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Predictive action tracking without motor experience in 8-month-old infants

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A B S T R A C T

A popular idea in cognitive neuroscience is that to predict others' actions, observers need to map those actions onto their own motor repertoire. If this is true, infants with a relatively limited motor repertoire should be unable to predict actions with which they have no previous motor experience. We investigated this idea by presenting pre-walking infants with videos of upright and inverted stepping actions that were briefly occluded from view, followed by either a correct (time-coherent) or an incorrect (time-incoherent) continuation of the action (Experiment 1). Pre-walking infants looked significantly longer to the still frame after the incorrect compared to the correct continuations of the upright, but not the inverted stepping actions. This demonstrates that motor experience is not necessary for predictive tracking of action kinematics. In a follow-up study (Experiment 2), we investigated sensorimotor cortex activation as a neural indication of predictive action tracking in another group of pre-walking infants. Infants showed significantly more sensorimotor cortex activation during the occlusion of the upright stepping actions that the infants in Experiment 1 could predictively track, than during the occlusion of the inverted stepping actions that the infants in Experiment 1 could not predictively track. Taken together, these findings are inconsistent with the idea that motor experience is necessary for the predictive tracking of action kinematics, and suggest that infants may be able to use their extensive experience with observing others' actions to generate real-time action predictions.

1. Introduction

From the moment they come into the world, infants are surrounded by people who are performing actions that they are unable to perform themselves. How infants form real-time predictions about these actions is an important question considering the crucial role action prediction plays in joint action, cooperation, and collaboration (Sebanz & Knoblich, 2009). It has often been suggested that to predict others' actions, observers need to map the actions onto their own motor repertoire (e.g. Knoblich & Flach, 2001; Neal & Kilner, 2010; Springer et al., 2011; Wilson & Knoblich, 2005). The results of several behavioural and neurophysiological studies indeed suggest that the motor system plays a functional role in action prediction in both infants and adults. For example, performing incongruent actions (Springer et al., 2011) or being restricted to act (Ambrosini, Sinigaglia, & Costantini, 2012) during action observation has been shown to interfere with participants' prediction abilities, and eye-tracking studies have demonstrated a relationship between infants' developing motor repertoire and their ability to predict other people's actions (Cannon & Woodward, 2012; Cannon, Woodward, Gredebäck, von Hofsten, & Turek, 2012; Falck-Ytter, Gredebäck, & von Hofsten, 2006; Gredebäck & Kochukhova, 2010; Gredebäck, Stasiewicz, Falck-Ytter, Rosander, & von Hofsten, 2009; Kanakogi & Itakura, 2011; Stapel, Hunnius, Meyer, & Bekkering, 2016). Furthermore, neurophysiological studies suggest that the motor system is recruited whenever observers are generating action predictions (Kilner, Vargas, Duval, Blakemore, & Sirigu, 2004; Ramnani & Miall, 2004; Southgate, Johnson, El Karoui, & Csibra, 2010; Southgate, Johnson, Osborne, & Csibra, 2009; Southgate & Vernetti, 2014). For example, Southgate et al. (2009) found that after observing a few repetitions of goal-directed reaching actions, 9-month-old infants began to show sensorimotor cortex activation prior to the onset of the action, suggesting that they were anticipating the impending action.

Although these studies demonstrate that the motor system plays a role in action prediction, there is still considerable debate

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concerning the precise nature of this role. The link between motor system activation and action prediction has led some to suggest that motor experience is crucial for action prediction. This account proposes that observers automatically activate the motor representations of the actions they observe, which in turn allows them to understand and predict the goal of those actions (Flanagan & Johansson, 2003; Green, Kochukhova, & Gredebäck, 2014; Möller, Zimmer, & Aschersleben, 2015; Rat-Fischer, O'Regan, & Fagard, 2014; Rizzolatti, Fogassi, & Gallese, 2001). Thus, it follows from this account that infants should be unable to predict actions that are outside their motor repertoire because they lack access to a corresponding functional motor representation.

Alternative accounts propose that actions are first interpreted at some level of visual and/or conceptual analysis before they are transformed into motor code (e.g., Csibra, 2007; Jacob, 2008; Kilner, Friston, & Frith, 2007). The reconstruction of the motor commands needed to perform the action allows the observer to predict the visual consequences of the action by invoking the forward model (Wolpert & Flanagan, 2001; Wolpert & Ghahramani, 2000), which is normally used to predict the sensory effects of the observer's own actions (Csibra, 2007). Furthermore, this account suggests that when the observer is unable to perform the observed action, he or she may activate the motor program for an action that could bring about similar effects (Csibra, 2007; Schubotz, 2007). Thus, while the first account claims that activation of a corresponding motor representation is a prerequisite for recognising the action and predict its further course (Flanagan & Johansson, 2003; Green et al., 2014; Rizzolatti et al., 2001), the second account advocates that visual information alone is sufficient to support action understanding, which in turn allows the observer to use the motor system to predict how the action will unfold.

In support of this latter account, recent studies have demonstrated that infants *can* predict actions irrespective of whether these actions can be mapped onto a corresponding functional motor representation (Biro, 2013). Furthermore, it has been shown that the motor system plays a role in the prediction of such non-executable actions (Southgate & Begus, 2013). However, as these studies used self-propelled objects and claws, it is currently unclear whether infants are also able to predict *human* actions that are outside their motor repertoire. Another limitation of previous work on action prediction in infancy is that the goal and the path of the observed actions are often conflated, making it unclear whether prediction of the goal state or movement path was measured (e.g., Cannon et al., 2012; Falck-Ytter et al., 2006; Southgate & Begus, 2013).

In the current study we aimed to address these issues, and advance the debate by focusing specifically on infants' ability to predict the *kinematics* of human actions and by asking whether there is a need for motor competence. Based on previous work with adult participants, we hypothesised that infants may be able to use their previous visual experience to support the real-time prediction[1] of actions that are outside their motor repertoire, and that they might activate motor programs for actions that can bring about similar effects when doing so. For example, Cross, Stadler, Parkinson, Schütz-Bosbach, and Prinz (2013) demonstrated that visual training improved adult participants' ability to predict intransitive actions they had never performed before (such as the movements of a gymnast or wind-up toy) and that this prediction process was associated with activation of the motor system. In this study, there was no goal object or location to guide participants' predictions. Nevertheless, visual experience with the actions may have allowed participants to extract information about the temporal dynamics of the observed actions, enabling them to activate motor programs for alternative actions with similar dynamics to generate predictions about how the actions would unfold (Schubotz, 2007). We hypothesised that infants, who spend a considerable amount of time simply watching the actions of people around them, may also be able to use visual experience to support the real-time prediction of actions that they have no motor experience with (Hunnius & Bekkering, 2010, 2014), possibly by activating motor programs for actions with similar temporal dynamics. The present study aimed to investigate this idea by testing pre-walking infants' ability to differentiate between walking actions that continued either correctly or incorrectly after a brief occlusion period, and the neural mechanisms supporting this ability.

2. Experiment 1: Looking time study

To measure predictive action tracking in infants, we adopted a paradigm that has previously been used to investigate real-time action prediction of point-light stimuli in adult participants (Graf et al., 2007; Parkinson, Springer, & Prinz, 2012; Sparenberg, Springer, & Prinz, 2012). Infants were presented with videos of upright and inverted (upside-down) infant stepping actions that were briefly occluded from view, followed by either a correct (time-coherent) or an incorrect (time-incoherent) continuation of the action. We then measured infants' looking times to static test postures after correctly versus incorrectly continued actions. We used infant stepping stimuli because a previous study suggested that visual experience with this type of action might trigger predictive processes (de Klerk, Johnson, Heyes, & Southgate, 2015). We used inverted stepping actions as control stimuli to check whether extrapolation from the movement prime would be sufficient to elicit predictive responses. We hypothesised that infants do not necessarily need active motor experience, but can rely on their previous observational experience with human actions to generate real-time action predictions. Therefore, we predicted that pre-walking infants would be able to distinguish between the correct and incorrect continuations of visually familiar upright stepping actions (as indicated by longer looking times to incorrectly continued actions compared to correctly continued actions), but not of unfamiliar inverted stepping actions.

2.1. Method

2.1.1. Participants

The final sample consisted of 24 pre-walking 8-month-old infants (M = 245 days; range 228–268 days). An additional nine infants were tested but excluded because they did not provide enough trials for analyses due to fussiness (N = 5), experimental error (N = 1) or failure to engage with the stimuli (N = 3). Two more infants were excluded because they did not fulfil the inclusion criteria: one infant was born 5 weeks pre-term and another was already cruising (walking while holding on to furniture). All included infants were born full-term, healthy and with normal birth weight. Written informed consent was obtained from the infant's caregiver prior to the start of the experiment.

2.1.2. Stimuli

The stimulus material for the test trials consisted of video clips of six different infants performing stepping actions on an infant treadmill filmed from a sagittal view (see de Klerk, Johnson, Heyes et al., 2015). All stepping actions were rightward movements but as the infants were on a treadmill, there was little horizontal translation. Familiarisation stimuli consisted of three infants performing bouncing actions on the infant treadmill. The

[1] In this paper, the terms 'predictive action tracking' and 'real-time action prediction' refer to mechanisms by which the kinematics or movement paths, rather than the goal or the outcome, of observed actions are tracked and predicted in real time.