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Mirroring and the development of action understanding

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The discovery of mirror neurons in the monkey motor cortex has inspired wide-ranging hypotheses about the potential relationship between action control and social cognition. In this paper, we consider the hypothesis that this relationship supports the early development of a critical aspect of social understanding, the ability to analyse others' actions in terms of goals. Recent investigations of infant action understanding have revealed rich connections between motor development and the analysis of goals in others' actions. In particular, infants' own goal-directed actions influence their analysis of others' goals. This evidence indicates that the cognitive systems that drive infants' own actions contribute to their analysis of goals in others' actions. These effects occur at a relatively abstract level of analysis both in terms of the structure infants perceive in others' actions and relevant structure in infants' own actions. Although the neural bases of these effects in infants are not yet well understood, current evidence indicates that connections between action production and action perception in infancy involve the interrelated neural systems at work in generating planned, intelligent action.

1. Introduction

There is not a single mirror neuron hypothesis. The discovery two decades ago of mirror neurons in the macaque motor cortex has inspired numerous, wide-ranging hypotheses about the cognitive, social, linguistic and affective implications of mirror neurons. The most obvious of these hypotheses concern the implications of mirror neurons for perceiving and understanding others' actions, but even this narrower lens encompasses many, specific hypotheses, for example, mirror neurons have been proposed to play a role in biological motion perception, the perception of bodies and their movements, the anticipation of action outcomes in others and the apprehension of others' intentions, among other aspects of action understanding. Evaluating any one of these possibilities requires integrating information about cognition, action and their neural correlates. In humans, of course, an added complication is that it is rarely tractable to study the activity of single neurons, and so these hypotheses can only be approached by considering the broader idea of mirroring—that is the idea that the neural and cognitive systems that are involved in action control also support the perception or understanding of others' actions.

In this paper, we evaluate one hypothesis about mirroring, namely, that the systems involved in action production support the analysis of goals in others' actions, and we will consider it with respect to early development. From the standpoint of exploring the potential social-cognitive implications of mirroring, early development offers a useful perspective. Action production and action understanding undergo foundational developments during infancy, and relationships among systems are often most evident during times of transition. Further, as we elaborate below, infancy research has developed methods for assessing a key component of action understanding (the analysis of action as goal directed), thus providing a tool for evaluating one potential way in which mirroring may support social-cognitive functioning. The body of work that has recruited these methods indicates that there are rich connections between motor development and the analysis of goals in others' actions.

Evaluating the hypothesis that action production and goal analysis are linked is also important from the standpoint of shedding new light on developmental processes. The study of skilled, goal-directed action production and the study of social-cognitive functioning have served as two major organizers in developmental science for nearly a century [1–3]. These two abilities emerge over periods of years in the course of human ontogeny, and each has been shown to provide a critical foundation for cognitive, social and linguistic development. Action development and social-cognitive development have largely been viewed as separate domains, studied with different methods in different laboratories. The discovery of mirror neurons suggests that fundamental new insights into development may be attained by more fully integrating these areas of study.

Indeed, findings in developmental science and developmental neuroscience provide broad evidence for connections between action perception and action production from early in life. Infants' behavioural responses to others' actions indicate that information is shared across systems that produce and perceive action in infancy, including neonatal imitation [4], and the effects of observed actions on infants' action control [5]. Further, infants' own actions correlate with and influence their responses to others' actions, including their ability to visually anticipate the endpoints of action trajectories [6–8] and their encoding of hand configurations relevant to interacting with objects [9,10] as well as broader patterns of social attention [11–13]. Finally, recent neurophysiological experiments have yielded evidence that the motor system is active during infants' observation of others' actions [14–16], and this activation during action observation has been shown to vary as a function of the infants' developing motor skill [17,18].

The question on which this paper focuses is whether these broad connections evident during infancy include the connection between action production and the analysis of goals in others' actions. There are three significant challenges to evaluating this question. The first is the need for measures that evaluate the critical aspect of social cognition in infants, in this case, the understanding that actions are structured by goals. How can we know whether infants understand others' actions as structured by goals? The analysis of action goals is inherently abstract, and so the second challenge is to understand how motor experience could contribute to it. In this paper, we address these two challenges by considering what recent research has shown us about infants' analysis of others' actions, the structure of their own actions and the relationships between them. The third challenge is to understand how these processes are organized at the neural level. Scientific knowledge on this front is limited, and so we end by considering the evidence relevant to this issue and the open questions it raises.

2. Infants' analysis of others' actions

Even the most concrete of actions, for example reaching out to grasp a ball, is seen by mature observers as structured by abstract relations. The hand's movement is understood not just as a physical body traversing space, but rather as an action directed towards a goal object, the ball. This way of viewing actions has been described in terms of 'intentional relations' [19] because actions are cognitively represented as structured by the relationship between the agent and object at which his or her actions are directed. Actions can be viewed as participating in intentional relations at varied levels of analysis, from proximal goals (reaching for a ball) to more complex and extended intentions (preparing to juggle, entertaining a crowd). This relational analysis of action is fundamental to social cognition and social learning, and it is at the core of what it means to understand an action as goal directed.

There is a great deal of evidence that infants understand others' actions as structured by intentional relations. In visual habituation experiments, when infants are habituated to repeated examples of an agent acting on a particular goal, for example grasping a ball, they subsequently show longer looking (a response to novelty) to events that disrupt the original relationship between the agent and her goal as compared to events that preserve this relationship while varying the physical details of the agent's movements (see [20] for a review). This pattern of response is evident by three to six months of age for simple instrumental actions, like grasping [21–24], and by nine to 12 months of age for actions that relate agents to objects at a distance or indirectly, like looking and pointing [25–29], reaching over obstacles [30] or using a tool or means to attain an object [31–35].

Much of the evidence for infants' analysis of intentional relations comes from visual habituation experiments. Even so, infants' sensitivity to the goal structure of action has also been documented using other experimental methods. For example, by seven months of age, when infants view a model which directs a goal-directed action towards one of two objects, they respond by selectively acting on the actor's prior goal [36,37]. In addition, by 11 months of age, when infants view video events in which an agent acts on an object, they generate visual predictions about the actor's actions in a new situation based on an analysis of her prior goal [38,39]. Finally, by nine months of age, neurophysiological data indicate differential brain responses when infants view goal-directed actions as compared with human movements that are not goal directed [16].

The selectivity of infants' responses in these paradigms makes it clear that they are responding to the relational structure of the actions they see, rather than to lower level features of the events or to repeated associations between a hand and an object. Infants do not respond selectively to 'goal' changes in control conditions involving ambiguous human movements or inanimate object motions that are closely matched to the experimental actions in terms of timing, movement and contact with an object [36–40]. For example, in one control condition, infants are shown a mechanical claw that moves towards and grasps an object. The claw's movements are closely matched, in timing, trajectory and contact with the object, to the movements of a human reach. Although this event entrains infants' attention to the object in the same way that a reaching hand does, infants do not respond selectively to changes in the goal for the claw events, they do not selectively imitate the goal of the claw's action and they do not generate goal-based predictions concerning the claw's next movements [38,40,41]. Interestingly, when older infants see that the claw is manipulated by a person, they do respond selectively to the goal structure of the experimental events [32], suggesting that the limiting factor is not the type of moving entity involved, but rather the extent to which the infant can understand the event as the action of an agent.

Perhaps, the strongest evidence that infants analyse intentional relations comes from work showing that they encode higher order goals, that is, goals that transcend specific actions on objects. A simple action, like grasping a cup, can be

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understood as directed at a downstream goal, such as clearing the table or having tea, depending on the context and the actions with which it co-occurs. Infants engage in this kind of action analysis, interpreting actions in a sequence in terms of their relationship to higher order goals: for example, when infants see an agent grasp a cloth in order to draw near and obtain a toy that sits on its far edge, they subsequently interpret grasps to the cloth as directed towards the toy, rather than the cloth itself; however, infants do not respond in this way if the same sequence of actions occurs without a means-end relationship (the agent grasps and pulls a cloth and then grasps a toy that sits beside the cloth) [31,34,35,42]. Thus, infants base their analysis of sequential actions on their relationship to higher order goals, rather than lower level patterns of association or linear order. Similarly, infants track agents' intentional relations over time and across variations in the form of the action and the context in which it occurs: for example, infants infer that a person will reach for an object that she has previously looked at [23,26,43; see also 44] or expressed a preference for [45].

Taken together, this body of work demonstrates that infants analyse others' actions in terms of intentional relations. This analysis is abstract in that it represents structure above the level of particular movements and physical contact with the environment. Infants' sensitivity to the goal structure of action does not necessarily imply that they possess rich, mentalistic concepts of intentions (see [20] for a discussion). Nevertheless, this analysis of action is likely to be foundational to social cognition in at least two senses: first, on the timescale of online processing of social events, goal-based action analysis is the necessary first step in social information processing, allowing the perceiver to generate appropriate responses to social partners in the moment. Second, on the timescale of developmental change, goal-based action analysis may provide a foundation for the development of folk psychological concepts later in childhood. Indeed, infants' responses in the kinds of visual habituation procedures described above predict their later performance, at 4 years of age, on explicit verbal tasks that assess their understanding of psychological processes in others [46,47].

Is mirroring involved in this aspect of social cognition? Infancy offers an interesting window on this question because at the same time that infants are beginning to analyse others' action goals, their own production of goal-directed actions undergoes fundamental developmental organization. Action development exerts broad effects on cognition and perception during infancy [48], and, as noted earlier, recent evidence suggests that action development influences infants' perception of and attention to other's actions [6–12]. The question is whether action development also influences infants' analysis of others' action goals. To address this question, we first consider the information inherent in action control that could support this kind of analysis. We then review evidence that this influence does, indeed occur. Following this evidence, we next consider the question of how the contributions of infants' own actions may engender development beyond the understanding of particular actions as goal directed.

3. Infants' actions are structured by goals

Human infants have an uphill road to climb in gaining motor skill. They are born with extremely limited abilities to control the movements of head, body and limbs. Therefore, much of early motor development involves gaining control of physical movements. Even so, it is clear that these efforts are organized with respect to goals from very early in life [49]. For example, from the earliest postnatal months, infants launch arm movements towards objects, and these efforts culminate in relatively smooth object-directed reaches by about six months of age [50,51]. Von Hofsten's pioneering work documented the ways in which even infants' earliest attempts to reach are prospectively directed towards goals. He showed that young infants aimed their reaches for a moving object in anticipation of the object's position at contact [52]. Further, like adults, infants preshape their hands to anticipate the size and orientation of objects as they reach for them [53,54]. Thus, from early in development, infants' actions are prospective and goal directed.

Towards the end of the first year, infants begin to organize action sequences in service of higher order plans. These plans are evident in the way that infants' initial actions are shaped by downstream goals. For example, Claxton *et al.* [55] found that 10-month-old infants adapt the speed with which they reached for a ball based on whether they planned to subsequently throw it versus place it into a container. They reached more slowly in the latter case, presumably because placing requires more precision than throwing (see [56] for a review of related findings). Infants at this age also engage in means-end actions that require action on one object in order to attain another object, which is the desired goal: to illustrate, by eight to 12 months, infants who are presented with an interesting toy placed out of reach at the far end of a cloth will produce well-organized solutions to the problem, visually fixating the toy while systematically drawing it within reach [3,57]. Goal structure also guides infants' learning of new actions: when eight-month-old infants first encounter a new means-end problem, they benefit more from training that highlights the goal as compared with training that highlights the means [58].

These examples elucidate the higher order cognitive components of infant action development. As Rosenbaum has shown in his studies of adult motor behaviour, goal information is inherent to motor control [59]. Even the simplest actions are shaped, monitored and corrected with respect to downstream goals. Infants' actions are no different. This perspective on action has a strong history in infancy research, perhaps because the organizing effects of goals on action are particularly salient in infants' prolonged and effortful attempts to solve motor problems. As Thelen and her colleagues wrote in describing how young infants gain control of their arm movements, 'Each reach is an effort to match current abilities to some desired goal. By repeating this matching effort over days, weeks, and months, infants find increasingly efficient and stable solutions' [60, p. 1094].

This aspect of infants' action production is isomorphic to the way that infants analyse others' actions. Just as infants' own actions are organized with respect to goals and higher order plans, their perception of others' actions is also organized in these ways. This structural similarity suggests that infants' action analysis may recruit information from action production. To be clear, the claim is not that subjective feelings of wanting or trying drive infants' actions and their action understanding. Rather, the proposal is that because goal information is inherent in motor control, mirroring could make this structural analysis available for analysing others' actions. This proposal predicts close relationships, during early development, between action production and goal analysis. As described next, there is growing evidence in support of this prediction.

4. Infants' actions influence their action understanding

If mirroring supports infants' action analysis, then developments in infants' own goal-directed actions, such as reaching or means-end coordination, should have implications for their analysis of others' actions. Consistent with this possibility, developments in infants' own actions correlate with their responses on tasks that measure their sensitivity to others' goals. For example, at 10 months of age, infants who are skilled at producing means-ends actions are able to recover the higher order goal of someone else's means-end actions, but infants of the same age who are less skilled cannot ([34] see also [29,61,62]). Thus, as infants become able to organize their own goal-directed actions, they also become more able to recognize goal structure in others' actions.

A stronger test of the relationship between infants' own actions and their action analysis is to ask whether motor experience causes changes in infants' apprehension of others' goals. A growing body of evidence indicates that it does. Training that supports infants' production of goal-directed actions also supports their ability to detect the goal structure of others' actions. For example, training with Velcro-covered 'sticky' mittens enables three-month-old infants to apprehend objects with their hands, and this training also leads infants to respond systematically to others' goal-directed actions in the visual habituation paradigm described earlier [22,24,62]. These effects have been found for higher order goals as well as for simple actions: training in a means-end task, such as using a cane to obtain a distant toy, enables eight- to 10-month-old infants to recover the higher order goal structure of another person's means-end actions. Having practiced using the cane to attain a goal, infants subsequently interpret another person's actions on the cane as directed at the ultimate goal rather than the cane itself [33,63,64].

Critically, there is evidence that it is the goal-directed aspects of infants' own actions that matter for these effects. Infants' responses to training paradigms vary in how well organized they are with respect to the goal, and this variation predicts infants' subsequent responses to others' actions in the visual habituation paradigm. Variability in three-month-old infants' tendency to engage in visually guided, object-directed activity with the mittens predicts their sensitivity to others' reaching goals [24,62]. In addition, eight- and 10-month-old infants' tendency to produce well-structured means-end actions during training predicts their subsequent analysis of higher order goals in others' actions [33,63]. Thus, actively engaging in goal-directed action changes how infants understand others' actions.

Further evidence is required to be sure that motor information, *per se*, matters for these intervention effects. Infants' actions generate many channels of information that may contribute to learning and development, including, but not limited to, motor information [48]. When they produce skilled reaching or tool-use actions, infants not only engage their motor processes, but also generate exemplars of action events that they can observe and learn from. Just watching someone use a tool, for example, provides information about the outcomes associated with tool movement and about the causal affordances of the tool. Does motor engagement matter for infants' analysis of others' actions above and beyond these opportunities for observational learning? Although mirroring, by definition, occurs during both the execution and observation of actions, during early development, execution should lead the way because the motor system is built via motor practice. Thus, action production would be predicted to be critical for acquiring new insight into the goal structure of others' actions. Similarly, research with adults supports the conclusion that active engagement in a specific, skilled action strongly shapes mirror system responses to that action [65].

Intervention experiments have tested this prediction in infants by including matched observational training conditions in which infants are shown multiple exemplars of reaching or tool-use events but do not have the chance to engage in the actions themselves [11,22,33,62,63]. To illustrate, Sommerville *et al*. [33] compared conditions in which 10-month-old infants either learned to pull a cane to obtain a toy or watched as an adult repeatedly did so. Subsequently, infants who received active training showed sensitivity to the goal structure of another person's cane-pulling actions, but infants who received only observational training did not, a finding mirrored in each of the studies that has used this logic. Across these studies, infants have been found to be highly attentive to the observational training events, and these events provide information that could, in principle, be useful for understanding the goal structure of the actions. Nevertheless, when infants do not themselves engage in the trained action, they seem not to glean information about the goal structure of that action. Thus, this work provides evidence that infants' actions influence their action understanding because acting involves the engagement of motor processes.

To summarize, there is a growing body of evidence that mirroring plays a role in the development of infants' action understanding. Learning to act in goal-directed ways leads infants to see the abstract, relational structure in others' actions. These effects of mirroring are relatively abstract, because they involve the goal and higher order plan structure of actions, both in terms of what infants produce and the structure infants perceive in others' actions. At the same time, these effects involve motor processes—they are driven by the infants' active engagement in the relevant action.

5. Infants' actions support the interpretation of novel actions in others

An open question is how broadly this kind of mirroring is involved in action understanding. One possibility is that mirroring only supports infants' analysis of the specific actions they have learned to produce, like reaching or using canes to obtain toys. In this case, although it would be useful some of the time, mirroring would be of limited value because infants often need to make sense of actions that they have not engaged in. However, recent findings from our group suggest that mirroring could play a broader role in analysing others' actions.

We have begun to explore the possibility that the goal-based action representations that infants derive from their own actions can serve as a base for generalization to broad instances, under the right conditions [41]. As we have highlighted in this paper, the cognitive processes involved in both action production and action understanding describe actions in terms their relation to a goal. Thus, the challenge, for the infant, is to generalize one instance of relational information (e.g. grasping in relation to a goal) to a novel case (e.g. using a tool in relation to a goal). Research on learning in other domains has shown that learners generalize relational information most effectively under conditions in which they can compare two instances with similar structural properties [65]. Infants and young children engage in this kind of cognitive learning, for example, using structural similarity to a familiar means-end problem in order to rapidly generate a solution to novel means-end problem [66,67].

We propose that this process could occur in contexts in which infants are able to simultaneously compare their own actions with the novel actions of another person. By comparing a new action, for example using a tool to pick up a toy, to one's own actions, for example grasping, infants may detect the relational similarity between these two actions and thus relate the goal structure of their own actions to the observed action. We reasoned that the context of joint action, in which the infants' own actions are directed towards the same goal as those of another person, might support this kind of comparison.

We evaluated this hypothesis by attempting to teach seven-month-old infants about a novel action, the use of a claw-shaped tool to grasp objects [41]. As noted earlier, prior findings had shown that infants at this age do not spontaneously view actions with a claw as goal directed. In the critical condition, the experimenter first used the claw to hand the infant several toys, and this ensured that the infants' grasping actions co-occurred with the tool's action on the toys. Following this experience, infants responded systematically in an imitation task that assessed their sensitivity to the goal structure of the experimenter's claw actions. That is, infants selectively acted on the experimenter's prior goal. By contrast, this result did not occur in control conditions in which infants interacted with the tool or saw the experimenter use it to move objects but did not engage in joint action. Infants in these conditions attended to the claw events to the same extent, and in the same ways, as infants in the joint action condition, but they did not glean information about goal structure from this experience. Thus, the opportunity to simultaneously compare their own actions to the observed actions with the claw seemed to be critical for infants' analysis of the goal structure of the claw action.

The second experiment tested whether infants' own engagement in the action was important for this effect. Infants either engaged in joint actions with a claw-wielding adult, as in the first experiment, or they observed this interaction occurring between two adults, with one reaching out to grasp the toys proffered by the other with the claw. Infants were equally attentive to the claw actions in these two conditions, but only infants who had engaged in joint actions (i.e. coordinated their own actions with the experimenter's claw actions) subsequently responded systematically to the goal structure of the claw actions. Thus, as was the case in the training studies, motor engagement seemed critical for infants' analysis of others' action goals. Even so, in a subsequent study, we found evidence that under more supportive training conditions, in particular, when linguistic cues to the experimenter's goal are included, 10-month-old infants detect relational similarity between grasping and claw actions even when their own motor processes are not engaged [68]. Thus, while infants' own actions may provide a particularly strong basis for generalizing to new actions, with development, infants may be able to use action information more flexibly.

These findings suggest that the knowledge which infants gain from their own actions can support their analysis of others' actions even when those actions differ from the infants' own. The conditions that enabled the generalization of action information in our experiments are ubiquitous in infants' daily lives—infants' own actions are often co-present and coordinated with the actions of other people. Social interactions, and in particular interactions in which infants' goals are coordinated with those of social partners, may provide rich opportunities for this kind of learning to occur [69]. Moreover, considering these effects as driven by general purpose cognitive learning mechanisms suggests a route by which action knowledge that is initially gleaned from motor experience could provide a developmental foundation for increasingly abstract goal concepts.

6. Open questions: mirroring and mirror neurons

Thus, current behavioural evidence from infants provides strong support for one hypothesis about mirroring. The cognitive systems that drive infants' own actions contribute to their analysis of goals in others' actions. This effect of mirroring occurs at a relatively abstract level of analysis both in terms of the structure infants perceive in others' actions and relevant structure in infants' own actions. Infants see others' actions as structured by goals and higher order plans, infants' own actions are structured in these ways, and infants' engagement in goal-directed actions and planned means-end actions renders changes in their understanding of these aspects of others' actions. Is this high-level action mirroring in infants supported by the mirror neuron system? The discovery of mirror neurons in monkeys suggested this hypothesis about the potential effects of mirroring on action understanding, but as yet, the neural bases of these effects in human infants are not known. Addressing this issue is the critical third challenge in evaluating the hypothesis we began with.

One approach to this issue is to ask whether there are parallels between the behavioural findings concerning action mirroring in infants and the response properties of mirror neurons in monkeys and the mirror neuron system in human adults. There are several such parallels. To start, mirror neurons in monkeys and the mirror neuron system in human adults are selectively sensitive to goal-directed or meaningful actions [70]. Monkey mirror neurons and the adult human mirror neuron system are also responsive to higher order plans, for example, differentiating responses to a grasping action depending on downstream goals [71,72]. These findings suggest that mirror neurons are modulated by goal- and plan-level action information and therefore raise the possibility that the mirror neuron system is involved in the mirroring effects in human infants' analysis of others' actions.

In addition, mirror neurons and the adult human mirror system are modulated by motor experience in ways that seem to parallel to the developmental effects of experience on infants' goal analysis. In monkeys, mirror neuron responses change when the animal is trained to use a new tool [73], and in humans mirror neuron system responses to others' actions are affected by the observer's motor expertise [74,75]. Further, engaging in joint actions has been found to influence mirror neuron system responsiveness in ways that are similar to the effects in our joint action studies with infants. For example, Kourtis *et al*. [76] found that mirror neuron system responses in adults were stronger when they viewed the actions of a person with whom they had just engaged in joint action (see [69] for further discussion).

Though suggestive, these findings leave open the question of the neural basis of action mirroring in human infants. A number of recent studies have begun to shed light on the potential neural correlates of the mirror neuron system in human infants. In adults, desynchronization of the electroencephalogram (EEG) mu rhythm has been shown to occur during both action execution and action observation and is thought to reflect activity in the mirror neuron system [77,78]. Infants evidence analogous patterns in EEG desynchronization during the observation and execution of action, suggesting that mirror neuron system activity can be identified in infants [14–17]. Similar patterns of EEG activity have also been observed in infant monkeys [79]. Critically, mu desynchronization in human infants has been found to vary as a function of motor development. Infants' own motor abilities predict the strength of their mu desynchronization response when they view others' actions [17,18].

Nevertheless, it is not yet known which aspects of social perception or action understanding are related to these patterns of neural activity in infants. Southgate and colleagues' work provides the best current evidence on this issue. They found that nine-month-old infants evidenced mu desynchronization when they viewed a hand reaching behind a barrier, but showed no such response when the hand reached to an empty location or when the hand moved in an ambiguous posture rather than reaching [16]. These findings thus suggest that infants demonstrate mirror neuron system activity that is selective for goal-directed actions. However, as the authors' interpretation of this finding makes clear, it is not certain whether this activation reflects the analysis of the agent's goal *per se*. Southgate *et al*. [16,80] have argued that because this neural response is anticipatory, occurring prior to the culmination of the action and under conditions in which the completion of the action can only be inferred, it reflects the generation of predictions about the outcome of the action, rather than analysis of the action goal. On the other hand, as discussed earlier, the motor system is inherently prospective and so it seems possible that motor processes could be involved in the prospective analysis of others' actions. Ultimately, resolving this issue requires integrating neural measures with the infant behavioural methods reviewed in this paper.

A further challenge in addressing this issue is the fact that the brain develops, and so investigating the neural correlates of the mirror neuron system during early ontogeny is not a simple matter of looking for adult patterns in infant brains. Because the motor system undergoes foundational development during infancy, it is not clear that mirror neuron system activity in infants would be evident in neural activity in the same way as it is in adults. Indeed, analyses of mu desynchronization in infants indicate more diffuse patterns in infants than adults, and other differences in the response that are not, as yet, fully understood (see [14,17] for discussions). More generally, understanding the developmental processes that shape the mirror neuron system is an important open question for the field [81].

Even so, the behavioural research reviewed here makes clear that, at the functional level, mirroring contributes to infants' analysis of others' goals. This body of work, and the methods it has generated, can provide an anchor for future approaches to understanding the neural correlates of the mirror neuron system during early development. In particular, the behavioural findings indicate that understanding this kind of mirroring at the neural level is going to require understanding the interrelated neural systems at work in generating planned, intelligent action. Infants' actions are structured by prospective goals [49] and higher order plans [56], and their actions are informed by cognitive analyses of the relational structure of problems [56,66]. Further, as the research reviewed here shows, infants engage these same processes in making sense of others' actions. Investigating the neural systems that ground these cognitive processes in infants will shed new light on the nature of the mirror neuron system, its limits and its potential.

7. One hypothesis among many

We began this paper by noting that there is not a single 'mirror neuron hypothesis', but rather, a broad set of hypotheses that stem from the discovery of mirror neurons. We have argued that one mirroring hypothesis looks like it has some truth to it, but this leaves open the question of whether others are true and, if true, what the relationships may be among different abilities that are structured by mirroring. One interesting property of monkey mirror neurons is that they vary in their response properties in ways that reflect many levels of analysis in the structure of an action, from exact movements (i.e. strictly congruent) to more general goals (i.e. broadly congruent) like obtaining with the hands or mouth and even to the affordances of objects [70]. Further, mirroring responses have been found in diverse regions in the adult human brain [82]. These facts suggest that mirroring could well influence the development of social perception and social cognition at multiple levels and in varied ways [81]. The challenge, going forward, is to integrate the methodological tools necessary to understand these distinct, yet potentially related, effects.

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