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# Do infants provide evidence that the mirror system is involved in action understanding? ☆

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ABSTRACT

The mirror neuron theory of action understanding makes predictions concerning how the limited motor repertoire of young infants should impact on their ability to interpret others' actions. In line with this theory, an increasing body of research has identified a correlation between infants' abilities to perform an action, and their ability to interpret that action as goal-directed when performed by others. In this paper, I will argue that the infant data does by no means unequivocally support the mirror neuron theory of action understanding and that alternative interpretations of the data should be considered. Furthermore, some of this data can be better interpreted in terms of an alternative view, which holds that the role of the motor system in action perception is more likely to be one of enabling the observer to predict, after a goal has been identified, how that goal will be attained.


## 1. Introduction

Human infants provide a compelling opportunity to explore the hypothesis that the mirror neuron system plays a functional role in action understanding. While the term 'action understanding' is used in different ways throughout the literature on mirror neurons, its most common usage seems to be synonymous with 'goal understanding'. That is, mirror neurons are proposed to enable the observer to infer the immediate target, or goal, of an action (Rizzolatti & Sinigaglia, 2010). Since 'goal understanding' is an ability that young infants are believed to possess, a promising test of the mirror neuron theory of action understanding is to ask whether the limited, but developing, motor capabilities of infants, influence their capacity to interpret others' actions as goal-directed. The process of identifying the goal of observed movements is proposed to happen via a mechanism that directly matches an observed movement onto a pre-existing motor representation of that action in the observer (Rizzolatti, Fogassi, & Gallese, 2001), or which codes the goal of the action in motor terms (Rizzolatti & Sinigaglia, 2010). An infant lacking a motor representation of the observed movement (because they have never performed that action) would thus presumably have no motor representation onto which they could map that movement. Therefore, the hypothesis that the mirror neuron system plays a role in action understanding via such a mechanism makes clear predictions about how the motor limitations experienced by young infants might impact on their ability to make sense of others' actions. As both types of sensory-motor transformation would require that the observer accesses a corresponding motor representation (either of the movements or the goal), an infant without motor experience with an action would not have access to a corresponding motor representation, and so should be unable to make sense of the observed action.

Independent of work on mirror neurons, a body of work had already emerged which suggested a relationship between infants' experience with an action and their ability to understand that action when performed by others. This work has since


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been cited by advocates of the mirror neuron theory of action understanding as support for their theory (e.g. Casile, Caggiano, & Ferrari, 2011), and has motivated numerous other infant studies aimed at confirming this hypothesis for the function of mirror neurons. Indeed, many infant studies have produced new data consistent with the hypothesis that mirror neurons support goal understanding. However, in the haste to promote the data as support for the theory, little attention has been given either to alternative interpretations of the data, or to other data which fail to support the theory. For example, despite the reported relationship between infants' action experience and their goal understanding, numerous studies have demonstrated goal understanding for actions for which infants could not possibly recruit a corresponding motor representation. Rather than an attempt to understand the existence of both supporting and non-supporting data within any alternative framework, data inconsistent with the theory has tended to be ignored[1]. Thus, the primary aim of this paper is to critically examine the claim that infant data provide strong evidence for the mirror neuron theory of action understanding, and to situate infant data within an alternative theory of the function of the motor system during action observation.

## 2. Evidence from infants

The claim that infant behaviour provides evidence for the mirror neuron theory of action understanding is based on the apparent relationship between infant's understanding of goals and their own motor abilities. The initial impetus for this claim came from pre-existing data demonstrating that infants could better attribute a goal to others' object-directed actions if those actions were performed by a human hand behaving in a typical way than if they were performed by a mechanical claw or stick (Woodward, 1998), or even a human hand behaving in an atypical fashion (e.g. approaching the object with the back rather than the front of the hand) (Woodward, 1999). The importance of experience was directly tested in a study by Sommerville and colleagues in which 3-month-old infants, who ordinarily do not reach for objects and do not appear to interpret others' actions as goal-directed, were given training with 'grasping' objects. The authors placed Velcro gloves on infant's hands which, when they swiped their hands in the vicinity of objects, would result in them inadvertently 'picking up' those objects. After this training, infants' goal-attribution abilities were tested, and only those infants who had this training experience could interpret the action of a gloved-hand as goal-directed (Sommerville, Woodward, & Needham, 2005). While not aimed at testing the mirror neuron theory of action understanding, these findings are certainly compatible. If mirror neurons indeed lead to goal understanding by recruiting a corresponding motor representation, the presumed effect of training in 3-month-olds was to provide them with a motor representation onto which they could match the observed action and understand its goal.

Following this, several studies aimed to test the hypothesis that infant's goal understanding was dependent on their being able to exploit a motor representation, acquired via first-person experience, of whatever action they were observing. As a measure of goal understanding, Falck-Ytter and colleagues asked whether infants would evidence prediction of the outcome of an action commensurate with their abilities to perform that action (Falck-Ytter, Gredeback, & von Hofsten, 2006). Goal understanding was operationalized as eye movements arriving at the location of the outcome of the action before the outcome was achieved. Infants observed either a human hand repeatedly placing balls in a bucket, or self-propelled balls following the same trajectory into the bucket. The authors found that older infants, who would likely be able to place objects into containers themselves, did generate predictive saccades towards the goal of the observed action. However, younger infants who were unlikely to be able to place objects in containers themselves did not show anticipatory saccades, suggesting that they were not able to infer the goal of this action. Furthermore, neither older nor younger infants generated anticipatory saccades when the movements observed were executed by self-propelled balls. Subsequent work has extended these findings by confirming that the ability to place objects into containers is indeed correlated with the ability to generate anticipatory saccades towards the outcome of the action when performed by others (Cannon, Woodward, Gredeback, von Hofsten, & Turek, 2011), and other work has shown that the maturity of infants' reaching is correlated with their ability to interpret a reach as goal-directed in others (Kanakogi & Itakura, 2011). These findings are interpreted as support for the mirror neuron theory of action understanding and hypothesized to reflect the importance of being able to access a motor representation of the observed action in order to understand that action as goal-directed.

In what follows, I will suggest a number of reasons why the data from infants is not unequivocal support for the mirror neuron theory of action understanding and suggest that such an interpretation is premature in the absence of further data.

## 3. Action specificity

While it has been shown that an infant's experience and competence with an action is related to their ability to interpret that action when performed by others, the specificity of this relationship has not been demonstrated. That is, we do not know whether it is specifically experience with the observed action that is crucial, or whether motor maturity more generally might facilitate action prediction. We do not know whether it is experience placing objects in containers that enables infants to predict the outcome of someone else placing objects in containers (Cannon et al., 2011; Falck-Ytter, Gredeback, & von Hofsten, 2006), or whether those infants who can place objects in containers are also more adept at other motor skills, and

[1] This data is often interpreted as resulting from an alternative, less important mechanism which results in a goal understanding that is inferior to that derived from a mirror mechanism (e.g. Gallese, Keysers, & Rizzolatti, 2004).

whether general motor maturity might be correlated with superior action prediction. In order for the correlation between action skill and predictive saccades during action observation to be evidence that predictive saccades reflect recruitment of corresponding motor plans, one would need to demonstrate that it is specifically skill with the observed action that leads to this improvement.

## 4. What is special about self-produced actions?

Infants can acquire experience with actions either from performing those actions themselves, or, through observing those actions performed by others. Consistent with the mirror neuron theory of action understanding, the experience acquired through action production appears to be superior to that acquired through action observation alone (Sommerville, Hildebrand, & Crane, 2008). If action understanding requires access to a motor representation of that action, then experience performing rather than observing that action would be crucial. However, this only provides incontrovertible evidence for the mirror theory if we can be sure that it is the addition of a motor representation generated from self-produced actions that is responsible for infants being better able to understand these actions when performed by others. What else, apart from a motor representation, could self-produced actions provide that other-produced actions could not? One possibility is that the experience obtained from self-produced actions provides a better learning opportunity than that obtained from other-produced actions. For example, children learn the labels for objects better when labelled objects are being manipulated by themselves, compared to when they are being manipulated by someone else (Yu & Smith, 2012), and information that is received by infants in response to their requests appears to be better retained than unsolicited information (Begus, Gliga, & Southgate, in preparation). One could hypothesize various reasons as to why self-produced information is better assimilated than other-produced information. For example, infants, like adults, may be more likely to learn information that they had a hand in eliciting (Kang et al., 2009), or self-produced effects may be especially arousing for infants (e.g. Lewis, Sullivan and Brooks-Gunn, 1985). Whatever the reason, the point is that there could be numerous explanations for why actions, with which the infant has first-person experience, are more readily understood when performed by others, only one of which is the availability of a motor representation onto which the observed action can be mapped.

## 5. How goal understanding is operationalized

Perhaps the most important reason why the infant data does not provide incontrovertible evidence for the mirror neuron theory of action understanding is that there are a number of reasons to question the assumption that what is taken as evidence of action understanding or a lack thereof, is really that. The interpretation of infant data as support for this theory is heavily dependent on the assumption that a particular behaviour reflects a goal attribution, and an absence of that behaviour reflects a failure to attribute a goal. The evidence discussed so far comes from two paradigms, one using infant looking-time as evidence of goal attribution and the other using infant predictive gaze. In the following sections, I will examine whether behaviour on these paradigms really provides the kind of evidence that the mirror neuron theory of action understanding requires.

### 5.1. The evidence from looking-time

In the first paradigm (Woodward, 1998), infants observe an agent repeatedly choosing one of two objects and then, after the objects have switched location, either continuing to choose the same object (in a new location) or switching her choice to the previously un-chosen object. When this action is a familiar reaching action, infants typically spend more time looking at the action towards the new object than the action towards the old object, even though, because of the location switch, the action towards the old object entails a change in path from what infants had seen during familiarization. The fact that infants look longer at the new object-directed action suggests that they had encoded the familiarization action in terms of the goal object, rather than other features like location of reaching. However, although the assumption that infants' looking behaviour reflects a goal attribution is rarely questioned, it is important to establish its validity, given that the argument that infants' behaviour provides support for the mirror neuron theory of action understanding relies on this assumption.

In a recent paper, Hernik and Southgate (2012) provide data that question the assumption that this paradigm reflects a goal attribution that could be generated by mirror neuron activity. One exception to infants' expectation that an agent who has previously approached a particular target will continue to approach that target is if that target was initially approached in isolation, rather than as one of a pair of objects (Luo & Baillargeon, 2005, 2007). The accepted interpretation of this caveat is that, while infants interpreted the approach towards the solitary object as goal-directed, they simply do not know which one the agent will approach now that there is a new object in the scene. In the classic two-choice paradigm, the infant has evidence that the agent does not choose the ignored object, but in the solitary object condition, they have no information as to the agent's disposition towards any new object, and so do not know whether she might actually prefer this one when it is available. The problem with this interpretation is that, as a mechanism of goal attribution, it would surely fail. One can imagine many situations where a goal attribution, which should endure the appearance of new potential targets for which the observer might lack information concerning the agent's disposition (Hernik & Southgate, 2012), would be abandoned if such information was necessary. For example, imagine an agent (A) chasing another (B) down a busy street. Under the Luo and

Baillargeon explanation, the appearance of all these new targets that comprise the busy street should lead the observer to abandon their goal attribution, and no longer expect A to continue chasing B. Thus, it is difficult to see how a mechanism which requires up-to-date dispositional information could support goal attribution. In fact, it turns out not to be the case that infants require knowledge of the agent's disposition towards all possible targets in order for them to generate an expectation concerning which target the agent should approach. Another paradigm which proposes to demonstrate goal understanding in infants is based on the interpretation of efficient action (Gergely & Csibra, 2003). In this paradigm, infants observe an agent repeatedly jumping over an obstacle to approach a target. In test trials, the obstacle is removed and infants see the agent either approaching the target with the same detour jumping action, or executing a straight path to the target. Despite the fact that the straight path is perceptually novel relative to the jumping action, infants appear to expect the agent to execute a straight path towards the goal, looking longer towards the jumping agent whose action is inefficiently related to the goal (Gergely, Nadasdy, Csibra, & Biro, 1995). Thus, infants can exploit action efficiency as a cue to goal-directedness. Now, if we make the approach to a solitary object an efficient action (by having the agent detour around a barrier on its approach), infants then continue to expect the agent to approach the same target object even in the presence of a new object towards which the infant has no knowledge of the agent's disposition (Hernik & Southgate, 2012). The fact that the infant continues to expect the agent to act on the same target irrespective of the arrival of new targets is consistent with the infant having attributed a goal to the agent. Similar effects have been reported by Biro (Biro, Verschoor, & Coenen, 2011) and when a different kind of alternative cue to goal-directedness is added to a solitary approach event (Luo, 2011). What this data suggests is that it is the presence of 'choice' (i.e. selecting one of two available objects) that is enabling infants to attribute a goal on the standard two-target paradigm, rather than simply the reach towards the object (as, in isolation, this does not seem to lead to an enduring goal attribution). That infants require this 'choice' or preference information in order to attribute an enduring goal presents a problem for those who wish to use infant's behaviour as evidence in support of the mirror neuron theory of action understanding. If a direct reach to the object does not result in a goal attribution, but rather other cues like a selective reach, or efficient action, are necessary, then it is difficult to see how mirror neurons could be playing a role in infant's goal attribution. Mirror neurons are hypothesized to enable the direct understanding of the action through a process of simulation, but in this paradigm, goal understanding appears to be mediated by the agent's 'choice' or preference.

### 5.2. The evidence from eye tracking

Infant's failure to attribute goals to a direct approach in the absence of additional cues such as choice or efficiency of the action has implications for other data interpreted as support for the mirror neuron theory of action understanding. While the success of 12-month-olds in predicting the goal of a hand action but their failure to predict the goal of a self-propelled ball is consistent with a mechanism which requires access to a motor representation for goal understanding, it is also possible that the condition with self-propelled balls lacked sufficient cues that the action was goal-directed. The direct movement of the balls into the bucket is devoid of any cues to efficiency of action in the same way as a direct path to a solitary object (Hernik & Southgate, 2012). While those who interpret infant's predictive gaze as support for the mirror neuron theory of action understanding would likely argue that such cues are also lacking in the hand condition, it may be that, by 12 months of age, placing actions are assumed to be goal-directed based on experience of seeing hands acting in goal-directed ways (Biro & Leslie, 2007). For unfamiliar agents like self-propelled balls, further cues to goal-directedness may be required – such as evidence that the ball's actions are efficiently related to the goal. In fact, a recent study has demonstrated that if a self-propelled ball detours over an obstacle en route to its goal, then 13-month-olds do evidence predictive gaze shifts to the goal (Biro, in press). These data suggest that it may not be the absence of a motor representation that precludes goal attribution in the self-propelled ball condition, but an absence of cues that indicate the movement is goal-directed.

However, even if these actions did contain sufficient cues for infants to interpret them as goal-directed, there are still reasons to question the assumption that predictive eye movements reflect a goal prediction achieved by a motor process. While the presence of predictive saccades have been cited as evidence in themselves of a motor contribution to goal understanding (Flanagan & Johansson, 2003), they may equally be mediated by conceptual knowledge of actions and their likely outcomes. For example, a commonly used paradigm in adults involves observers watching a hand approaching a small and a large object (Ambrosini, Costantini, & Sinigaglia, 2011; Costantini, Ambrosini, Cardellicchio & Sinigaglia, in press). When the hand is pre-shaped so that it is in a whole-hand grasp, observers generate saccades towards the large object in advance of the hand arriving at that object, but when the hand is closed into a fist, observer's eye movements do not show evidence for prediction of the goal. The authors argue that the grasping hand provides motor information which presumably can be matched to a motor representation associated with large objects whereas the closed hand does not provide any motor information that would lead to the prediction that one object is more likely to be the target than the other. However, it is also likely that we have accumulated experience that hands in whole-hand grasps are more likely to be reaching for bigger objects than smaller objects, but it is unlikely that we would have any associated outcome for a hand approaching objects in a fist shape. There is no inherent reason why predictive saccades should be interpreted as supporting one hypothesis over the other.

Nevertheless, studies do show that if the motor system is unavailable, even adults fail to make predictive saccades towards a familiar action outcome. For example, studies using Transcranial Magnetic Stimulation (TMS) have shown that if the motor system is rendered temporarily unavailable, adult participant's predictive saccades to goal outcomes are impaired (Constantini, Ambrosini, Cardellicchio, & Sinigaglia, in press; Elsner, D'Ausilio, Gredeback, Falck-Ytter, & Fadiga, 2013). These data have been interpreted as evidence that a process of direct matching, implemented in the motor system, is required for generating a goal prediction. However, while these data clearly do suggest a role for the motor system in predictive tasks, what kind of prediction it is involved in generating is ambiguous. The ability to predict the goal of an action also permits one to predict a likely way in which that goal will be fulfilled; the path that the action will take en route to this goal and the kinematics involved (Csibra & Gergely, 2007). In an action such as a direct reach for an object, the location of saccades reflecting a goal prediction and those reflecting a prediction about how that goal will be achieved would be the same. While saccadic data cannot distinguish these two possibilities, only if they reflected a process of goal prediction would they be support for the mirror theory of action understanding. The same criticism applies to the infant studies using predictive saccades as evidence for motor involvement since in all studies the path direction and the goal location are the same.

While the presence of predictive saccades towards an action outcome surely implies that the observer has generated a goal prediction regardless of whether they reflect the *process* of goal prediction, an absence of predictive saccades does not imply that no goal prediction has taken place. In order to generate a predictive saccade, an observer would not only need to generate a prediction (concerning either the goal or the action path), but they would also need to disengage from whatever they were currently attending to. While action familiarity might facilitate predictive saccades because generating predictive saccades may require the availability of a motor program, action familiarity might also facilitate attention disengagement. Since infants receive both motor and visual feedback from self-produced actions (Del Giudice, Manera, & Keysers, 2009), actions that the infant can produce would be more visually familiar than actions that they cannot produce. In studies measuring predictive saccades, the test of success is the speed with which the observer generates saccades away from a salient moving stimulus (e.g. a hand, mechanical claw or self-propelled ball) towards the action end point. The ability to visually disengage from an interesting stimulus, thought to reflect endogenous attention control, continues to improve across the first year of life, with infants at 7 months being slower to disengage than infants at 14 months (Elsabbagh et al., in press). Thus, an alternative explanation for the difference in predictive saccades in the familiar and unfamiliar action conditions of the studies discussed above is that they reflect infant's developing capacity for attention disengagement. While the human action is likely highly familiar to infants, the mechanical claw (or any other non-familiar action), by virtue of its novelty, may be more difficult for infants to disengage from, and thus more difficult to generate predictive saccades away from. Furthermore, 12-month-olds might simply be better at shifting their attention from a moving stimulus to a static one than 6-month-olds. A possible test would be to occlude a portion of the movement in both conditions. Occluding the salient movement element may make it easier for infants to visually disengage from the action and saccade towards the outcome. If predictive saccades result from access to a corresponding motor representation then occlusion of the movement should have no effect and the results should be the same. In all of the studies using predictive saccades as a measure of goal understanding, the observed action has been something that the infants cannot produce themselves, and is unlikely to have ever seen before (i.e. self-propelled balls and mechanical claws). Clues to whether it is the lack of visual or motor experience that results in the lack of predictive saccades, could be found in looking time studies. When the measure is looking-time, 6-month-old infants appear to more readily attribute a goal to a walking human adult (Kamewari, Kato, Kanda, Ishiguro, & Hiraki, 2005), than to an animate box, or a mechanical claw (Woodward, 1998), even though both of these actions are outside of their motor repertoire. But while they would likely have accumulated plenty of visual experience with walking adults, they would be unlikely to have any prior visual experience with self-propelled boxes or mechanical claws.

Finally, despite not generating predictive saccades towards the target of a mechanical claw (Cannon & Woodward, 2012; Kanakogi & Itakura, 2011), a different measure of action prediction suggests that infants do generate predictions for such unfamiliar actions. Based on a documented correlation between motor activity and action prediction (Kilner, Vargas, Duval, Blakemore, & Sirigu, 2004; Southgate, Johnson, Osborne, & Csibra, 2009), we asked whether infants would exhibit motor activation when they could expect either a human hand or a mechanical claw to act (Southgate & Begus, in press). Infants were familiarized to a hand or claw consistently approaching and 'grasping' one of two objects. After familiarization, infants saw the two objects presented individually at the top of a screen with either the hand or the claw resting at the bottom of the screen. We hypothesized that if infants could predict the goal of an action, we should see motor activation during this static period. We used EEG to look for a reduction in the sensorimotor alpha rhythm, indicating motor activation (Hari & Salmelin, 1997; Hari et al., 1998), during this rest period and found that infants recruited their motor system when they saw the target object, irrespective of whether the effector they saw was a hand or a mechanical claw. This suggests that even if infants fail to make anticipatory saccades when they observe a mechanical claw approaching a target object, they can still interpret these actions as target related. Furthermore, the presence of motor activation when infants see the target object suggests that they are using their motor system for some part of this process. In the following section, I will discuss how data like this – suggesting that infants recruit their motor system during a phase in which action can be predicted, irrespective of the familiarity of that action – can be interpreted.

## 6. What is the role of the motor system in action observation?

I have argued that the oft-made assumption that the superiority of familiar actions for goal understanding in infancy implies that the motor system plays a causal role in this goal understanding is unwarranted, and that there are various alternative possible interpretations that should be considered. Furthermore, the wealth of evidence suggesting that infants can attribute goals to numerous actions for which they could not recruit a motor representation suggests that access to corresponding motor representations is unnecessary for goal understanding. An alternative to the mirror neuron theory of action understanding is the cue-based view (e.g. Biro & Leslie, 2007). As discussed throughout the preceding sections, researchers have identified a number of different cues which infants appear able to exploit in order to identify an action as goal-directed. These include that the action can be interpreted as efficiently related to an outcome, the presence of a choice or selection on the part of the agent, action variability and salient action effects (for further discussion see Hernik & Southgate, 2012). Goals are identified and understood based on the presence of these cues rather than the familiarity of the action. However, action familiarity may still influence goal attribution. As Biro and Leslie (2007) have noted, familiar human actions (like reaching or grasping) may become associated with goal-directed behaviour to the point where they become cues to goal-attribution. Furthermore, the ease with which one can infer a goal is likely to be influenced by experience with an action; certain actions are likely to become associated with certain outcomes (e.g. a hand in a pincer grip is likely usually followed by the picking up of a small object rather than a large object).

While proponents of the mirror neuron theory of action understanding have conceded that these cues could be helpful for actions that are outside of the motor repertoire of the observer, for actions for which the observer could access a motor representation, this would be the preferred route and would result in a superior understanding of the action (Gallese et al., 2004). However, data which demonstrate the recruitment of the motor system during the observation of non-executable actions (e.g. Southgate & Begus, in press) is difficult to reconcile with this view. The motivation for positing a secondary, non-motor route to goal understanding derives from the logical assumption that a mirror mechanism that matches form and motion could not be recruited for making sense of actions for which the observer would lack a corresponding motor representation. The fact that the motor system is recruited irrespective of action familiarity suggests that it is doing something quite different from matching the observed action onto a corresponding motor representation.

Thus, an alternative explanation for the presence of motor activation during action observation is that it reflects a process of action anticipation, or prediction. According to this view, goals are identified outside of the motor system but, once they are, the motor system is recruited in order to predict how that goal will be achieved (Csibra, 2007; Jacob, 2009; Prinz, 2006), including predicting the unfolding kinematics of the observed action (Kilner, 2011). Generating an action prediction is not only crucial for basic needs like fleeing a predator for whom you have identified yourself as its target, but for successful engagement in cooperative and collaborative activities (Sebanz, Bekkering, & Knoblich, 2006). This hypothesis accounts for the fact that goal understanding itself appears possible without any reliance on corresponding motor representations, while at the same time explaining the well-documented involvement of the observer's motor system during predictive tasks. For example, Schubotz and colleagues have shown that areas of the observer's motor system are activated when they generate a wide range of predictions, even those which have no relation to action such as what tone will come next in a sequence (Schubotz, 2007; Schubotz & von Cramon, 2002), and other findings also strongly implicate the observer's motor system in predictive tasks (Cross, Stadler, Parkinson, Schütz-Bosbach, & Prinz, 2011; Kilner et al., 2004; Southgate et al., 2009). Furthermore, this hypothesis fits well with the fact that the motor system functions in a predictive fashion during action execution (Miall & Wolpert, 1996), and thus its predictive involvement in action observation is a natural product of its inherently predictive modus operandi.

A further hypothesis concerning how the motor system facilitates action prediction is that it operates in an emulative fashion. Once the observer knows the goal of the agent, they can ask how they themselves would fulfil this goal; what motor commands they would execute to this end, and it is this emulative process that recruits the motor system (Csibra, 2007). Insofar as we generally attempt to achieve our goals in the most efficient way possible, when the actor and observer share the same motor capabilities, the observer will likely emulate the effect via a motor program that matches that which the actor will actually use. However, under the emulation hypothesis, when the observer lacks the motor program that the actor is using, they may nevertheless recruit an alternative motor program that could bring about the same outcome that the observer has identified as being the goal of the action. For example, it has been shown that adults who are born without hands recruit their foot motor region when observing hand actions (Gazzola et al., 2007), a finding that is consistent with the hypothesis that the motor system is recruited to emulate the goal of an action. Similarly, a 6-month-old infant who lacks a motor program for walking could identify a goal such as 'approach target' or 'contact target' based on available cues and then recruit whatever motor program they themselves could use to bring about this goal (e.g. a motor program for crawling or reaching).

This view of the role of the motor system is also consistent with numerous findings, including that the mirror system appears sensitive not to the effectors used to achieve a goal, but to the goal itself (Umiltà et al., 2008). If the role of the motor system in action interpretation were one of predicting action unfolding (post goal identification), the ease with which the goal can be ascribed would be crucial to the subsequent involvement of the motor system in prediction. For example, motor system involvement in action perception is modulated by the presence of a visible goal. The fact that observation of pantomimed actions does not lead to motor activation (Muthukumaraswamy, Johnson, & McNair, 2004) would be expected because, in the absence of a known outcome, the observer has no basis on which to predict how the action will unfold. Similarly, the ostensibly conflicting finding that infants recruit their motor system while observing a mechanical claw reaching for an object, suggesting that motor activation is not dependent on motor experience (Southgate & Begus, in press) and findings in adults that expertise with an observed action such as ballet (Calvo-Merino, 2004; Cross, Hamilton, & Grafton, 2006; Orgs, Dombrowski, Heil, & Jansen-Osmann, 2008) or piano playing (Haslinger et al., 2005) results in greater motor activation can be reconciled under the prediction hypothesis. While the visible presence of a goal in the infant study and the inclusion of known visual cues to goal attribution (see Hernik & Southgate, 2012 for further discussion of cues) could have enabled infants to emulate the goal via an alternative motor program, only experts with knowledge of ballet sequences or piano pieces would be able to predict how the sequence would unfold, and thus we would expect to see a relationship between expertise and motor involvement, especially during the prediction of intransitive actions.

The ease with which a goal can be identified and its effect on motor activation was also demonstrated in a recent study with infants (Southgate, Johnson, Karoui, & Csibra, 2010). In this study, infants were shown a grasping hand or an unfamiliar back-of-hand disappearing behind an occluder. Crucially, infants had no prior knowledge of what, if anything was behind the occluder. Infants exhibited motor activation in the case of the grasping hand, but not when the hand was in a back-of-hand posture. A control condition confirmed that this was not simply because the infants could match the kinematics of the grasping hand but not of the back-of-hand. Instead, a possible explanation is that, while the familiarity of the grasping hand permitted infants to generate a hypothesis about the likely outcome of the action (perhaps based on an association that they had acquired during the first 9 months of their life, in which they likely often saw grasping hands approaching objects), the unfamiliar back-of-hand action did not. Armed with this goal knowledge in the grasping hand condition, infants could then recruit their motor system to generate a prediction concerning how that grasping action would unfold in pursuit of the goal. In the absence of any goal knowledge for the back-of-hand condition, infants would have had no basis on which to generate a prediction concerning how the action would unfold, and thus they did not recruit their motor system.

## 7. Conclusions

Much has been made of the documented correlations between infant's motor skills and their performance on tasks of action understanding, in part because they ostensibly provide good evidence for the mirror neuron theory of action understanding. This paper has attempted to expose the limitations in the existing infant data as support for the mirror neuron theory of action understanding. In an attempt to find supporting evidence for this theory, findings which are consistent with the theory have been hastily assimilated without sufficient consideration of alternative explanations.

Advocates of the theory that actions are understood by motor matching accept that we can make sense of actions outside of our motor experience, arguing that there is likely to be both a motor and a non-motor route to action understanding, but that a motor route offers a 'richer' understanding of the action (Gallese et al., 2004; Rizzolatti & Sinigaglia, 2010). However, there is no evidence that a 'richer' understanding of an action is attained via a motor route, and, given that both infants (Southgate & Begus, in press) and adults (Cross et al., 2011; Schubotz, 2007) recruit their motor system for actions both within and outside of their motor repertoire, it is not clear on what basis we should postulate two distinct routes to action understanding. After all, this secondary route was only suggested in response to the assumption that the motor system would not be recruited for actions that are outside the observer's own motor history.

The fact that infants can make sense of actions outside of their motor repertoire, and that they recruit their motor system during the perception of non-executable actions, fits better with the alternative view of action understanding. Under this view, goals are identified on the availability of various cues, only one of which might be action familiarity. However, once a goal is attributed, the motor system may be recruited to help the observer predict how the goal will be attained. As with the mirror neuron theory of goal understanding, this is essentially a simulative process. However, rather than simulating the observed movements in order to identify a goal, the observer identifies the goal and then simulates a way in which this goal might be fulfilled.

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