and 'to tidy' could equally be described as goals or as intentions (see Uithol et al., 2011b, for fuller discussion of this point). We therefore define an intention as a hidden mental state which motivates an action, such as 'to help' versus 'to hurt' (a definition shared by authors such as Jacob and Jeannerod, 2005; Spunt et al., 2011). This definition, when applied to the example above, encompasses 'to quench thirst' but would not include superordinate action goals such as 'to drink'.

2.4. Which definition of 'action understanding' should be adopted?

Defining action understanding as *action identification* has the disadvantage that action identification is very similar to action perception. If action understanding is to be conceptualised as a distinct psychological process, then the definition of that process needs to specify how it differs from action perception. This is also problematic when designing studies investigating action understanding, as a clear distinction between action identification and action perception is required in order to design appropriate experimental and control conditions. This disadvantage does not apply to *goal identification* and *intention identification*, since these definitions each include an aspect– the identification of a goal or intention – that is separate from action perception, making it more feasible that these terms may correspond to psychological processes that are distinct from action perception.

Defining action understanding as *intention identification*, on the other hand, has the disadvantage that intention identification involves the identification of the actor's underlying, hidden, mental state. Identifying the mental state of others, including their beliefs, desires and (crucially, here) their intentions, is a process termed mentalizing (Frith and Frith, 2006). Mentalizing is a well-established psychological process with a long history of research, and therefore (as discussed above regarding action perception), any definition of action understanding must also specify how it differs from mentalizing. Proponents of the view that action understanding involves identifying the intention underlying observed actions have clearly stated that intention identification involves a psychological process that is distinct from mentalizing (see, for example, the discussion in Rizzolatti and Sinigaglia, 2010), but the precise nature of the distinction between mentalizing and intention identification remains opaque. It is claimed, for example, that intention identification of the kind subserved by mirror neurons relates to "motor intentions" only, and that these intentions are distinct from other types of intention (identification of which relies on mentalizing) (Rizzolatti and Fogassi, 2014), but the nature of this distinction has not been specified. For example, "motor intentions" have been defined as the "final outcome of an action that leads to positive or negative reinforcement" (Rizzolatti and Fogassi, 2014, p.7), but the lack of specificity in this definition means that it is not clear whether motor intentions are distinguished from other types of intention on the basis of the content of the intention (save for the fact that they do not include representation of propositional attitudes), the format in which it is encoded, or any one of several other possible variables. Relatedly, since mentalizing is thought to involve other, non-motor, brain regions, such as the temporoparietal junction, the temporal poles and the medial prefrontal cortex (Frith and Frith, 2003), the intention identification definition of action understanding needs to specify how the brain areas involved in mentalizing interact with the motor regions believed to be involved in intention identification, and what the processes performed in those additional brain areas add to the identification of "motor intentions".

A further limitation that applies to both the *goal identification* and *intention identification* definitions of action understanding is that there is rarely a one-to-one mapping between actions and goals or intentions (e.g. Bach et al., 2005; Csibra, 2007; Jacob and Jeannerod, 2005; Uithol et al., 2011a). With respect to goal identification, different actions can be performed to achieve different goals (Hamilton and Grafton, 1993; Jacob and Jeannerod, 2005; Kilner et al., 2007); for example, the goal 'to grasp' can be achieved using a precision grip, a whole-hand grip, or even another effector such as the mouth. Thus, adopting this definition of action understanding would require that the mechanisms involved in this process need to encode abstract representations that generalise across different actions, while also simultaneously distinguishing between different goals which are achieved using the same action (Caramazza et al., 2014; Dinstein et al., 2008; Oosterhof et al., 2013).

The requirement for generalisation, and the difficulties this produces, is even more extreme under the *intention identification* definition of action understanding. The same intention can be realised via different goals, each of which can be achieved using different actions. Identification of a specific underlying mental state from an action alone has therefore been argued to be impossible (Jacob and Jeannerod, 2005).

Interestingly, kinematic cues can be used to distinguish between certain intentions in certain controlled situations (Becchio et al., 2014, 2008; Georgiou et al., 2007; Naish et al., 2013; Sartori et al., 2009), and observers are sensitive to at least some of these kinematic differences (Cavallo et al., 2016; Donnarumma, Dindo, & Pezzulo, 2017). This set of findings suggests that in some cases, action kinematics are affected by the actor's underlying mental state. This is potentially problematic, however, for designing well-controlled measures of intention identification, because if different intentions are confounded with different kinematics it is not clear whether differential patterns of data reflect intention identification or, instead, representation of kinematics without inference of intention. In any case, these findings do not negate the requirement that if either the *goal identification* or *intention identification* definition of action understanding is adopted, any action understanding mechanism must be able to generalise across different actions which have the same underlying goal or intention.

In sum, the preceding analysis suggests that there may be several different processes that are currently described as 'action understanding'. Action identification depends on the selectivity of the response; that the observation of an action causes the activation of the specific motor program that would produce the same action in the observer. The other two definitions, however, require a lack of selectivity: a generalization across the motor features of observed actions. It is possible therefore that these definitions may relate to distinct cognitive processes. In deciding which definition of action understanding is the most appropriate to adopt, researchers should bear in mind the requirements outlined above: any definition of action understanding should clearly distinguish this process from action perception and from mentalizing; and should specify whether this process does or does not require generalisation across motor features of observed actions.

3. Measuring action understanding

Once consensus has been reached regarding the most appropriate definition of action understanding to adopt, a valid measure of action understanding is required. A problematic aspect of many previous studies of action understanding is that researchers have inferred from mirror neuron responses in the monkey, or from neural activity in mirror neuron areas of the human brain, that action understanding has occurred (e.g. Caggiano et al., 2011, 2009; Ferrari et al., 2005; Fogassi et al., 2005; Umiltà et al., 2001). However, if mirror neuron activity is

taken as an indicator of action understanding, then the claim that action understanding relies on mirror neuron activity becomes unfalsifiable (Cook et al., 2014; Steinhorst and Funke, 2014). The process of action understanding must therefore be operationalized via the completion of a specific task[1] . The most appropriate task to use will depend on the definition adopted, but here we outline some general considerations.

First, as outlined above, action understanding must be distinguished from action perception and from mentalizing. At a minimum, this implies that performance on an action understanding task must be compared with performance on a task (or tasks) measuring action perception and / or mentalizing, ideally utilising the same stimulus set. By using the same stimuli across tasks measuring action understanding, action perception, and / or mentalizing, any difference in performance between tasks cannot be due purely to perceptual differences between the stimuli used in those tasks.

Next, within an action understanding task, stimuli should be selected to vary such that they differ only as a function of the action understanding definition under investigation. In particular, it is essential to ensure that stimuli which differ in terms of the goal or intention, but not the action identity, do not introduce the confound of different goal objects (Cattaneo et al., 2007; Fogassi et al., 2005; Ruggiero and Catmur, 2018), or different action kinematics. Finally, when testing *goal identification* and *intention identification*, the task should require the observer to generalise goals or intentions across stimuli depicting specific action representations.

4. Are mirror neurons involved in action understanding?

We now turn to the existing literature investigating the neurocognitive mechanisms underlying action understanding, with a specific focus on whether this ability is subserved by mirror neurons (or, in human research, brain areas thought to contain mirror neurons; mirror neuron areas, hereafter). Since the previous sections in this paper have demonstrated that there is a conceptual distinction between identifying actions and generalising across actions to identify goals and intentions, we will contrast studies of *intention identification* and *goal identification* with studies of *action identification*.

4.1. Intention identification versus action identification

4.1.1. Single cell studies

Single cell recordings are an important source of evidence for claims of the involvement of specific neurons in a particular cognitive function. In a study that attempted to target *intention identification*, Fogassi et al. (2005) trained monkeys to grasp food and either to bring it to their mouth in order to eat it, or to place it in a container. The monkeys also observed the experimenter performing these same actions. For each action the movement was similar (the container was near the mouth), but the end state of the action was different. Recording from single cells in the premotor cortex, the authors found that out of nineteen sensorimotor neurons that fired selectively for 'to place' or 'to eat' during action execution, sixteen of these also fired selectively to the same end state during observation of 'to place' (three neurons) or 'to eat' (thirteen neurons) grasping actions. Since the bodily configurations of the 'eat' and 'place' actions were very similar, the researchers concluded that these neurons demonstrated selective responses to the actor's underlying intention. However, describing 'to eat' versus 'to place' as different 'intentions' is problematic since these terms do not describe hidden mental states (see section 2.3).

Similar results have subsequently been found in studies involving both monkeys and humans (the latter using electromyography to measure muscle responses during observation; Bonini et al., 2010; Cattaneo et al., 2007). However, Heyes (2010) commented that a container was always present in the place trials but never in the eat trials. Therefore, the presence or absence of the container may have become a conditional cue differentially activating two groups of grasping sensorimotor neurons. Similarly, the object's identity (food or non-food) was also confounded with, and thus a cue to, the actor's 'intention' in the majority of these studies. In a recent study, Ruggiero and Catmur (2018) unconfounded object identity (food or non-food) and the end state of the action (to eat or to place), and demonstrated that muscle responses during action observation encode the object identity rather than the end state of the action. Thus, the results described above could be due to learned stimulus-response associations between objects and their corresponding motor plans, rather than the encoding of a specific action end state. Furthermore, since terms such as 'to eat' and 'to place' do not necessarily describe hidden mental states, even if these studies did reflect the encoding of 'to eat' versus 'to place', this could be better characterised as sensitivity to forthcoming superordinate action goals rather than to the actor's underlying mental state.

In support of a role for mirror neurons in *action identification*, several single cell studies have shown that strictly congruent mirror neurons fire to the execution and observation of a particular action, performed in a specific way (e.g. Gallese et al., 1996; Mukamel et al., 2010). Since the configural relationship between body parts in the observed action is identical to that in the observer, were they to perform the action, this implies that mirror neurons are encoding the specific action, rather than the actor's intention. Therefore, these studies support (strictly congruent) mirror neuron involvement in action identification, but are harder to reconcile with intention identification, which relies on generalization across multiple observed actions, each of which could realise the actor's intention.

4.1.2. Disruptive TMS

An additional method to determine an association between a brain region and a cognitive function involves the use of disruptive transcranial magnetic stimulation (TMS). The logic of these studies is that if disruption of brain area Y causes cognitive process X to be disrupted, then cognitive process X relies upon brain area Y. Michael et al. (2014) used continuous theta-burst stimulation (cTBS) over mouth and hand areas of premotor cortex while participants completed three tasks. For each trial, an image depicting a context was presented, followed by a brief video of a pantomimed action (either hand or mouth), and subsequently a choice of three images. The first task was a purely perceptual task in which participants were required to select from three action images the one that perceptually corresponded to the action depicted in the video. The second, an object-action task, required participants to select from three object images the appropriate object that matched the pantomimed action; and finally the third, a context-dependent object-action task, required participants to integrate both the context and the observed action in order to select from three object images the most appropriate object for that action given the context – a task that was hypothesised to involve *intention identification*. The results showed a double dissociation: when cTBS was applied over the hand area of premotor cortex, participants performed worse on all three tasks for the hand actions compared to the mouth actions, and vice versa when cTBS was applied over the mouth area. Michael et al. claimed that because disruption to the two areas of premotor cortex disrupted accuracy in all tasks as a function of the presumed motor properties of each area, premotor brain areas – and, by extension from the macaque data, mirror neurons – are involved in intention identification. However, performance was reduced equally on the first task, which required purely perceptual matching of the observed actions, and the contextual task, which required both perceptual matching and analysis of the actor's 'intention'. If mirror neuron areas are involved in intention identification, then performance should have decreased more for the contextual task theorised to involve intention identification than it did for

[1] Because of this requirement, in Section 4 we focus mainly on studies where participants have a particular task to perform, rather than reporting the results of passive action observation studies.

the purely perceptual task. Therefore, the results do not provide evidence for the role of mirror neuron areas in a process other than perceptual matching of actions (see Catmur et al., 2014).

4.1.3. fMRI studies

A further class of experiment uses functional magnetic resonance imaging (fMRI) in order to locate brain regions where activity is modulated by performance of a specific task. Studies using fMRI to investigate the neurocognitive mechanisms underlying *intention identification* have contrasted an intention identification condition – identifying 'why' the action is being performed – against an *action identification* condition – identifying 'how' the action is being performed. In an early study of this kind, Iacoboni et al. (2005) found that the right inferior frontal cortex showed a greater response in the context of a hand grasping a full cup of tea, hypothesised to represent the intention 'to drink', compared to when the hand was grasping an empty cup of tea, hypothesised to represent the intention 'to clean up'. However, the question of whether 'to drink' and 'to clean up' should be characterised as intentions in the sense of hidden mental states (see section 2.3) also applies to this study. Furthermore, the contrast of the task thought to invoke intention identification with that thought to invoke action identification was confounded by the fact that the stimuli were not matched for the number of objects they contained. Differential activity of motor cortical areas may therefore have been the result of the objects' motor affordances (or the activity of canonical neurons (neurons that respond to the sight of objects and which are co-located with mirror neurons)) rather than reflecting anything to do with intention identification. Finally, these data do not explain why, if the inferior frontal cortex is coding intentions (or even if it is encoding superordinate action goals), there is a greater response for one type of 'intention' – drinking – than another.

In a study that is also often considered to provide evidence for the involvement of mirror neuron areas in *intention identification*, participants were asked to decide, as quickly as possible, 'why' actions were being performed: to use an object (such as a hairdryer) or to move it (Ortigue et al., 2009). Responses in areas including inferior parietal lobule and inferior frontal gyrus were greater for the presentation of new, compared to repeated, end states (i.e. for 'to use' followed by 'to move' and vice versa). However, again, these end states are not 'intentions' in the sense of hidden mental states, but can be considered superordinate action goals. Furthermore, this study also contains stimulus confounds: the 'use' and 'move' actions differed in terms of the hand configurations that were used to grasp the objects, and thus this result may reflect responses to repetition of particular grasps, rather than particular end states.

Subsequent studies do not suffer from stimulus confounds as they used the same stimuli in both *action identification* and *intention identification* conditions: the only difference between conditions being the task participants were required to do. For example, Spunt and Adolphs (2014) presented participants with the same images in two conditions: a 'how' condition, in which participants had indicate whether the image contained hands or an emotional expression, and a 'why' condition, in which participants had to judge whether the action was being carried out in order to fulfil a particular intention. In this study the 'why' condition did require understanding of hidden mental states such as 'to help'. During the 'how' task, mirror neuron areas, such as the intraparietal sulcus, showed increased response, while during the 'why' task, mentalizing areas, such as the dorsomedial prefrontal cortex, showed a significantly greater response. However, Spunt, Kemmerer and Adolphs (2016) recently highlighted the need to control for the level of abstraction in the 'how' versus 'why' contrast: 'why' questions are often more abstract than 'how' questions, and at least for certain sets of actions, the same action description can produce responses in mirror neuron areas or mentalizing brain areas as a function of whether it is associated with a 'how' or a 'why' question, respectively. This effect is driven by 'how' questions producing decreases, and 'why' questions producing increases, in the level of abstraction required in the answer (Spunt et al., 2016). This raises interesting questions regarding whether mirror and mentalizing areas represent actions and intentions per se, or instead respond to the *process* of identifying actions or intentions. Nevertheless, similar studies (de Lange et al., 2008; Spunt and Lieberman, 2012, 2013), and a meta-analysis of fMRI studies of action versus intention identification (Van Overwalle and Baetens, 2009) support the conclusion that mirror neuron areas are likely to be involved in action identification rather than intention identification.

Altogether, this research suggests that mirror neuron areas are unlikely to directly encode the intentions (i.e. the hidden mental states) underlying observed actions, but may instead support the identification of configural relationships between body parts that allow actions to be distinguished from one another. It is possible that the information encoded by mirror neurons is then used by different brain areas in order to identify the mental state underlying an observed action. This possibility is supported by studies demonstrating increased connectivity between mirror neuron areas (e.g. inferior frontal gyrus and inferior parietal lobule) and brain areas involved in mentalizing (e.g. dorsomedial prefrontal cortex and temporoparietal junction) when participants are asked to judge the intention underlying an observed action, compared with judging how an action is performed (Cole et al., 2019; Libero et al., 2014).

4.2. Goal identification versus action identification

4.2.1. Single cell studies

Many researchers have argued that the response properties of mirror neurons show that they encode goals (Bonini and Ferrari, 2011; Rizzolatti and Craighero, 2004; Rizzolatti and Sinigaglia, 2010; but see Cook and Bird, 2013, for a rebuttal of this claim). For example, Umiltà et al. (2001) recorded cells in area F5 of the monkey while they watched an experimenter reach for an item of food, and while they watched an experimenter reach for an item of food that was hidden from view behind a screen. They found that more than 50% of the mirror neurons still fired even when the food was hidden, and half of these did so as strongly as when the food was in view. The authors suggested that these cells are responding to the goal of the action rather than the specific action itself, as the grasping action is not seen. However, Paulus (2012) notes that the monkeys used in this study observed the reaching and grasping action sequence many times before mirror neuron activity was recorded. This prior experience suggests that the observer would already be aware of the goal of the action (grasping the object), at the beginning of the action, and therefore, if mirror neuron responses are indeed encoding the action goal, they should fire as soon as the action begins. However, since these neurons only fired later, once the observed action reached its grasping phase, this indicates that they are encoding the specific grasping action, and not the goal. Furthermore, the prior experience argument proposes that the neuron may fire because, due to the experience gained during training, the monkey has learned to predict a grasp action in this context, regardless of the presence or absence of a barrier occluding the end of the grasp action. This implies that the firing of mirror neurons reflects a learnt association between a contextual cue and an action, rather than the encoding of a goal (Cook et al., 2014). Finally, Uithol and colleagues (2011b) argue that, because mirror neuron firing was dependent on the presence of an object, these data do not support goal identification from the observation of an action alone.

In support of goal encoding by mirror neurons, Ferrari et al. (2005) found that 21% of sensorimotor neurons sampled from the premotor area responded to the execution and observation of actions which had the same goal (to take possession of an object), but whereas during action *execution* these neurons were responsive to the performance of actions made with biological effectors (e.g. hand or mouth actions performed by the monkey), they responded preferentially to the *observation* of actions made with tools. The authors concluded that this

demonstrates mirror neurons are encoding the goal of the action, rather than the configuration of body parts required to produce that action, and are therefore involved in *goal identification*. Similarly, Rochat et al. (2010) found the same pattern of firing in premotor neurons when the monkey observed grasping actions with the hand as when it observed grasping using 'reverse' pliers, in which the actor had to open their fingers in order to close the pliers and grasp the object. They concluded that since the body part configurations involved in producing these actions are different, these neurons must be generalizing across the specific actions (open or close hand) and instead are encoding the goal of the actions (grasping), implying that mirror neurons perform goal identification. However, similar to Umiltà et al. (2001), the monkey received a long period of training (over 6 months) before the testing phase began, in which it obtained correlated experience of seeing tool actions and performing hand closing actions in order to grasp food. Therefore, the prior experience argument would suggest that these neurons are firing due to a learnt association between a stimulus (tool opening) and the associated action (hand closing), rather than the encoding of a goal (Cook et al., 2014).

In line with this criticism, Cook and Bird (2013) noted that the majority of mirror neurons are sensitive to low-level features of observed actions, such as which hand is used (Gallese et al., 1996), the direction of movement (Gallese et al., 1996), distance traversed (Caggiano et al., 2009) and observer's viewpoint (Caggiano et al., 2011). They pointed out that if mirror neurons encode goals, their firing rate would be invariant to these features, which change the visual features of the action, but not the goal. Overall, although some findings (particularly those involving single-cell recordings where the monkey receives extensive prior training) suggest that mirror neurons can generalise across low level properties of observed actions, this is likely to be due to learned sensorimotor associations. When these studies are removed, the majority of the remaining evidence indicates that mirror neurons encode low-level features, fulfilling the criteria for performing *action identification*.

4.2.2. TMS studies

Cavallo et al., 2012 conducted an analogue of Rochat et al. (2010)'s reverse plier experiment in humans using single-pulse TMS and found results incompatible with those obtained in the monkey. They recorded motor-evoked potentials produced by TMS while participants observed and executed grasping movements with classic and reverse pliers. Motor-evoked potentials were recorded from the opponens pollicis and the first dorsal interosseous muscles, which are strongly involved in the execution of closing movements of the hand. The results showed that the greatest activation of these muscles was obtained during the observation of tool actions performed using classic pliers. Since these pliers involve a closing movement of the hand, whereas the reverse pliers involved an opening movement, they concluded that this demonstrates that motor cortex excitability reflects the configural relationship between body parts in the observed hand movements (closing versus opening the hand), rather than the goal of closing the pliers. These results suggest that humans, when observing another individual performing a task with pliers, encode the configural body part relationships involved in the action, rather than the goal of the action.

Other studies, using TMS to disrupt rather than to measure neural activity, have also found support for the involvement of mirror neuron areas in *action identification* rather than *goal identification*. Weight judgement tasks, in which participants observe an actor lifting a box and, from observing this action, estimate the relative weight of the box, target action identification rather than goal identification, as the goal of the observed movement – to lift the box – is always the same. Pobric and Hamilton (2006) found that stimulating the inferior frontal gyrus, using TMS, impaired participants' performance on this task but did not affect performance on a control bouncing ball weight evaluation task. However, Valchev et al. (2017) found no effect of cTBS over primary motor cortex and superior parietal lobule on either the weight judgement or bouncing ball tasks. These contrasting results suggest that more tasks specifically targeting action identification need to be designed in order to further explore the involvement of mirror neuron areas in this process.

4.2.3. fMRI studies

Following the same logic as Cook and Bird (2013), who pointed out that if mirror neurons encode goals, their firing rate should be invariant to low-level features such as the observer's viewpoint (see section 4.2.1), several studies have used fMRI in humans to determine whether mirror neuron areas encode goal representations, or whether, instead, activity in such areas is modulated by low-level features of action (Kable and Chatterjee, 2006; Oosterhof et al., 2012; Tucciarelli et al., 2015).

Using multivoxel pattern analysis, Hafri et al. (2017) demonstrated that neural responses generalised across specific exemplars of actions within categories such as 'brushing' and 'pulling', both in brain areas traditionally considered to carry out perceptual processing (bilateral occipitotemporal cortex) and in areas thought to contain mirror neurons (inferior parietal lobule, left premotor cortex, and left middle frontal gyrus). The responses to these action categories in these areas were invariant to differences in actors, objects, scene context, or viewpoint, suggesting that some or all of these brain areas may contribute to *goal identification*. In contrast, Wurm and colleagues (Wurm and Lingnau, 2015; Wurm et al., 2016) found that although neural responses in the inferior parietal lobule and the lateral occipitotemporal cortex generalized across specific exemplars of actions within categories such as 'open' and 'close', the premotor cortex encoded specific exemplars of actions, based on configural relationships between observed body parts. Further evidence of generalization across actions, in terms of stimulus type (observed action versus written description), was shown using multivoxel pattern analysis in lateral posterior temporal cortex, but not in premotor or parietal areas (Wurm and Caramazza, 2019).

It is possible that the contrasting response in premotor cortex across these studies is due to the type of action categories they employed. The categories used by Hafri et al. (2017) are more perceptually distinct than those used by Wurm and colleagues. Specifically, in Hafri et al.'s study there is less variation between exemplars within a category, and more variation across categories, in terms of both body part configuration and body part itself (i.e. hand versus mouth versus leg), than in Wurm and colleagues' studies. This means that it is possible to identify which category an action belongs to by focusing on the body part, or configuration of body parts, in specific action exemplars, rather than by generalising across exemplars. Therefore, in Hafri et al.'s study, the apparently generalised activation of premotor cortex across exemplars may in fact be due to discrimination of these perceptual differences across action categories.

Another recent fMRI study also found that mirror neuron areas were not necessary for *goal identification* (Nicholson et al., 2017). Participants watched sequences of instrumental actions while focusing on the action performed, the goal of the action or the objects used. The neural response during goal identification was largely overlapping with that related to processing of object identity, and not with processing of the configural body posture of the action itself. In contrast, premotor and parietal 'mirroring' areas responded specifically when the actions were either unfamiliar or the goals were ambiguous. These results suggest that mirror neuron areas may aid in discriminating unfamiliar actions, but the processing of this information in regards to goal identification is performed by object processing areas. These results are not compatible with theories suggesting that mirror neuron areas contribute to goal identification.

Altogether, these findings suggest that neural populations in non-motor areas, such as the lateral occipitotemporal cortex, can generalize across perceptually different examples of an action, demonstrating that they fulfil the criteria for *goal identification*. However, the available

evidence largely indicates that neural populations in premotor cortex encode specific perceptual features of actions relating to configural relationships between body parts, fulfilling the criteria for *action identification*.

It is useful at this stage to reflect back on the considerations regarding study design which we outlined in section 3, emphasising the importance of control tasks, the need to avoid stimulus-related confounds, and the requirement of testing for generalisation of goals or intentions across action exemplars. The new generation of multivoxel pattern analysis studies described above determine whether a particular brain region can identify the same action when performed using different objects (Wurm et al., 2016) or in different contexts (Wurm and Caramazza, 2019), thereby fulfilling the requirement of testing for generalisation of goals. However, these studies still lack control tasks measuring action perception and/or mentalizing (Hafri et al., 2017; Wurm et al., 2016; Wurm and Caramazza, 2019; Wurm and Lingnau, 2015). Moreover, some of these studies are still subject to stimulus-related confounds, for example, by using different body parts to perform different actions (Hafri et al., 2017). These considerations make the results of these studies problematic to interpret with respect to the contribution of specific brain areas to goal identification, and should be taken into account in future studies.

Overall, these findings fit with the conclusions of previous authors including Csibra (2007), Jacob (2009, 2013) and Hickok (2013). One final consideration is that although our paper suggests some evidence for the involvement of mirror neurons, or mirror neuron areas, in action identification, this does not imply that mirror neurons are essential for action identification. For example, individuals born without upper limbs (and without motor representations of those limbs) can recognise actions as fast and as accurately as those with upper limbs (Vannuscorps and Caramazza, 2016); on the other hand, one recent meta-analysis of neuropsychological patients with damage to mirror neuron areas supports a causal role of these areas in action identification (Urgesi et al., 2014; but see Tarhan et al., 2015, for a contrasting finding in a large sample of stroke patients). Further studies should investigate the causal involvement of mirror neuron areas in action identification in typical individuals, taking into account the task design considerations specified in section 3.

5. Conclusion

The term ‘action understanding’ has been defined in several ways since it was first proposed to describe the psychological process purportedly carried out by mirror neurons. We suggest that the most commonly used definitions correspond to three discrete potential psychological processes: *action identification*, *goal identification* and *intention identification*. Action identification involves using the configural relationships between body parts to distinguish one observed action from another. Goal identification, on the other hand, involves generalising across different observed actions to identify the immediate goal of the action. Intention identification also involves generalising, not only across observed actions, but also across different goals, in order to identify the hidden mental state motivating the action.

We have argued that each of these definitions is problematic for different reasons. First, it is not clear how action identification differs from action perception; or how intention identification differs from mentalizing. If there is no distinction between these pairs of processes then using the term ‘action understanding’ to describe either action identification or intention identification is superfluous; and investigation of whether mirror neurons support action understanding should instead focus on whether they support action perception or mentalizing. The goal and intention identification definitions of action understanding are also potentially problematic for mirror neuron accounts, because they require that any action understanding mechanism must generalise across different observed actions which have the same underlying goal or intention, and it is far from clear that the firing patterns of mirror neurons accord with this requirement (Cook and Bird, 2013).

Building on this analysis, we propose that future tasks testing action understanding should: clearly define the action understanding process that is being tested; distinguish action understanding from related processes; avoid stimulus-related confounds; and test for generalisation across motor features of observed actions.

Finally, after analysing the existing literature, we conclude that although there is some evidence to suggest that mirror neurons, or brain areas containing mirror neurons, contribute to action identification, there is little evidence to support the claim that they contribute to goal or intention identification. Generalisation of goals across multiple exemplars of observed actions appears instead to involve non-motor regions such as the lateral occipitotemporal cortex, whereas identifying intentions involves regions such as medial prefrontal cortex that are traditionally considered to be involved in mentalizing.

In conclusion, mirror neurons, and brain areas which contain them, may indeed be involved in a process that has been termed ‘action understanding’, but only if action understanding is defined as action identification. Based on our analysis above, we contend that there is currently no reason to distinguish action identification from action perception. That motor areas are involved in action perception was exciting when first proposed, and remains intriguing today, without requiring a novel psychological process to be defined. We therefore recommend that future research should focus on establishing the extent to which motor areas contribute to action perception, and on how any such contribution may contribute to social behaviour and its dysfunction.

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Conflict of interest

None.

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