Motor Activation During the Prediction of Nonexecutable Actions in Infants

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Abstract
Although it is undeniable that the motor system is recruited when people observe others' actions, the inferences that the brain generates from motor activation and the mechanisms involved in the motor system's recruitment are still unknown. Here, we challenged the popular hypothesis that motor involvement in action observation enables the observer to identify and predict an agent's goal by matching observed actions with existing and corresponding motor representations. Using a novel neural indication of action prediction—sensorimotor-cortex activation measured by electroencephalography—we demonstrated that 9-month-old infants recruit their motor system whenever a context suggests an impending action, but that this recruitment is not dependent on being able to match the observed action with a corresponding motor representation. Our data are thus inconsistent with the view that action prediction depends on motor correspondence; instead, they support an alternative view in which motor activation is the result of, rather than the cause of, goal identification.

Anticipating other organisms' actions in order to make quick decisions, such as whether to approach or flee, is crucial to the survival of many species. In humans, however, the ability to anticipate what other people will do next and adjust one's own response accordingly underpins the unique propensity to engage in joint action, cooperation, and collaboration (Sebanz & Knoblich, 2009).

Recent research suggests that the motor system plays a functional role in the ability to anticipate other people's actions. For example, adult observers who are engaged in a motor task (Cannon & Woodward, 2008) or who have their motor abilities artificially restricted (Ambrosini, Sinigaglia, & Costantini, 2012) show an impaired ability to anticipate other people's actions. Human infants, who are naturally restricted in their motor abilities, also exhibit a relationship between motor ability and action anticipation. Specifically, previous studies have shown that only those infants who can competently perform a particular action appear able to anticipate that action when it is performed by someone else (Cannon & Woodward, 2012; Falck-Ytter, Gredebäck, & von Hofsten, 2006; Gredebäck & Kochukhova, 2010; Gredebäck, Stasiewicz, Falck-Ytter,

Rosander, & von Hofsten, 2009; Kanakogi & Itakura, 2011).

Action anticipation in all of these studies was measured by evaluating the observer's ability to generate anticipatory saccades toward a target ahead of an ongoing action. Given that the pattern of predictive saccades during action observation closely resembles the pattern seen during action execution, it has been hypothesized that these predictive saccades depend on the observer having recruited a motor representation similar to that which he or she would have recruited for executing that same action (Falck-Ytter et al., 2006; Flanagan & Johansson, 2003). Thus, the apparent absence of goal-directed action anticipation when adults or infants observe actions for which they cannot access a corresponding motor representation, either because their motor system is otherwise engaged or because they have no prior motor experience with that

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action, is interpreted as evidence for the importance of possessing a motor representation with which the observed action can be matched and consequently understood (Ambrosini, Costantini, & Sinigaglia, 2011; Ambrosini et al., 2012; Cannon & Woodward, 2012; Kanakogi & Itakura, 2011).

The assumption underlying all of these studies is that the involvement of the motor system in the generation of anticipatory saccades enables the observer to understand and predict the goal of an action via a process of direct matching (Rizzolatti, Fogassi, & Gallese, 2001). However, although it is clear that an observer's motor system does indeed play a role in prediction (Schubotz, 2007), what kind of prediction it facilitates is far less clear. Attributing a goal permits one to generate a prediction that the goal will be attained, but it also enables one to predict how an ongoing action will unfold in pursuit of that goal (Csibra & Gergely, 2007). An alternative account of the involvement of the motor system in action perception is thus that it enables the observer to generate a prediction about how an ongoing action will unfold in pursuit of a previously attributed goal (Csibra, 2007). Crucially, whereas the direct-matching view logically requires the observer to possess a motor representation of the observed action in order to understand and subsequently predict that action's goal, the alternative hypothesis proposes that because the same goal can often be achieved in different ways, an observer may recruit a different motor representation of an action with a similar end and use this to predict how another action may unfold (Csibra, 2007).

There are several reasons to question the assumption that involvement of the motor system in action anticipation implies the recruitment of a corresponding motor representation. First, although there is a relationship between infants' motor skill and their ability to anticipate actions, it is not clear that it is specifically skill with the observed action, as opposed to motor maturity more generally, that is driving this relationship. Given that cognitive and motor development are likely to be interrelated (Diamond, 2000), it may be that infants with superior motor skills are just better at predicting actions or events. Second, evidence suggests that, in adults, areas of the motor system are recruited when the observer is predicting a broad range of actions, irrespective of whether the observer could have recruited a corresponding motor representation of that action (Cross, Stadler, Parkinson, Schütz-Bosbach, & Prinz, 2013). Thus, the involvement of the motor system in action anticipation need not imply that the underlying mechanism is one that depends on motor correspondence.

Finally, the assumption that the relationship between motor capability and action anticipation is mediated by access to a corresponding motor representation neglects consideration of a wealth of evidence suggesting that both adults and infants can make sense of numerous actions for which they could not possibly possess a corresponding motor representation (Biro & Leslie, 2007; Csibra, 2008; Heider & Simmel, 1944; Hernik & Southgate, 2012; Luo & Baillargeon, 2005; Ramsey & Hamilton, 2010; Southgate & Csibra, 2009). Such evidence suggests that adults and infants can understand the goals of actions irrespective of whether they would have available a corresponding motor representation.

In the current study, we challenged the hypothesis that the documented relationship between motor capability and action anticipation in human infants is driven by access to a corresponding motor representation. We exploited the fact that the motor system is recruited when observers are generating action predictions (Kilner, Vargas, Duval, Blakemore, & Sirigu, 2004; Southgate, Johnson, Karoui, & Csibra, 2010; Southgate, Johnson, Osborne, & Csibra, 2009), and we used motor activation as a novel measure of action anticipation. Specifically, we asked whether 9-month-old infants would recruit their motor system when the context suggested an impending action, even if that action was one for which they could not recruit any corresponding motor representation. If the motor system were recruited during the prediction of nonexecutable actions, it would indicate not only that infants are able to interpret and anticipate actions outside of their motor repertoire, but also that motor involvement in action observation is unlikely to reflect a process of matching observed actions with existing and corresponding motor representations (Falck-Ytter et al., 2006; Kanakogi & Itakura, 2011).

Infants were first familiarized with an action repeatedly directed toward one object (the target) in the presence of another object (the distractor). For one group of infants, this action was a human hand reaching and grasping (hand condition), but for two further groups, either the action was a mechanical claw reaching and grasping (claw condition) or the target object moved by itself (self-propelled condition). Following familiarization, infants saw trials in which still frames of either the target or distractor object were presented in isolation, and we asked whether infants would exhibit motor activation, which would suggest that they were anticipating an action, when presented with the target but not when presented with the distractor object. We used electroencephalography (EEG) to measure suppression of the sensorimotor alpha rhythm from baseline as our measure of motor activation (Marshall, Young, & Meltzoff, 2011; Southgate et al., 2010; Southgate et al., 2009). If lacking a corresponding motor representation for an observed action results in failure to generate action predictions, we should see motor activation for target objects only in the hand condition. In contrast, if the motor system is broadly involved in action prediction irrespective of the motor capacities of the observer and motor activation does not

reflect a direct matching process (Rizzolatti & Sinigaglia, 2010), we would expect to see motor activation when infants see the target object regardless of the action type.

Method

Participants

The final sample consisted of thirty-three 9-month-old infants (18 males, 15 females; mean age = 275 days, range = 259–297 days) who were randomly assigned to three conditions (hand, claw, or self-propelled). An additional 32 infants were excluded because they did not provide enough artifact-free trials for analysis as a result of movement, fussiness, or poor-quality EEG signal ($n = 30$) or because they did not provide any usable trials in the first half of the experiment ($n = 2$). This exclusion rate is typical of EEG studies with human infants (Marshall et al., 2011; Southgate et al., 2010; Southgate et al., 2009). All infants were born full term, were healthy, and had normal birth weight.

Stimuli and procedure

Stimuli were created using Apple Final Cut Pro and presented on a computer screen with MATLAB (The

MathWorks, Natick, MA) using the Psychophysics Toolbox extension (Brainard, 1997; Pelli, 1997). We chose two novel, featurally distinct but similarly sized objects as stimuli (Fig. 1); the objects serving as the target and distractor were counterbalanced across infants. Infants first observed four familiarization events in which the distractor object remained stationary while a hand (hand condition) or claw (claw condition) reached for and grasped the target object or the target object appeared to move by itself (self-propelled condition). In each case, the target object moved or was moved from the top right or left of the display toward the center of the display. The objects switched locations on Familiarization Trials 2 and 3 and returned to their original locations on Trial 4.

Each experimental trial was 4,000 ms and comprised a baseline period (1,000 ms), a static period (1,500 ms), and an outcome period (1,500 ms). In the baseline period, a moving screensaver-like image was shown. On target trials, the baseline period was followed by a static period, in which infants saw a still frame of the target object positioned at the top center of the screen, and in the hand and claw conditions, the hand or claw positioned at the bottom of the screen. During the outcome period, the target object moved or was moved toward the center of the screen as in familiarization trials. On
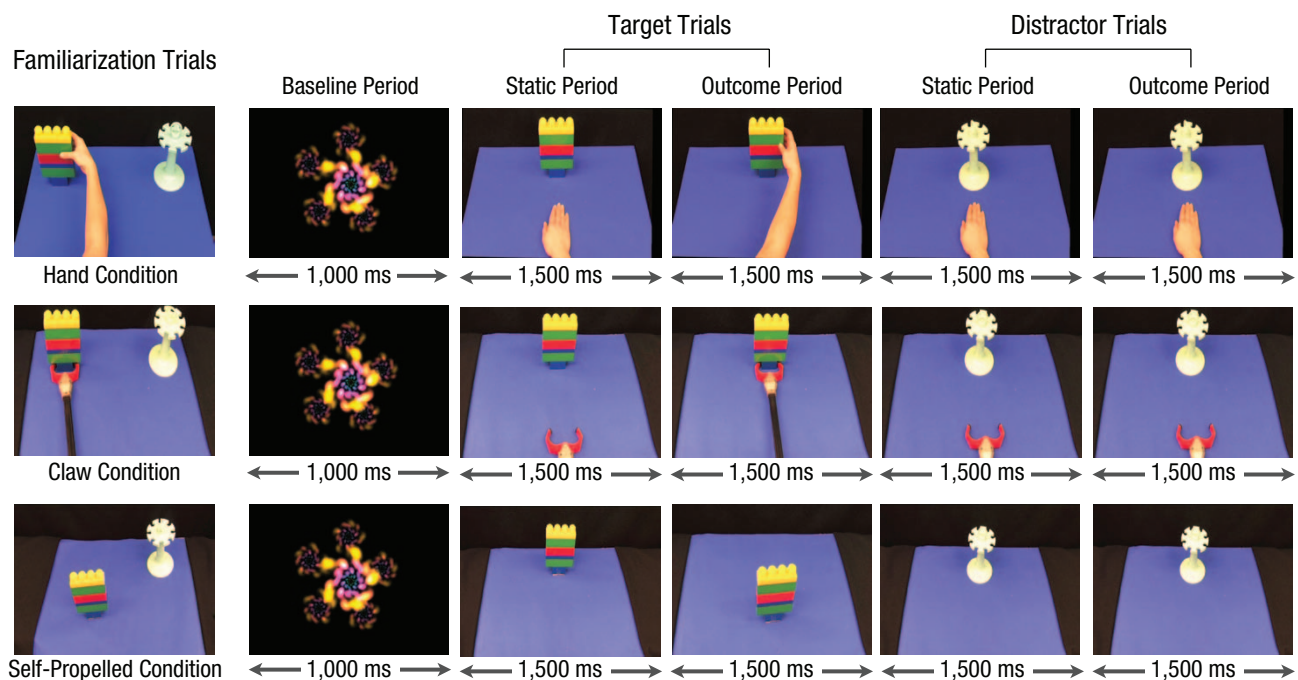
Fig. 1. Experimental paradigm. Infants first saw four familiarization trials, in which one of the two presented objects (target) was consistently moved toward the center of the screen by a hand or a claw (hand and claw conditions) or moved by itself (self-propelled condition) while the other object (distractor) remained stationary. Familiarization was followed by repeated experimental trials, which started with a static image of only one of the objects (with a hand, a claw, or by itself, according to the condition) presented for 1,500 ms. After the static period, either the object was moved or moved by itself toward the center of the screen (target trials) or the object remained static for the entire length of the trial (distractor trials). Each trial was preceded by a 1,000-ms baseline depicting a moving screensaver-like pattern.

distractor trials, the static period was the same as on target trials, but the display continued to remain static during the outcome period.

Infants who did not complete at least nine target and nine distractor trials were excluded from analysis. Infants were video-recorded throughout the session, and we excluded any trials in which infants made limb movements or were inattentive. Included infants completed a mean of 18 target trials and 17 distractor trials. Infants were seated in a darkened room on a caregiver's lap roughly 80 cm from a 30 cm × 40 cm monitor. Brief attention-getting sounds were played at random to maintain infants' attention, and infants watched trials for as long as they were willing. As in previous studies (Southgate et al., 2010; Southgate et al., 2009), we identified a 3-Hz-wide frequency band that best reflected activity of the sensorimotor cortex on an individual basis (this band was determined based on infants' own reaches for objects). The frequency band that best reflected activation of infants' sensorimotor cortex was then analyzed for a decrease from baseline to the anticipatory period. The frequency bands analyzed were 6 to 8 Hz (25 infants), 7 to 9 Hz (7 infants), and 8 to 10 Hz (1 infant).

EEG acquisition

EEG was recorded using a 128-electrode Hydrocel Geodesic Sensor Net (EGI, Eugene, OR). EEG was sampled at 500 Hz, recorded with respect to the vertex electrode, and rereferenced to the average reference prior to analysis. Following recording, EEG was segmented into 4,000-ms segments (beginning 1,000 ms before the beginning of the analysis period and ending 3,000 ms after the onset of the analysis period). Time-frequency analyses were performed on each artifact-free trial using continuous wavelet transform with Morelet wavelets at 1-Hz intervals in the range of 5 to 25 Hz.

To eliminate distortion created by the wavelet transform, we removed the first and last 400 ms of each trial and chose a 400-ms baseline period beginning 600 ms before the onset of the analysis period. Activity was averaged across each infant's individual 3-Hz-wide frequency band, and activity in the 400-ms baseline period was subtracted from activity in the first 500 ms of the analysis period. Average wavelet coefficients within infants were calculated by taking the mean across trials. As in previous studies, we analyzed activity over a cluster of four left-hemisphere sensorimotor electrodes (30, 36, 37, and 42) and four right-hemisphere sensorimotor electrodes (87, 93, 104, and 105). The approximate 10-10 electrode equivalents are C1, C3, CP1, CP3, C2, C4, CP2, and CP4. In addition, to be sure that our data specifically reflected changes in the sensorimotor alpha rhythm and not the more posterior occipital alpha rhythm, we included for comparison a cluster of occipital channels (electrodes 70, 71, 76, and 83, which approximate O1 and O2 in the 10-10 layout), where previous studies have shown the infant visual alpha rhythm to be dominant (Stroganova, Orekhova, & Posikera, 1999). Finally, to confirm that any effect was specifically a motor effect, we also analyzed activity at left and right frontal sites (electrodes 19, 23, 24, and 27 on the left and 3, 4, 123, and 124 on the right, which approximate F3 and F4, respectively, in the 10-10 layout). In all reported analyses, amplitudes were averaged over these clusters of channels.

Results

A repeated measures analysis of variance (ANOVA) was conducted with time (400-ms baseline period vs. 500-ms analysis period), object (target vs. distractor), and electrode location (left central vs. right central vs. left frontal vs. right frontal vs. occipital) as within-subjects factors and condition (hand, claw, or self-propelled) as a between-subjects factor. Results revealed significant interactions between time and object, $F(1, 30) = 5.77$, $p = .02$, $\eta_p^2 = .16$, and time and electrode location, $F(4, 27) = 6.07$, $p = .001$, $\eta_p^2 = .47$. There were no main effects or interactions involving condition.

Follow-up repeated measures ANOVAs were then conducted separately for each electrode location. These revealed a significant interaction between time and object, $F(1, 30) = 9.40$, $p = .005$, for left-hemisphere channels. Separate repeated measures ANOVAs on each trial type (target vs. distractor) revealed that there was a significant decrease in sensorimotor alpha amplitude from baseline to the anticipatory period during target trials, $F(1, 30) = 12.9$, $p = .001$, but there was no such decrease during distractor trials ($p = .44$). Again, these effects were not modulated by the kind of action the infant saw, as there was no interaction involving condition ($p = .95$). These data demonstrate that infants recruited their sensorimotor cortex (as evidenced by a decrease in sensorimotor alpha amplitude from baseline to the anticipatory period; see Fig. 2) when the context suggested an impending action. There were no significant main effects nor interactions for data from right-hemisphere channels, which confirmed previous findings that sensorimotor alpha suppression during action prediction occurs predominantly in the left hemisphere in infants (Southgate et al., 2010; Southgate et al., 2009).

Finally, there was a main effect of time in the occipital cluster, $F(1, 30) = 13.25$, $p = .001$, that was not mediated by either trial type or condition ($ps > .2$). A paired-samples t test on data collapsed over object and condition showed that, for occipital channels, there was a significant increase in alpha amplitude from baseline to the anticipatory period, $t(65) = 4.16$, $p = .0001$. Occipital alpha is known to
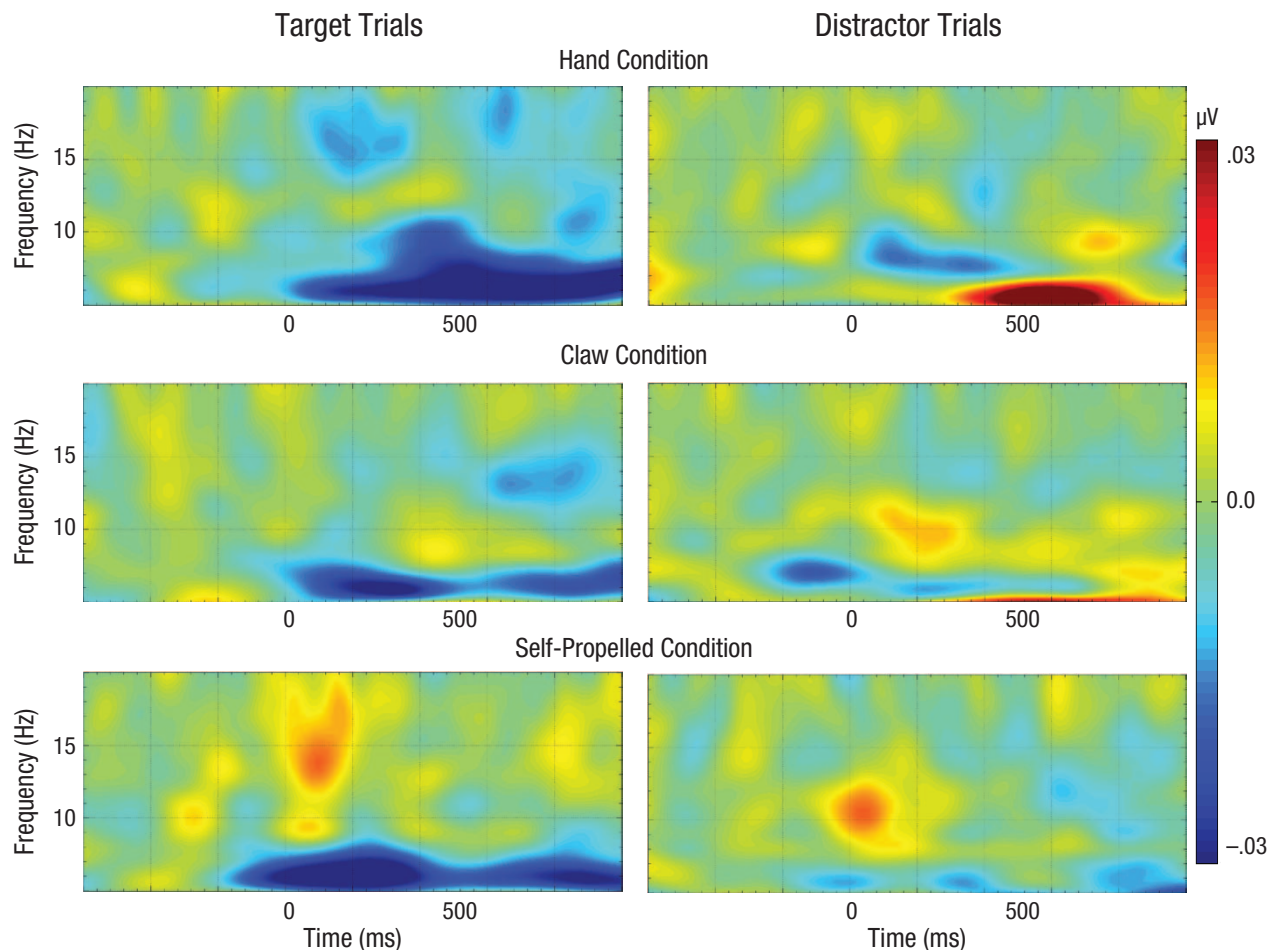
Fig. 2. Time-frequency plots showing observed changes in sensorimotor alpha amplitude for target and distractor trials in the three conditions. Each plot shows baseline-corrected activity (averaged over the first 400 ms of each segment) averaged over the four left sensorimotor channels and over all infants in each condition. Zero is the onset of the static analysis period. Results reported in the text are based on comparison of the 400-ms baseline period with the first 500 ms of the analysis period.

be modulated by task demands (Herrmann, Senkowski, & Röttger, 2004), so one interpretation of this increase is that it reflects the need for infants to remember whether the object they were seeing was associated with an impending action. Whatever the reason for the increase in occipital alpha, the absence of alpha suppression at occipital sites confirmed that the left-hemisphere sensorimotor alpha suppression we observed was a central phenomenon and independent of the visual alpha rhythm. There were no significant effects of time, object, or condition in either the left or right frontal sites. There was an interaction between time and object in right frontal channels that approached significance, $F(1, 30) = 3.19$, $p = .08$. This effect was driven by an increase in alpha from baseline during distractor trials, $F(1, 30) = 3.70$, $p = .06$.

Discussion

The data we obtained using a novel measure of action prediction suggest that human infants can generate action predictions regardless of whether they have access to a motor representation of that action. That we found motor activation during a period when there was no movement but the context implied impending action suggests two conclusions. First, the previously reported finding that motor activation occurs when both adults and infants are making action predictions (Kilner et al., 2004; Southgate et al., 2010) suggests that infants were generating action predictions for actions that they could not have matched with actions in their own motor repertoire. Second, although the motor system seems to play a role in action anticipation, it is not a role that is dependent on the observer possessing a corresponding motor representation. Although it could be argued that a mechanical claw is viewed as isomorphic to a human hand and could be matched based on similar form and motion, this cannot be the case for the object moving alone in the self-propelled condition.

To accommodate the fact that observers can provide rich interpretations of actions that they cannot perform

(e.g., Heider & Simmel, 1944), proponents of the direct-matching view concede that there may be an alternative, nonmotor route through which goals can be identified and actions understood (Rizzolatti & Sinigaglia, 2010). However, our data show that the motor system is recruited when infants anticipate nonexecutable actions and thus provide little basis for positing two distinct routes for action understanding. We found that the motor system was recruited regardless of whether the infant could have mapped the observed action onto a corresponding motor representation, yet the presence of selective motor activation on target trials nevertheless strongly suggests that infants identified a goal and expected an action. Considering these findings, our data provide evidence against the view that action understanding or prediction are achieved through a process of direct matching.

Although predictive paradigms permit both a prediction about what goal will be attained as well as how that goal might be attained, previous work has related motor skill to the ability to identify the goal of other people's actions (Ambrosini et al., 2012; Falck-Ytter et al., 2006; Kanakogi & Itakura, 2011). However, the current data demonstrating that infants identified the goal irrespective of motor correspondence, together with previous evidence demonstrating that goal understanding is influenced by the presence of abstract cues (Biro & Leslie, 2007; Hernik & Southgate, 2012), suggests that it is more likely that the role of the motor system in action observation lies in action anticipation (Csibra, 2007; Jacob, 2008). Further support for this view can be garnered from studies showing that goal familiarity is more important than action familiarity in eliciting motor involvement (Gazzola, Rizzolatti, Wicker, & Keysers, 2007). A mechanism that directly matches observed movement with existing motor representations in order to generate a goal understanding is inconsistent with this finding. However, if the motor system were recruited in order to generate a prediction concerning how an action will unfold, the ease with which the intended goal can be inferred would be crucial.

Previous studies have cast doubt on the hypothesis that infants require experience performing an action in order to understand that action when performed by other people (Biro & Leslie, 2007; Csibra, 2008; Luo & Baillargeon, 2005; Southgate & Csibra, 2009). However, the growing number of eye tracking studies demonstrating a relationship between motor skill and predictive saccades, particularly in infants, have given renewed support to the direct-matching hypothesis and the importance of direct matching for action understanding early in development. However, the current study suggests that infants can identify goals and generate action predictions accordingly without having a motor representation of the observed action. A question that remains is how to reconcile our findings with studies showing a relationship between action experience and anticipatory saccades. It is important to note that the specificity of this relationship has not been demonstrated. We do not know whether experience with a specific action leads to the ability to anticipate that action when other people perform it or whether motor maturity more generally is related to the ability to anticipate actions performed by others. Furthermore, a possible problem for paradigms using anticipatory looking to assess infant's ability to predict actions that differ in their familiarity is that anticipatory looking relies on the infant disengaging from the action. Because the actions that are not in the infant's motor repertoire (e.g., mechanical claws grasping or balls propelling themselves) are inherently more novel, it may be that infants make less anticipatory saccades in these instances because they are less likely to disengage as quickly from a more novel stimulus. Recent research suggests that the ability to disengage from interesting stimuli increases across the first year of life (Elsabbagh et al., 2013).

The presence of motor activation during the prediction of nonexecutable actions supports the view that the motor system is broadly involved in event prediction (Schubotz, 2007). What predicted event motor activation reflects likely depends on the timing of the activation because for any given action, what should be predicted will depend on where the action is in its course. In a previous study, we found an absence of motor activation just prior to the outcome of an action that had no visible goal (Southgate et al., 2010). In the current study, however, we found motor activation prior to the onset of the action of a self-propelled object despite the fact that this action also had no visible goal. This difference may reflect the fact that the onset of the action in the self-propelled condition could be predicted without considering the outcome of the action, whereas in the previous study, predicting what would happen next was more dependent on consideration of the outcome.

Although it is not clear how the motor system facilitates action anticipation, one possibility is that motor activation reflects the observer's recruitment of a motor program that, although it may differ from the motor program recruited by the actor, could nevertheless bring about the same effect (Csibra, 2007). As people generally attempt to achieve goals in the most efficient way, when the observer and the actor share the same motor capabilities, the observer will likely emulate the effect via a motor program that corresponds to that which the actor will actually use. In contrast, when the observer lacks the same motor capability, he or she may use an alternative motor program to emulate the same goal. Empirical evidence showing that adults born without hands recruit areas involved in foot movements when observing hand actions provides some support for this view (Gazzola,

van der Worp, et al., 2007). However, there will be cases in which such an emulative mechanism will fail. In a previous study, infants who saw an unfamiliar action progressing toward a hidden outcome did not show motor activation (Southgate et al., 2010). In the absence of any way to infer the likely outcome, the observer would have no basis on which to recruit an alternative motor program that could emulate that outcome.

A similar problem arises during the observation of intransitive actions, such as dancing. With no knowledge of what the outcome of each movement should be, a naive observer would have no basis on which to recruit an alternative motor program. This may go some way toward explaining why reports of experts recruiting their motor systems more during the observation of actions with which they are expert come primarily from studies of intransitive actions (Calvo-Merino, Glaser, Grèzes, Passingham, & Haggard, 2005; Haslinger et al., 2005).

Whatever the role of the motor system in prediction, the fact that it appears to facilitate the prediction of a broad range of events both within and outside of the observer's own motor skill would provide infants who are limited in their motor skills with a means to generate predictions about other people's actions. Because action prediction is a crucial component of collaborative activities, and collaborative activities are an important way in which young humans learn the traditions of their cultural group (Tomasello, Carpenter, Call, Behne, & Moll, 2005), an action-anticipation mechanism that is independent of motor skill may allow infants to benefit from the actions of other individuals at a time when their own action capabilities are just developing.

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