Chapter 17

Mirroring and the ontogeny of social cognition

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Introduction

Making sense of the actions and intentions of others is critical for human social functioning and for social-cognitive development. Despite a great deal of interest in the development of action understanding and the broad impact that it can have on the emergence of social abilities (e.g., Brune and Woodward 2007; Wellman et al. 2008; Yamaguchi et al. 2009; Paulus et al. 2014; Krogh-Jespersen et al. in press), relatively little is known about the neural underpinnings of this foundational social-cognitive skill. In this chapter, we review recent research that suggests that mirroring—the process of activating one's own action control system while observing someone else acting—may be linked to the development of action understanding.

The hypothesis that the brain's action control system shapes the ability to process and respond appropriately to the actions of others was initially inspired by research in animal neuroscience. Rizzolatti and colleagues (1996) identified individual neurons (mirror neurons) in the monkey motor cortex that discharge not only during action production but also when the animal observes another agent produce the relevant action. This finding, combined with parallel discoveries in neuroimaging studies with human adults, has led to wide-ranging proposals about the role that the motor system may play in supporting social cognition and social behavior. Among these predictions is the idea that activating one's own motor system during perception allows the observer to interpret the actions of others in meaningful ways. Drawing on these action control resources could have wide-ranging implications for early development, a time when both motor and social abilities undergo foundational organization (Ferrari et al. 2013; Woodward and Gerson 2014). In this chapter, we consider one of these potential implications by exploring the evidence that mirroring may facilitate a fundamental aspect of action understanding—interpreting others' actions in terms of their goal structure—in the first years of life.

For adults, the perception of others' actions as goal-directed is robust and automatic (Spunt and Lieberman 2013). When others reach for objects, for example, adults rapidly decipher the meaning behind this action at several levels, from the most basic (e.g., reaching for a plate) to the increasing abstract (e.g., beginning to clear the table). In this chapter, we will focus our discussion of infant action understanding at the most fundamental level—the ability to understand that other people's actions are directed toward goals rather than simply movements through space. This attention to the agent–goal relation is a necessary foundation for tracking and anticipating the actions of social partners, and it is critical for many aspects of social behavior that emerge early in development, including imitative learning, joint attention, and prosociality.

Because mirror neurons in monkeys, and analogous mirroring responses in the human brain, are selective for goal-directed actions, it has been hypothesized that they play a role in the perception of action goals (e.g., Rizzolatti and Craighero 2004). Research over the past decade has begun to evaluate this possibility with respect to early development, but, as we detail below, there are still pressing gaps in the empirical record. We consider two, related, bodies of research with infants: one that investigates the neural correlates of action observation, and one that investigates infants' understanding of others' goals. Together, these bodies of work provide suggestive evidence that neural mirroring may support social-cognitive development during infancy, although the existing evidence also leaves critical questions unanswered. In particular, assessing the limitations of the previous research on this topic makes it clear that integrating neural and behavioral measures is critical for assessing the functional role of motor system activation during development. Combining neural measures with behavioral assessments of action understanding will allow researchers to assess whether, and how, recruiting the motor system in infancy functions to facilitate action understanding. New research from our group demonstrates that this approach can shed new light on the functional significance of neural mirroring in infants. We close by highlighting the power in this method and the new questions that this question could help us answer.

Mirroring in infancy

When adults view another person acting, they show activation in regions of the brain that are associated with motor control (Buccino et al. 2001; Grezes and Decety 2001; Iacoboni et al. 2005), and they evidence similar electrophysiological responses to those shown during action production (Muthukumaraswamy et al. 2004; Pineda 2005; Arnstein et al. 2011). These responses appear to be selective for goal-directed actions, rather than for meaningless movements, and the strength of the mirroring response relates to the observer's own motor competence and experiences (e.g., Calvo-Merino et al. 2006; Cannon et al. 2014).

A burgeoning body of work suggests that, like adults, infants show activation in the motor system when observing the actions of other people. While there are a number of ways to record the adult motor system response (e.g., functional MRI [fMRI], EEG, and EMG), some of these methods are not feasible to use with infants. EEG is a method that allows us to compare measures of motor system engagement in adults to that of infants. In adults, power in the mu frequency range is reduced (mu desynchronization) over sensorimotor cortex during both action execution and action observation, and simultaneous fMRI and EEG recordings show that this component of EEG is correlated with activation of several cortical areas of the mirror neuron system (Arnstein et al. 2011). Infant EEG patterns present similarly to those of adults (Marshall and Meltzoff 2011; Cuevas et al. 2014). While the infant mu frequency range is lower (6–9 Hz) than that of adults (8–13 Hz; see Marshall and Meltzoff 2011), mu desynchronization in infancy seems to have many of the same characteristic features of the adult neural mirroring response. To start, infants, like adults, show attenuation in the mu frequency range over sensorimotor regions of the scalp both when they perform actions themselves and when they observe the actions of others (Southgate et al. 2009; Southgate et al. 2010; Stapel et al. 2010; Marshall et al. 2011; Saby et al. 2013; Southgate and Begus 2013; Warreyn et al. 2013).

Further, similar to the adult neural mirroring response, infants' neural mirroring is modulated by their own motor development and motor experience. For example, van Elk and colleagues (2008) found that those infants with more crawling experience have a stronger neural mirroring response when they observe others' crawling. This correlational finding suggests that motor experience may be linked to the strength of the neural mirroring response early in life (see also Cannon et al. 2015). Additional research has demonstrated that self-produced experience with actions and objects can influence the extent to which the motor system is activated (Van Elk et al. 2008; Stapel et al. 2010; Paulus et al. 2012; Virji-Babul et al. 2012; Marshall et al. 2013; de Klerk et al. 2014). To illustrate, Marshall and colleagues (2013) gave infants experience interacting with two rattles—one rattle was heavy and the other was light. Infants then observed an experimenter reach for each rattle one at a time, while counterbalancing the actual weight of the rattle that the experimenter was lifting. The authors found that, when infants observed an experimenter reach for a rattle that they had experienced as heavy, infants showed a stronger motor system response than when they observed an actor reach for the rattle that they had experienced as light. These studies suggest that both fundamental changes to infants' motor repertoires (i.e., motor skills that are well established and central to motor development) and short-term motor experiences (e.g., experiencing one object as heavy) influence infants' neural responses when viewing others' actions.

Critically, as has been observed in the adult literature, this neural response in infants seems to be related to meaningful interpretation of others' actions as goal-directed. For example, Southgate and colleagues (2010) found that the neural mirroring response was selectively present when infants observed actions that could viewed as being directed toward a goal: infants showed mu desynchronization when they observed a person reaching toward a toy previously hidden behind a screen, but not when they observed a person reaching to an empty location behind a screen. Thus, neural mirroring response was selectively present in situations where the action outcome could be inferred—even if the outcome was not directly visible. Findings from Stapel and colleagues (2010) further suggest that the interpretability of the observed action modulates the mu desynchronization response in infants. The authors found greater mu desynchronization in infants when they observed surprising action outcomes (e.g., holding a cup to one's ear) than when they observed expected outcomes (e.g., holding a cup to one's mouth).

Thus, a growing body of evidence suggests that in infants, as in adults, neural mirroring occurs. Even so, a central question remains unanswered: what does mirroring buy infants? Neural mirroring appears to occur when infants view others' goal-directed actions but, in itself, this co-occurrence does not clarify the social-cognitive functions that it may support. Indeed, Cook, Heyes, and their colleagues (2014) have hypothesized that neural mirroring responses in infants reflect relatively shallow associations between the feelings associated with acting and visual information about actions that derived from the experiences of watching one's own actions and acting in coordination with others, and that such responses may have no important function for social perception (see also Hickok 2014; but see Krogh-Jespersen et al. 2014; Simspon et al. 2014).

Even if the most deflationary possibility can be ruled out, there are a number of hypotheses about the potential functional roles that mirroring could play in infancy, and, as yet there is little evidence available to directly evaluate them or distinguish among them. Researchers have hypothesized that mirroring may support infants' cognitive analysis of goal structure in others' actions (Woodward and Gerson 2014), infants' imitative social behavior (Simpson et al. 2014; cf. Meltzoff 2007), and infants' predictions about the outcomes of others' actions (Csibra 2007; Southgate et al. 2009; Hunnius and Bekkering 2014). These possibilities are not necessarily mutually exclusive, but each involves specific predictions that have not, as yet been fully articulated and investigated. To begin to evaluate these possibilities, it is necessary to draw on behavioral measures that can identify particular social-cognitive functions during infancy and, ultimately, use these methods to evaluate whether these functions are dependent on neural mirroring. Developmental psychologists have implemented a number of behavioral methods for investigating infants' action knowledge and related social responses, and these methods provide initial evidence concerning the potential functions of neural mirroring as well as potential tools for use in research that fully integrates neural and behavioral measures of mirroring and its functions in infants. In the following sections, we first consider the behavioral evidence for infants' action understanding, its expression in social behavior, and its connection to motor experience. Then we turn to the question of the potential relation between neural mirroring and these social-cognitive abilities in infants.

Infants' actions and action understanding

During infancy, there are foundational advances in both action control and action understanding. In the first year, infants undergo dramatic changes in the control of their own goal-directed actions, including the abilities to gain control of arm movements and generate skilled goal-directed reaches (e.g., Thelen et al. 1993; von Hofsten 2004), engage in prospective control of reaching actions (e.g., von Hofsten 1980; von Hofsten and Ronnqvist 1988; Robin et al. 1996), and organize increasingly complex sequences of actions in service of higher-order goals (e.g., Claxton et al. 2003; Gerson and Woodward 2013). Alongside these developments in action control, infants also become able to apprehend meaningful structure in the actions of other people. During the first year, infants begin to encode others' reaching actions as structured by goals (e.g., Woodward 1998; Cannon and Woodward 2012) and become able to apprehend increasingly complex goals that structure sequences of actions (e.g., Sommerville and Woodward 2005) and social interactions (e.g., Henderson and Woodward 2011).

Much of the evidence concerning infants' apprehension of action goals comes from visual habituation studies. Infants are first habituated to a stimulus, for example, a person reaching toward and grasping an object. Following habituation, infants view events in which either the goal (the object grasped) or the movement pattern of the actor's reach has changed, and their novelty response (longer looking) is assessed (e.g., Woodward 1998). By 5–6 months of age, infants show selective responses when the goal of a reaching action changes (Woodward 1998; see Woodward et al. 2009), and by 12–14 months infants show similar responses to changes in higher-order goals, such as those involved in means–end and collaborative actions (Sommerville and Woodward 2005; Henderson and Woodward 2011). Infants do not show this selective response to goal changes for the movement of inanimate objects (Woodward 1998) or for ambiguous human movements (Woodward 1999)—that is, infants' responses are specific to the goal-directed actions of agents (see Woodward and Gerson 2014 for a discussion). Infants' responses in these experiments have been found to correlate with their own motor abilities: at ages when new motor abilities are first emerging, infants who show more skill at the relevant action also show stronger responses to goal changes in others' actions (e.g., Sommerville and Woodward 2005; Brune and Woodward 2007; see also Loucks and Sommerville 2012).

Eye-tracking studies have revealed infants can also generate rapid, online, visual predictions about how a goal-directed action will unfold (Falck-Ytter et al. 2006; Gredebäck et al. 2009; Hunnius and Bekkering 2010; Kanakogi and Itakura 2011; Cannon et al. 2012). Critically, by 11 months of age, infants can reliably predict an actor's subsequent action based on an analysis of her prior goal (Cannon and Woodward 2012; Krogh-Jesperson and Woodward 2014). This ability to generate rapid online predictions about action outcomes correlates with the infant's own motor abilities. For instance, those infants who are more skilled at performing precision grips are faster to predict the outcomes of others' precision grips (Ambrosini et al. 2013). Similar relations between infants' own actions and their ability to visually anticipate others' actions have been observed for a number of different kinds of actions (Gredebäck and Kochukhova 2009; Kanakogi et al. 2011; Cannon et al. 2012). More generally, as is true for adults, infants show similar visual anticipation in their own actions and when viewing the actions of others (von Hofsten 2007; Rosander and von Hofsten 2011).

Infants' overt imitative responses to others' actions also reveal their sensitivity to action goals. Across a number of different ages and test conditions, researchers have found that infants don't automatically copy the actions of social partners—rather, they selectively reproduce the goal-relevant aspects of those actions (Meltzoff 1995; Carpenter et al. 1998; Hamlin et al. 2008). To illustrate, Hamlin and colleagues (2008) showed seven-month-old infants events where a person grasped one of two toys; the authors then allowed the infants the opportunity to choose one of the toys themselves. When infants were given the opportunity to choose a toy, they selectively acted on the same object that the actor grasped. Critically, infants' propensity to selectively reproduce the actor's goal was specific to well-formed, goal-directed actions. Infants did not respond in this way when they viewed ambiguous human movements or the movements of inanimate objects (Hamlin et al. 2008; Mahajan and Woodward 2009; Gerson and Woodward 2012).

These findings provide converging evidence that infants see others' actions as structured by goals. The various methods that have been used with infants (visual habituation, imitation, and eye-tracking) each reveal a core ability in infants to apprehend the goal-directed nature of others' actions. Even so, each method provides potentially unique evidence about the ways in which infants respond to others' goals. Visual habituation methods may be a very sensitive measure of infants' cognitive encoding of events, because they allow infants ample time to study and respond to the actions they view. In contrast, eye-tracking and imitation procedures are more demanding, as they require the generation of relatively rapid online responses (see Krogh-Jespersen et al. in press). Imitation tasks have the further demand of producing a response in the context of a social interaction and thus may depend on social motivation as well as cognitive encoding and the rapid generation of a response.

As noted above, these studies have also provided initial evidence for a connection between infants' action understanding and their own actions, in that infants' responses in these tasks have been found to correlate with measures of their own motor expertise. Even so, further evidence is needed to evaluate whether motor experience influences infants' sensitivity to others' action goals. This issue is addressed by studies of the effects of motor training interventions on infants' responses to others' actions. For instance, when ten-month-old infants are trained to use a cane to retrieve an out-of-reach object, they subsequently show sensitivity to the goal structure of cane actions in a visual habituation paradigm (Sommerville et al. 2008). Thus, learning to perform novel actions can facilitate infants' understanding of the action in others. Critically, providing infants with opportunities to observe others' use of the cane did not influence their subsequent responses to others' cane actions. That is, active motor experience uniquely supports infants' action understanding (see also Henderson et al. 2013).

Training studies indicate that self-produced actions support even the earliest aspects of infants' action understanding. When infants are three months old, they have generally not mastered skilled reaching and thus have a limited ability to reach for and grasp objects. Needham and her colleagues (2002) developed a method for allowing infants at this age to "grasp" objects using "sticky," Velcro-covered mittens. Visual habituation studies have demonstrated that, following sticky-mittens training (but not before), infants interpret the actions of others as goal-directed (Sommerville et al. 2005; see also Libertus and Needham 2010). This effect is unique to instances where the infant is provided active training obtaining their goals—observational experience is not sufficient for facilitating three-month-old infants' goal analysis (Gerson and Woodward 2014). Thus, first-person motor experience seems to provide unique information for infants concerning the structure of others' actions.

The evidence from behavioral experiments with infants supports two general conclusions. First, from early in life, infants are sensitive to the goal-directed nature of others' actions. Infants do not seem to regard actions as mere movements through space but, instead, they analyze actions in terms of the agent's likely goals. Second, there are clear links between infants' motor experience and their understanding of others' actions. Infants' own actions seem to provide them with information that they can use to make sense of other people's behavior. These findings raise the possibility that neural mirroring lies behind the observed connection between infants' actions and their action understanding, and they provide methods that can be recruited to explore this possibility. They do not, however, fully answer the question. There are other mechanisms by which active experience could inform infants' action understanding. Neural mirroring may or may not drive these effects. We turn now to the question of how to bridge this gap.

A new strategy for assessing the functional role of mirroring in infancy

The research reviewed so far is suggestive. Neural measures with infants reveal responses that would be expected if neural mirroring were to support action understanding. Behavioral measures of infants' action understanding reveal patterns that would be expected if action understanding were to draw structure from neural mirroring. But in the end, making progress in understanding the mechanisms that support infant social-cognitive development requires bridging the gap between these two bodies of work. That is, to know whether and how neural mirroring is linked to social cognition, we need to record infants' neural responses and their social-cognitive behavior together. Without independent and integrated measures of action understanding and neural mirroring, the question cannot be fully answered.

Research with adults has successfully addressed this issue and consequently provides clear evidence that some aspects of action understanding depend on neural mirroring. For example, disruption to neural processing using transcranial magnetic stimulation over the premotor cortex reduces adults' ability to recognize actions (Michael et al. 2014) and slows their ability to generate visual predictions about the outcome of an action sequence (Stadler et al. 2012). Behavioral methods that tax the motor system have similar effects (Cannon and Woodward 2008; Ambrosini et al. 2012). Furthermore, when adults are asked to consider how an action was performed versus why an action was performed, there is differential activation of mirroring regions (Iacoboni et al. 2005); this finding suggests that mirroring is linked to particular types of behaviors and interpretations of events in adulthood. This work is convincing because it provides independent assessments of neural activity and behavior.

Obviously, manipulating task directions and neural activity are not options when trying to understand the functional significance of mirroring in preverbal infants. A different strategy is needed in order to examine what mirroring buys preverbal infants. There are fewer tools available to investigate contingencies between neural and behavioral responses in infants than in adults. Even so, infants offer a vantage point on this issue that adults cannot: in adults, perceiving and responding appropriately to others' actions is robust and automatic (Spunt and Lieberman 2013), but these abilities first emerge, and are therefore more variable, during infancy. When new skills are first emerging, behavior is variable, and this variability can reflect differences in developmental trajectories. Indeed, variability in infants' behavioral responses to others' goal-directed actions reflects meaningful individual variation in developmental trajectories both concurrently (e.g., Sommerville and Woodward 2005) and longitudinally (e.g., Wellman et al. 2008). Further, there is reason to think that there may be detectable, and informative, individual variation in mu desynchronization during infancy, because, as noted earlier, the strength of the desynchronization response has been found to correlate with variation in infant motor development (Cannon et al. 2015; van Elk et al., 2008).

When infants are tested using the behavioral measures described in this chapter (i.e., visual habituation, goal reproduction paradigms, and eye-tracking measures), performance is variable. Individual infants differ from one another and, within a given infant's responses, there is variability from trial to trial. We propose that exploiting this between- and within-infant variability is an infant-friendly way to assess contingent links between neural activity and social-cognitive behavior. If neural mirroring is contingently linked to performing a particular social-cognitive behavior, then this suggests that neural mirroring functions to facilitate that behavior. In the next section, we describe initial research from our lab group that takes a first step in this direction (Filippi et al. under review).

Integrating behavioral and neural measures in infants

In a first attempt to pursue this strategy with infants, we integrated the Hamlin and colleagues (2008) goal imitation paradigm with EEG to measure mu desynchronization (Filippi et al. under review). Since previous research has suggested that seven months is an age when infants' foundational motor skills (such as reaching) are still developing and this is a time when infants begin to selectively reproduce the goals of others, we chose to test whether the variability in seven-month-olds' behavior is selectively linked to neural mirroring. On each trial, infants observed an experimenter who grasped one of two toys, and they were then given an opportunity to select between the toys. Infants could either choose to act on the same toy that the experimenter had selected (goal response) or the toy that the experimenter did not select (non-goal response). Based on previous research (see Hamlin et al. 2008), we reasoned that, if infants acted on the experimenter's prior goal, then they had perceived the experimenter's action as goal-directed.

To assess whether neural mirroring was contingently linked to goal perception, we examined whether there were differences in motor system involvement as a function of infants' subsequent behavior during the choice phase of the experiment. We segmented neural activity as infants observed the experimenter select between two toys (i.e., the action-observation phase) and binned each trial based on infants' subsequent behavior (i.e., whether infants generated a goal response or a non-goal response). Critically, in order for any segment of neural data to be included in our sample, infants had to attend to the experimenter's action and then produce a clear behavioral response. This inclusion criterion was critical for demonstrating that the findings reflected variations in infants' sensitivity to the actor's goal during observation rather than variations in attentiveness, engagement, or motor preparation. We reasoned that, if mirroring is related to goal-based social behaviors, then infants should show more motor system activation prior to generating a goal response then when generating a non-goal response.

To assess neural mirroring, we examined attenuation of the mu rhythm (6–9 Hz) over central electrode sites when compared to a 1 s baseline segment that preceded the action-observation phase. Assessing mu rhythm attenuation in comparison to a baseline is the traditional method of assessing sensorimotor system involvement during action-execution and action-observation events (see Pfurtscheller and Aranibar 1979). As such, we measured change from baseline scores to determine the extent of sensorimotor system involvement during action observation. Upon binning neural activity during the action-observation phase as a function of subsequent behavior, we found that infants showed significant attenuation of the mu rhythm over central sites during action observation for goal-response trials but not for non-goal-response trials. This finding demonstrates that the motor system was recruited when infants observe an action and subsequently generated goal responses. The motor system did not show significant involvement when infants observed actions and subsequently generated non-goal responses. These results provide novel evidence that the recruitment of motor system is contingently linked to social cognition in infants.

As a further test of the relation between neural mirroring and goal-based responding, we also considered between-infant variation, this time focusing on mu desynchronization when infants acted themselves. We predicted that if infants are recruiting the same neural system that during action observation that is engaged when infants execute action themselves, then we would expect that individual differences in neural activity during action execution would also be linked to infants' propensity to generate goal responses over the course of the experiment. Consistent with this hypothesis, we found a significant correlation between motor system recruitment during action execution and the proportion of goal responses that infants generated over the course of the experiment. Infants who showed greater mu desynchronization during their own reaching later went on to imitate more of the experimenter's goals.

These results raise the possibility that motor system recruitment may be broadly linked to developments in social behavior. They also indicate that considering developmental variation during infancy may provide a rich vantage point on the neural correlates of action understanding, and the functional roles of neural mirroring. This approach could be used to evaluate whether other social-cognitive abilities, including cognitive encoding of action goals (independent of initiating a social response), and action anticipation are supported by neural mirroring. That is, applying this approach will shed light on the breadth of social-cognitive functions that are related to neural mirroring.

Earlier, we noted that the three major behavioral methods that have been used with infants, although each depends on goal understanding, these methods each also carry distinct demands of their own. Our initial integrative study involved imitation, an ability that requires rapid implementation and (perhaps) social motivation as well as a cognitive encoding of the action goal. Thus, from the findings so far it is not clear which of these component abilities is dependent on neural mirroring. Recruiting neural methods may provide a vantage point for better understanding the distinct cognitive and motivational components of these infant responses. Conversely, integrating neural and behavioral methods can pave the way toward understanding why neural mirroring may matter for infant social life. Does neural mirroring support the basic cognitive ability to analyze goals in actions? Or does it support the implementation of this knowledge in the context of a rapid visual prediction or social response?

In addition, this approach could be used to better understand the nature of the training effects reviewed earlier. The finding that active motor experience renders changes in infants' responses to others' actions is consistent with the possibility that neural mirroring is at play, but it is also the case that other neurocognitive mechanisms could explain this effect (see Gerson and Woodward 2012). Integrated neural and behavioral measures could provide a vantage on the question of whether the effects of motor training on infant action understanding are mediated by changes in neural mirroring or are driven by some other mechanism.

More generally, these initial findings demonstrate that a developmental perspective offers novel insight into the functional role that the motor system plays in this foundational social-cognitive ability. This work raises new questions about the development of the neural systems that underlie skilled action production and action perception, and it provides a methodological approach—using variability during early development—to address these questions.

Conclusion

In seeking to understand the proposal that neural mirroring may support the development of action understanding, we have reviewed two bodies of infancy research. One body of work has used EEG to evaluate the neural response that occurs when infants view others' actions. The findings from this approach suggest that action control systems are active when infants watch others' actions. The other body of work has used behavioral methods to ask how infants understand others' actions and how they use their knowledge to generate social responses. The findings from this body of work indicate strong connections between infants' action understanding and their own experiences as agents. While each of these separate approaches has shed important light on early social-cognitive development, our conclusion is that even greater insights will result from the integration of the two approaches.

To conclude, research to date demonstrates that infants show characteristic features of mirroring in their early social behavior and neural response. While these characteristic features of mirroring in infancy are in line with adult literature demonstrating that the motor system is functionally linked to action understanding, it is an open question whether and how the motor system relates to action understanding and social behavior early in life. Determining whether or not infants recruit their motor systems to understand others' actions requires not only assessing infants' neural responses but also their behavior.

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References

Ambrosini, E., Reddy, V., de Looper, A., Costantini, M., Lopez, B., and Sinigaglia, C. (2013) Looking ahead: Anticipatory gaze and motor ability in infancy. PLoS ONE, **8**, e67916.

Ambrosini, E., Sinigaglia, C., and Costantini, M. (2012) Tie my hands, tie my eyes. Journal of Experimental Psychology: Human Perception and Performance, **38**, 263–6.

Arnstein, D., Cui, F., Maurits, N. M., and Gazzola, V. (2011) μ-suppresssion during action observation and execution correlates with BOLD in dorsal premotor, inferior parietal and SI cortices. Journal of Neuroscience, **31**, 14243–9.

Brune, C. W., and Woodward, A. L. (2007) Social cognition and social responsiveness in 10-month-old infants. Journal of Cognition and Development, **8**, 133–58.

Buccino, G., Binkofski, F., Fink, G. R., Fadiga, L., Fogassi, L., Gallese, V., et al. (2001) Action observation activates premotor and parietal areas in a somatotopic manner: An fMRI study. European Journal of Neuroscience, **13**, 400–404.

Calvo-Merino, B., Grezes, J., Glaser, D., Passingham, R. E., and Haggard, P. (2006) Seeing or doing? Influence of visual and motor familiarity in action observation. Current Biology, **16**, 1905–10.

Cannon, E. N., Fox, N. A., Vanderwert, R. E., Woodward, A. L., and Ferrari, P. F. (2015). The mirror neuron system in infant development: Relations between emerging motor skill and event-related desynchronization in EEG.

Cannon, E. N., and Woodward, A. L. (2008) Action anticipation and interference: A test of prospective gaze. In B. C. Love, K. McRae, and V. M. Sloutsky, eds., Proceedings of the 30th Annual Conference of the Cognitive Science Society.Cognitive Science Society, Austin, TX, pp. 981–4.

Cannon, E. N., and Woodward, A. L. (2012) Infants generate goal-based action predictions. Developmental Science, **15**, 292–8.

Cannon, E. N., Woodward, A., Gredebäck, G., von Hofsten, C. von, and Turek, C. (2012) Action production influences 12-month-old infants' attention to others' actions. Developmental Science, **15**, 35–42.

Cannon, E. N., Yoo, K., Vanderwert, R. E., Ferrari, P. F., and Woodward, A. L. (2014) Action experience, more than observation, influences mu rhythm desynchronization. PloS ONE, **9**, e92002.

Carpenter, M., Akhtar, N., and Tomasello, M. (1998) Fourteen- through 18-month-old infants differentially imitate intentional and accidental actions. Infant Behavior and Development, **21**, 315–30.

Claxton, L. J., Keen, R., and McCarty, M. E. (2003) Evidence of motor planning in infant reaching behavior. Psychological Science, **14**, 354–6.

Cook, R., Bird, G., Catmur, C., Press, C., and Heyes, C. (2014) Mirror neurons: From origin to function. Behavioral and Brain Sciences, **37**, 177–92.

Csibra, G. (2007) Action mirroring and action understanding: An alternative account. In P. Haggard, Y. Rosetti, and M. Kawato, eds., Attention and Performance. Sensorimotor Foundations of Higher Cognition, Vol. 22. Oxford University Press, Oxford, pp. 435–80.

Cuevas, K., Cannon, E. N., Yoo, K., and Fox, N. A. (2014) The infant EEG mu rhythm: Methodological considerations and best practices. Developmental Review, **34**, 26–43.

de Klerk, C. C. J. M., Johnson, M. H., Heyes, C. M., and Southgate, V. (2014) Baby steps: Investigating the development of perceptual-motor couplings in infancy. Developmental Science, 18, 270–80.

Falck-Ytter, T., Gredebäck, G., and Hofsten, C. von. (2006) Infants predict other peoples' action goals. Nature Neuroscience, 9, 878–9.

Ferrari, P. F., Tramacere, A., Simpson, E. A., and Iriki, A. (2013) Mirror neurons through the lens of epigenetics. Trends in Cognitive Sciences, 17, 1095–104.

Filippi, C., Cannon, E. N., Fox, N. A., Thorpe, S., and Woodward, A. L. (under review) Neural mirroring predicts goal analysis in 7-month-old infants.

Gerson, S. A., and Woodward, A. L. (2012) A claw is like my hand: Comparison supports goal analysis in infants. Cognition, 122, 181–92.

Gerson, S. A., and Woodward, A. L. (2013) The goal trumps the means: Highlighting goals is more beneficial than highlighting means in means-end training. Infancy, 18, 289–302.

Gerson. S. A., and Woodward, A. L. (2014) Learning from their own actions: The unique effect of producing actions on infants' action understanding. Child Development, 85, 264–77.

Gredebäck, G., and Kochukhova, O. (2009) Goal anticipation during action observation is influenced by synonymous action capabilities, a puzzling developmental study. Experimental Brain Research, 202, 493–7.

Gredebäck, G., Stasiewicz, D., Falck-Ytter, T., Rosander, K., and Hofsten, C. von. (2009) Action type and goal type modulate goal-directed gaze shifts in 14-month-old infants. Developmental Psychology, 45, 1190–4.

Grezes, J., and Decety, J. (2001) Functional anatomy of execution, mental simulation, observation, and verb generation of actions: A meta-analysis. Human Brain Mapping, 12, 1–19.

Hamlin, J. K., Hallinan, E. V., and Woodward, A. L. (2008) Do as I do: 7-month-old infants selectively reproduce others' goals. Developmental Science, 11, 487–94.

Henderson, A. M. E., Wang, Y., Eisenband Matz, L., and Woodward, A. (2013) Active experience shapes 10-month-old infants' understanding of collaborative goals. Infancy, 18, 10–39.

Henderson, A. M. E., and Woodward, A. L. (2011) Let's work together: What do infants understand about collaborative goals? Cognition, 121, 12–21.

Hickok, G. (2014) The Myth of Mirror Neurons. W. W. Norton and Company, New York, NY.

Hunnius, S., and Bekkering, H. (2010) The early development of object knowledge: A study of infants' visual anticipations during action observation. Developmental Psychology, 46, 446–54.

Hunnius, S., and Bekkering, H. (2014) What are you doing? How active and observational experience shape infants' action understanding. Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences, 369.

Iacoboni, M., Molnar-Szakacs, I., Gallese, V., Buccino, G., Mazziotta, J. C., and Rizzolatti, G. (2005) Grasping the intentions of others with one's own mirror neuron system. PLoS Biology, 3, e79.

Kanakogi, Y., and Itakura, S. (2011) Developmental correspondence between action prediction and motor ability in early infancy. Nature Communications, 2, 341.

Krogh-Jespersen, S., Filippi, C., and Woodward, A. L. (2014) A developmental perspective on action and social cognition. Commentary, Behavioral and Brain Sciences, 37, 208–9.

Krogh-Jespersen, S., Liberman, Z., and Woodward, A. L. (in press) Think fast! The relationship between goal prediction speed and social competence in infants. Developmental Science.

Krogh-Jesperson, S., and Woodward, A. L. (2014) Making smart social judgments takes time: Infants' recruitment of goal information when generating action predictions. PloS ONE, 9, e98085.

Libertus, K., and Needham, A. (2010) Teach to reach: The effects of active versus passive reaching experiences on action and perception. Vision Research, 50, 2750–7.

Loucks, J., and Sommerville, J. A. (2012) The role of motor experience in understanding action function: The case of the precision grasp. Child Development, 83, 801–9.

Mahajan, N., and Woodward, A. (2009) Seven-month-old infants selectively reproduce the goals of animate but not inanimate agents. Infancy, 14, 667–79.

Marshall, P. J., and Meltzoff, A. N. (2011) Neural mirroring system: Exploring the EEG mu rhythm in human infancy. Developmental Cognitive Neuroscience, 1, 110–23.

Marshall, P. J., Saby, J. N., and Meltzoff, A. N. (2013) Infant brain responses to object weight: Exploring goal-directed actions and self-experience. Infancy, 18, 942–60.

Marshall, P. J., Young, T., and Meltzoff, A. N. (2011) Neural correlates of action observation and execution in 14-month-old infants: An event-related EEG desynchronization study. Developmental Science, 14, 474–80.

Meltzoff, A. N. (1995) Understanding the intentions of others: Re-enactment of intended acts by 18-month-old children. Developmental Psychology, 31, 838–50.

Meltzoff, A. (2007) "Like me": A foundation for social cognition. Developmental Science, 10, 126–34.

Michael, J., Sandberg, K., Skewes, J., Wolf, T., Blicher, J., Overgaard, M., et al. (2014) Continuous theta-burst stimulation demonstrates a causal role of premotor homunculus in action understanding. Psychological Science, 25, 963–72.

Muthukumaraswamy, S. D., Johnson, B. W., and McNair, N. A. (2004) Mu rhythm modulation during observation of an object-directed grasp. Cognitive Brain Research, 19, 195–201.

Needham, A., Barrett, T., and Peterman, K. (2002) A pick-me-up for infants' exploratory skills: Early simulated experiences reaching for objects using "sticky mittens" enhances young infants' object exploration skills. Infant Behavior and Development, 25, 279–95.

Paulus, M., Hunnius, S., van Elk, M., and Bekkering, H. (2012) How learning to shake a rattle affects 8-month-old infants' perception of the rattle's sound: Electrophysiological evidence for action-effect binding in infancy. Developmental Cognitive Neuroscience, 2, 90–6.

Paulus, M., Licata, M., Kristen, S., Thoermer, C., Woodward, A., and Sodian, B. (2014) Social understanding and self-regulation predict preschoolers' sharing with friends and disliked peers: A longitudinal study. International Journal of Behavioral Development, 39, 53–64.

Pfurtscheller, G., and Aranibar, A. (1979) Evaluation of event-related desynchronization (ERD) preceding and following voluntary self-paced movement. Electroencephalography and Clinical Neurophysiology, 46, 138–46.

Pineda, J. A. (2005) The functional significance of mu rhythms: Translating "seeing" and "hearing" into "doing." Brain Research Reviews, 50, 57–68.

Rizzolatti, G., and Craighero, L. (2004) The mirror neuron system. Annual Review of Neuroscience, 27, 169–92.

Rizzolatti, G., Fadiga, L., Gallese, V., and Fogassi, L. (1996) Premotor cortex and the recognition of motor actions. Cognitive Brain Research, 3, 131–41.

Robin, D. J., Berthier, N. E., and Clifton, R. K. (1996) Infants predictive reaching for moving objects in dark. Developmental Psychology, 32, 824–35.

Rosander, K., and Hofsten, C. von. (2011) Predictive gaze shifts elicited during observed and performed actions in 10-month-old infants and adults. Neuropsychologia, 49, 2911–17.

Saby, J. N., Meltzoff, A. N., and Marshall, P. J. (2013) Infants' somatotopic neural responses to seeing human actions: I've got you under my skin. PloS ONE, 8, e77905.

Simpson, E. A., Murray, L., Paukner, A., and Ferrari, P. F. (2014) The mirror neuron system as revealed through neonatal imitatôn: Presence from birth, predictive power and evidence of plasticity. Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences, 1644, 20130289.

Sommerville, J. A., Hildbrand, E. A., and Crane, C. C. (2008) Experience matters: The impact of doing versus watching on infants' subsequent perception of tool-use events. Developmental Psychology, 44, 1249–56.

Sommerville, J. A., and Woodward, A. L. (2005) Pulling out the intentional structure of human action: The relation between action production and processing in infancy, Cognition, 95, 1–30.

Sommerville, J. A., Woodward, A. L., & Needham, A. (2005). Action experience alters 3-month-old infants' perception of others' actions. *Cognition*, *96*, B1-B11. doi: 10.1016/j.cognition.2004.07.004

Southgate, V., and Begus, K. (2013) Motor activation during the prediction of nonexecutable actions in infants. Psychological Science, 24, 828–35.

Southgate, V., Johnson, M. H., El Karoui, I., and Csibra, G. (2010) Motor system activation reveals infants' on-line prediction of others' goals. Psychological Science, 21, 355–9.

Southgate, V., Johnson, M. H., Osborne, T., and Csibra, G. (2009) Predictive motor activation during action observation in human infants. Biology Letters, 5, 769–72.

Spunt, R. P., and Lieberman, M. D. (2013) The busy social brain: Evidence for automaticity and control in the neural systems supporting social cognition and action understanding. Psychological Science, 24, 80–6.

Stadler, W., Ott, D. V. M., Springer, A., Schubotz, R. I., Schütz-Bosbach, S., and Prinz, W. (2012) Repetitive TMS suggests a role of the human dorsal premotor cortex in action prediction. Frontiers in Human Neuroscience, 6, 20.

Stapel, J. C., Hunnius, S., van Elk, M., and Bekkering, H. (2010) Motor activation during observation of unusual versus ordinary actions in infancy. Social Neuroscience, 5, 451–60.

Thelen, E., Corbetta, D., Kamm, K., Spencer, J. P., Schneider, K., and Zernicke, R. F. (1993) The transition to reaching: Mapping intention and intrinsic dynamics. Child Development, 64, 1058–98.

Van Elk, M., van Schie, H. T., Hunnius, S., Vesper, C., and Bekkering, H. (2008) You'll never crawl alone: Neurophysiological evidence for experience-dependent motor resonance in infancy. NeuroImage, 43, 808–14.

Virji-Babul, N., Rose, A., Moiseeva, N., and Makan, N. (2012) Neural correlates of action understanding in infants: Influence of motor experience. Brain and Behavior, 2, 237–42.

von Hofsten, C. (1980) Predictive reaching for moving objects by human infants. Journal of Experimental Child Psychology, 30, 369–82.

von Hofsten, C. von. (2004) An action perspective on motor development. Trends in Cognitive Sciences 8, 266–72.

von Hofsten, C. (2007) Action in development. Developmental Science, 10, 54–60.

von Hofsten, C. von, and Ronnqvist, L. (1988) Preparation for grasping an object: A developmental study. Journal of Experimental Psychology: Human Perception and Performance, 14, 610–21.

Warreyn, P., Ruysschaert, L., Wiersema, J. R., Handi, A., Pattyn, G., and Roeyers, H. (2013) Infants' mu suppression during the observation of real and mimicked goal-directed actions. Developmental Science, 16, 173–85.

Wellman, H. M., Lopez-Duran, S., LaBounty, J., and Hamilton, B. (2008) Infant attention to intentional action predicts preschool theory of mind. Developmental Psychology, 44, 618–23.

Woodward, A. L. (1998) Infants selectively encode the goal object of an actor's reach. Cognition, 69, 1–34.

Woodward, A. L. (1999) Infants' ability to distinguish between purposeful and non-purposeful behaviors. Infant Behavior and Development, 22, 145–60.

Woodward, A. L., and Gerson, S. A. (2014) Mirroring and the development of action understanding. Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences, 369, 20130181.

Woodward, A. L., Sommerville, J. A., Gerson, S., Henderson, A. M. E., and Buresh, J. S. (2009) The emergence of intention attribution in infancy. In B. Ross, ed., The Psychology of Learning and Motivation, Vol. 51. Academic Press, Burlington, VT, pp. 187–222.

Yamaguchi, M., Kuhlmeier, V. A., Wynn, K., and VanMarle, K. (2009) Continuity in social cognition from infancy to childhood. Developmental Science, 12, 746–52.