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Motor system contribution to action prediction: Temporal accuracy depends on motor experience

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ABSTRACT

Predicting others' actions is essential for well-coordinated social interactions. In two experiments including an infant population, this study addresses to what extent motor experience of an observer determines prediction accuracy for others' actions. Results show that infants who were proficient crawlers but inexperienced walkers predicted crawling more accurately than walking, whereas age groups mastering both skills (i.e. toddlers and adults) were equally accurate in predicting walking and crawling. Regardless of experience, human movements were predicted more accurately by all age groups than non-human movement control stimuli. This suggests that for predictions to be accurate, the observed act needs to be established in the motor repertoire of the observer. Through the acquisition of new motor skills, we also become better at predicting others' actions. The findings thus stress the relevance of motor experience for social-cognitive development.

1. Introduction

Predicting others' actions is crucial for acting in a social world. For social interaction to run smoothly, accurate predictions of the precise timing of the partner's movements are necessary (Sebanz & Knoblich, 2009). According to the simulation account (Wilson & Knoblich, 2005), the motor system generates predictions of how observed actions will continue in time and space. These predictions are thought to be based on the motor program a person uses for executing the same action (Kilner, Friston, & Frith, 2007; Prinz, 2006; Wolpert, Doya, & Kawato, 2003). Studies contrasting human and non-human movements provide a first indication that the motor system is indeed involved in the prediction of actions and their timing: Though human motion should be much harder to predict due to its complexity, empirical results show the opposite (Saunier, Papaxanthis, Vargas, & Pozzo, 2008; Stadler, Springer, Parkinson, & Prinz, 2012). The current study investigated whether the motor system is crucially involved in action prediction by comparing how well groups with different motor experiences can predict different actions.

Previous neuroimaging studies showed that the motor system is not only involved in action execution, but also in action observation (e.g., Candidi, Sacheli, Mega, & Aglioti, 2014; De Bruijn, Schubotz, & Ullsperger, 2007; Glenberg et al., 2010; Hari et al., 1998; Malfait et al., 2009; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996). Motor activation in adults is found to be stronger if the observer has more motor experience with this action (Calvo-Merino, Glaser, Grèzes, Passingham, & Haggard, 2005; Calvo-Merino, Grèzes, Glaser, Passingham, & Haggard, 2006; Cross, Hamilton, & Grafton, 2006). The same holds for infants as shown in a study by van Elk, van Schie, Hunnius, Vesper, and Bekkering (2008). The tested 14- to 16-month-old infants, who were experienced crawlers but inexperienced walkers, displayed stronger motor activation while watching crawling compared to walking movements. Motor experience thus changes action perception. But does it also have an impact on the accuracy of for example temporal action predictions? Presumably, the internal model that predicts the sensory consequences of a motor command, also called a forward model (Wolpert et al., 2003), becomes more fine-grained through action experience. Such an experience-based forward model would then result in predictions of observed actions that become more accurate with increasing action experience.

Converging evidence suggests that the motor system plays an important role in the prediction of perceived actions. That is, the motor system is active during action prediction tasks (Fontana et al., 2012) prior to goal attainment (Umiltà et al., 2001), and sometimes even prior to action onset (Kilner, Vargas, Duval, Blakemore, & Sirigu, 2004). Motor activation is stronger when the observed action is not yet completed than when the goal is attained (Urgesi, Moro, Candidi, & Aglioti, 2006; Urgesi et al.,

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2010). The accumulating evidence from the neuroimaging literature, however, leaves open the question whether there is a measurable behavioral benefit of the involvement of the motor system when observing another person's action. One benefit illustrated in many recent studies is that infants more readily infer the end location of an observed action if that action is part of their motor repertoire. For instance, infants are quicker to infer the end location of a human compared to a non-human action (Cannon & Woodward, 2012; Falck-Ytter, Gredebäck, & von Hofsten, 2006; Kanakogi & Itakura, 2011) and quicker to make a goal inference if they are more proficient in the action they observe (Ambrosini et al., 2013; Gredebäck & Kochukhova, 2010; Kanakogi & Itakura, 2011). Opponents of this interpretation argue that goal inference improves due to general motor maturation rather than as a result of increased active experience with the specific actions involved (Southgate, 2013). It thus still needs to be examined whether the prediction of an action benefits from experience with specifically this action and whether motor involvement supports precise temporal predictions which are needed in everyday social interactions.

To answer these questions, the current study compares the prediction accuracy of actions that are either part of the observer's motor repertoire or not. To that end, the participant groups were selected such that they had different motor capabilities because of their age. This developmental approach provides a unique opportunity to study the benefits of action experience for the prediction of observed actions in a natural training setting, namely by examining the impact of real-life experiences. Initially, testing and comparing prediction accuracy over different age groups might appear difficult, as reaction times tend to be slower and more variable in young children, making it hard to weigh their reactions against those of older age groups. However, the oculomotor system reaches adult levels of functioning early in life (Hunnius, 2007), which makes gaze location and gaze timing suitable measures to test action prediction performance across age groups (Falck-Ytter et al., 2006; Hunnius & Bekkering, 2010). When predicting the trajectory of objects reappearing from behind an occluder, even infants have been shown to take into account complex velocity profiles of moving objects (e.g., circular movement by 9 months of age, Gredebäck, von Hofsten, & Boudreau, 2002). In a similar fashion, gaze timing to a post-occluder area was used as a measure of action prediction accuracy in the current study. All participants observed videos of an actor or object moving from one side of the scene to the other. The actor briefly disappeared behind an occluder and then reappeared on the other side (see Fig. 1). The participants' ability to accurately predict when the actor or object would reappear was investigated. Besides prediction accuracy, the stability of the predictions was measured, which also provides information about the underlying prediction process: whereas high variability in prediction accuracy might reflect guessing, little variability likely stems from a well-established process (Zanone & Kelso, 1997).

To investigate whether differences found in action prediction accuracy between age groups are not due to general (motor) maturation, but related to motor experience with the specific actions observed, different actions were used. Experiment 1 served as a proof of concept, comparing 14-month-old infants (experienced crawlers, inexperienced walkers) with 30-month-old toddlers and adults (experienced in both walking and crawling). The infant group was expected to be more accurate and stable in predicting crawling compared to walking, whereas the other age groups were to be equally stable and accurate in predicting both actions. In Experiment 2, 18- to 20-month-old toddlers were investigated to test whether relatively little walking experience would be sufficient to accurately predict walking.

In both experiments, a third condition was included which displayed an object moving through the scene. This allowed for a comparison between predictions of movements that can be generated by the motor system and movements that are probably predicted using other brain areas, such as Medial Superior Temporal area (MST) and Middle Temporal area (MT, Newsome, Wurtz, Dursteler, & Mikami, 1985; Tanaka & Saito, 1989). These areas respond to non-biological movements in a visual scene in macaque monkeys, and especially MST is responsive to the direction of movement in humans as well (Smith, Wall, Williams, & Singh, 2006). In line with previous research (Saunier et al., 2008; Stadler et al., 2012), predictions of human movements were expected to be more accurate and stable than predictions of the non-human movements.

2. Experiment 1

2.1. Methods

2.1.1. Subjects

Sixteen right-handed adults (11 females, mean age = 22.8 years, *SD* = 3.6), seventeen infants (10 females, mean age = 14.0 months, *SD* = 0.26), and twenty-three toddlers (6 females, mean age = 29.9 months, *SD* = 0.33) were tested. Two additional infants and two additional toddlers were tested but data were not included in the analyses due to insufficient calibration of the eye-tracker. All children were recruited via the database of the Baby Research Center Nijmegen, which consists of parents who signed up for participation in child research. Infant participants were only invited to the lab if parents reported that their child displayed the ability to crawl on hands and knees. The adults were recruited via the university's participant database. Participants in the adult sample and parents of the child participants gave written informed consent for participation (either their own or their child's) in the study.

2.1.2. Procedure

All participants were presented with the same set of stimuli on a Tobii 1750 eye-tracker (Tobii Technology, Stockholm, Sweden). First, a calibration procedure was administered, during which participants viewed contracting and expanding circles placed on a 3 by 3 (children) or 4 by 4 grid (adults). Data included in the analyses if sufficient information for minimally 7 (children) or 14 (adults) calibration points was available. After calibration, 48 (children)

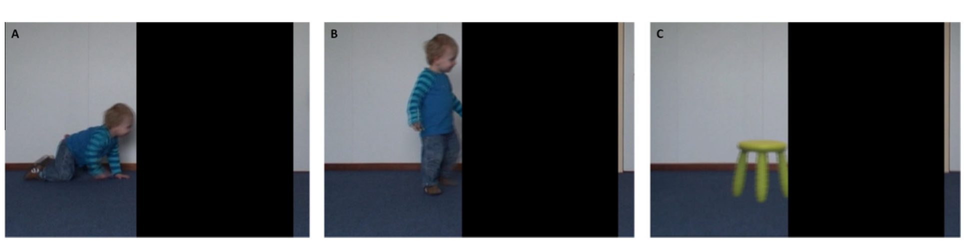

Fig. 1. Example frames from the three stimulus conditions, (A) infant crawling, (B) infant walking, and (C) moving object.