

# Eye Movements During Action Observation

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## Abstract

An important element in social interactions is predicting the goals of others, including the goals of others' manual actions. Over a decade ago, Flanagan and Johansson demonstrated that, when observing other people reaching for objects, the observer's gaze arrives at the goal before the action is completed. Moreover, those authors proposed that this behavior was mediated by an embodied process, which takes advantage of the observer's motor knowledge. Here, we scrutinize work that has followed that seminal article. We include studies on adults that have used combined eye tracking and transcranial magnetic stimulation technologies to test causal hypotheses about underlying brain circuits. We also include developmental studies on human infants. We conclude that, although several aspects of the embodied process of predictive eye movements remain to be clarified, current evidence strongly suggests that the motor system plays a causal role in guiding predictive gaze shifts that focus on another person's future goal. The early emergence of the predictive gaze in infant development underlines its importance for social cognition and interaction.

## Keywords

action, performance, development: infant, neuroscience, social cognition

When you observe a family member reaching for a piece of candy, you do not reactively track the movement of his or her hand. Rather, you fixate on the candy before the hand reaches it. This predictive gaze shift allows you to overcome the internal processing lag of the perception-action system (i.e., the time it takes to perceive the surrounding world) and pay attention to important events as they unfold. When you are after the same sweet, this predictive gaze provides the time you need to plan and execute an action toward the goal. Without prediction, your perception of the surrounding world would be fragmented and lag behind real-world events, and you would certainly never get hold of the candy. In short, the ability to perform predictive gaze shifts while observing actions is fundamental for successful interactions with the environment (Hayhoe & Ballard, 2005; Henderson, 2003; Land, 2009; von Hofsten, 2004), irrespective of whether the overarching goal is to collaborate or compete.

It has long been known that predictive eye movements play an important role in guiding our own actions. A large body of work has shown that predictive eye movements are functionally integrated into most everyday actions that we perform (von Hofsten, 2004), including reaching (Johansson, Westling, Bäckström, & Flanagan, 2001), walking (Patla & Vickers, 1997), driving (Land & Lee, 1994), playing sports (Land & McLeod, 2000;

Vickers, 1996), and cooking (Hayhoe, Shrivastava, Mruzek, & Pelz, 2003; Land, Mennie, & Rusted, 1999). Typically, we move our eyes to a goal several hundred milliseconds before that goal is reached. The exact timing of one's gaze depends on the task at hand (Land & Hayhoe, 2001) and the proficiency of the actor (Abernethy, 1990; Franchak, Kretch, Soska, & Adolph, 2011; Sailer, Flanagan, & Johansson, 2005; von Hofsten, 2004).

## Embodied Account of Predictive Eye Movements

However, it was not until 2003 that Flanagan and Johansson (2003) discovered that predictive gaze shifts are not only important in guiding our own actions but are also integral to action observations—that is, observing another person's goal-directed actions. In their study, Flanagan and Johansson demonstrated that adults predicted action goals by fixating on the end location of an action before it was reached, both when they executed an action themselves and when they observed someone

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else executing an action (the task involved moving three small blocks in the coronal plane).

The similarity in the eye movements of the actor and the observer led Flanagan and Johansson to suggest that the prediction of another's goal could result from a mechanism that mapped an observed action onto the motor representation of that action and that this basic process operated during both the execution and the observation of the action. The idea was that when you see someone else act, you activate your own motor plans for similar actions, and these motor plans include instructions for the oculomotor system to implement goal-directed, predictive saccades. In other words, Flanagan and Johansson proposed that a goal-directed gaze shift would be initiated by activating a single underlying neural network, irrespective of who performed the action. This hypothesis was consistent with the discovery of mirror neurons (Dipellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992; Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Rizzolatti, Fogassi, & Gallese, 2001) and the notion that action understanding is rooted in the motor system. As with the mirror-neuron system (Iacoboni & Dapretto, 2006; Molenberghs, Cunnington, & Mattingley, 2012), the tendency to predict a goal while observing another person's action was assumed to reflect a quick, automatic, visuo-motor matching process, rather than a process based on the cognitive interpretation of visual information (Flanagan & Johansson, 2003).

In this article, we refer to this view as the *embodied account* of predictive eye movements. In general, embodied accounts emphasize the notion that cognition is situated in activity and that it is the outcome of a history of active manipulations of the environment (Barsalou, 2008). This view contrasts with theories that assume that cognition is an abstract manipulation of symbols (Mahon & Caramazza, 2008).

Flanagan and Johansson (2003) argued that the presence of the predictive gaze spoke against the possibility that eye movements during action observations were driven by pure visual analysis, without involving the motor system (p. 770). According to those authors, visually driven eye movements are typically reactively linked to the events we observe. To confirm this, in addition to conditions in which participants either performed or observed another actor, Flanagan and Johansson included a control condition in which the blocks appeared to be moving to their final location by themselves (the experimenter performing the actions was not visible to the observer). As expected, when observing these apparently self-propelled objects, participants fixated on the goal only after the object had arrived there—that is, their gaze shifts were reactive rather than predictive. Taken together, those results suggested that it was necessary to see a hand-object interaction to elicit a predictive gaze; that

conclusion was consistent with the notion that the observer must use his or her own motor knowledge to predict the goal. Of course, given that only behavioral data was available at the time, the suggestion that this process was mediated by the observer's motor system was a speculation.

The present article reviews the research that followed from the Flanagan and Johansson study (2003). Simultaneously, we evaluate the proposed embodied account of predictive eye movements and present studies that have directly manipulated brain activity, with the aim of better understanding the neural networks involved. We also review recent work that has investigated action prediction in infancy. Overall, the evidence supports the central claim made by Flanagan and Johansson (2003), but, as always, the story is more complicated than originally assumed.

Unless otherwise stated, all empirical findings cited below refer to eye tracking studies that have investigated the tendency of adults or infants to predict (with their eyes) another person's goal-directed actions, which, for the sake of simplicity, we refer to as *action prediction* in this article. The majority of the studies used the timing of gaze to another person's goal as the dependent variable, although some also used the accuracy of gaze shifts when multiple possible goals were present.

### ***Behavioral analyses of human adults that have replicated and extended the initial findings of Flanagan and Johansson***

Research subsequent to Flanagan and Johansson (2003) has replicated and extended their initial findings. These studies have demonstrated that an adult gaze can predict the goal of a wide range of manual actions performed by others, including stacking objects (Rotman, Troje, Johnson, & Flanagan, 2006), reaching (Kanakogi & Itakura, 2011), eating (Kochukhova & Gredebäck, 2010), drinking (Hunnius & Bekkering, 2010), placing objects in containers (Eshuis, Coventry, & Vulchanova, 2009; Falck-Ytter, Gredebäck, & von Hofsten, 2006; Melzer, Prinz, & Daum, 2012; Rosander & von Hofsten, 2011), and pouring (Myowa-Yamakoshi, Scola, & Hirata, 2012). The key findings of these studies are consistent with the embodied account of action prediction. First, they show that a predictive gaze can be triggered by point light hands (in which only motion profiles are maintained, represented as moving dots). This finding suggests that basic kinematic information is sufficient to elicit the predictive process (Elsner, D'Ausilio, Gredebäck, Falck-Ytter, & Fadiga, 2013; Elsner, Falck-Ytter, & Gredebäck, 2012). Second, they showed that it is important that the goal of the

perceived action is within the reaching space of the agent reaching for the goal (Costantini, Ambrosini, & Sinigaglia, 2012b). Last but not least, they also employed control stimuli that displayed apparently self-propelled objects, similar to those used by Flanagan and Johansson, to study action prediction in adults. As expected, consistent with the initial findings, the predictive goal-directed gaze shifts were not observed in the control conditions (Eshuis et al., 2009; Falck-Ytter, 2010; Falck-Ytter et al., 2006) or were observed to a lesser degree than in conditions involving human action (Eshuis, Coventry, & Vulchanova, 2009; Kochukhova & Gredebäck, 2010). Taken together, the findings suggested that there is something special about human actions that can trigger predictive eye movements. However, a convincing test of the embodied account proposed by Flanagan and Johansson would require a different type of data—that is, data that could provide a causal link between motor-system activation and predictive eye movements during action observation.

### ***Direct evidence: Motor activity is causally linked to action prediction***

The premise that action prediction depends on the observer's own motor proficiency was tested by interfering with the action-production system and then determining whether action prediction was inhibited. According to the embodied account, action prediction should be task-specific; thus, interference should occur primarily when the task performed and the task observed require the same effector (e.g., the same hand).

The first study to use this approach was reported by Cannon and Woodward (2008). They instructed adult participants to observe a goal-directed manual action (similar to the one used by Flanagan and Johansson) while performing one of two distracting tasks: Participants either tapped their fingers or counted backward. Action prediction was diminished by simultaneous finger tapping but not by counting backward (a working memory task). The authors argued that taxing the motor system interferes with the process of matching perceived events to one's own motor plans for similar actions. In contrast, they argued that working memory tasks have little to do with the embodied processes that are assumed to guide predictive eye movements, and thus these tasks were expected to have little impact on action prediction. Assuming that the interfering effect of finger tapping was due to a specific tax on the motor system, that study provides selective support for the embodied account.

Costantini, Ambrosini, and Sinigaglia (2012a) let adults hold either a small or a large object while observing either a hand approaching objects with a whole-hand grip (suitable for large objects) or a hand approaching objects with a precision grip (suitable for small objects). It was found

that performing a grip that was different from the one observed resulted in fewer predictions relative to a baseline condition, in which the hand of the participants rested freely. Ambrosini, Sinigaglia, and Costantini (2012) demonstrated that the latency of adults' predictive eye movements increased (i.e., they became less predictive) when an observer's arms were tied behind his or her back, compared to when the hands were free to move.

Again, those studies suggested that motor interference could affect action prediction, but the evidence is purely behavioral, and hence it was not fully satisfactory, given the nature of the hypothesis. Arguably, the most direct support for the embodied account of predictive eye movements was obtained in two studies that used joint transcranial magnetic stimulation (TMS) and eye tracking methods (Costantini, Ambrosini, Cardellicchio, & Sinigaglia, 2013; Elsner et al., 2013). In one of those studies (Elsner et al., 2013), adult participants observed goal-directed reaching actions, represented as point-light displays, while TMS pulses selectively stimulated the hand or leg areas in the primary motor cortex. Results were compared to those produced in the absence of TMS activation at each site. Consistent with the embodied account, the participants exhibited delayed fixation on the goal when TMS pulses interfered with the hand area of the primary motor cortex, compared to when no TMS was performed or when the TMS targeted the leg area of the primary motor cortex. In the other study (Costantini et al., 2013), participants viewed manual reaching actions while TMS pulses were directed either to the ventral premotor cortex or to one of two control sites (the superior temporal sulcus or the frontal eye field). Stimulating the premotor area caused specific interference effects that were not observed in the two control conditions.

In summary, five studies experimentally manipulated activity in the motor cortex (either through TMS or behavioral manipulations) while participants observed another individual's actions (Ambrosini et al., 2012; Cannon & Woodward, 2008; Costantini et al., 2013; Costantini et al., 2012b; Elsner et al., 2013). All studies demonstrated an interference effect, consistent with the embodied account. These five studies have provided the strongest evidence that the motor cortex is somatotopically recruited and contributes causally to action predictions.

### **The Development of Action Prediction**

Given the importance of action prediction in our ability to encode and interact with the surrounding world, much attention has been devoted to investigating these processes during infancy and early childhood. This recent line of research has demonstrated uniformly that action prediction develops early in life (Ambrosini

et al., 2013; Biro, 2013; Brandone, Horwitz, Aslin, & Wellman, 2014; Cannon, Woodward, Gredebäck, von Hofsten, & Turek, 2012; Daum, Attig, Gunawan, Prinz, & Gredebäck, 2012; Falck-Ytter, 2010; Falck-Ytter et al., 2006; Fawcett & Gredebäck, 2013, 2015; Geangu, Senna, Croci, & Turati, 2015; Gredebäck & Kochukhova, 2010; Gredebäck & Melinder, 2010; Gredebäck, Stasiewicz, Falck-Ytter, Rosander, & von Hofsten, 2009; Green, Kochukhova, & Gredebäck, 2014; Henrichs, Elsner, Elsner, & Gredebäck, 2012; Henrichs, Elsner, Wilkinson, Elsner, & Gredebäck, 2014; Hunnius & Bekkering, 2010; Kanakogi & Itakura, 2011; Melzer et al., 2012; Paulus, Hunnius, & Bekkering, 2011; Rosander & von Hofsten, 2011; Senju, Southgate, Snape, Leonard, & Csibra, 2011; Southgate, Senju, & Csibra, 2007). By attaining the ability to predict another person's action goals, infants can fixate on future goals, and thus they proactively pay attention to the person's actions as they unfold. From this perspective, action prediction is a fundamental cornerstone of our ontogenetic development. Without this ability, learning from others through observation and interaction would be far reduced.

Several developmental studies have studied infants of different age groups and demonstrated that action prediction develops at the same time as the ability to perform an action. For example, 4-month-olds have poor reaching skills, and they fail to predict the goals of reaching actions. Six-month-olds have recently developed the ability to reach for objects, and they have the ability to predict the goal of other people's reaching actions (Kanakogi & Itakura, 2011; see also Ambrosini et al., 2013). They are also highly proficient at placing objects in their mouths, and they can predict the goal of other peoples' eating actions (Kochukhova & Gredebäck, 2010). In contrast, 6-month-olds cannot predict the movements of mechanical claws (Kanakogi & Itakura, 2011), spoons that appear to move on their own, or combing actions that they cannot perform (Kochukhova & Gredebäck, 2010).

The ability to place objects into a container typically develops between 6 and 12 months of age, and 12-month-olds, but not 6-month-olds, can predict the goal of such actions (Falck-Ytter et al., 2006). However, 12-month-olds (and even adults) cannot predict the goal of a ball that appears to move on its own into a container. Moreover, at the age of 1 year, prediction of an initial act (in this case, reaching) will become modulated by the overarching goal of the action sequence (placing the object either on a table or inside a container). This finding suggests that prediction is controlled by a system of *action understanding* that is hierarchically organized (Gredebäck et al., 2009).

Several of those studies also analyzed individual manual ability. There are clear correlations (when age is controlled for) between predictive eye movements and

various measures of manual capability, including the ability to reach for something (Kanakogi & Itakura, 2011; Melzer et al., 2012), the number of times an infant places objects in a container (Cannon et al., 2012), and the number of attempts made before accurately placing a puzzle piece on a puzzle board (Gredebäck & Kochukhova, 2010). Also, the ability to predict the goal of feeding actions correlated with an infant's lifetime experience of being fed (Gredebäck & Melinder, 2010).

In summary, developmental studies have demonstrated that the ability to predict action emerges in early infancy. This finding underlines the role of prediction in social cognition and interactions in general. Also, the correlation between the actions that infants can perform and actions they can predict suggests that social cognition and social learning might be bound by the developing action repertoire of the infant. This result is consistent with the embodied account of action prediction.

### How Is Prediction Related to Action Understanding?

According to Flanagan and Johansson (2003), action prediction and action understanding occur simultaneously. That is, low-level sensory information from performing an action taps directly into the motor system, which then in turn outputs the estimated goal (the direct-matching hypothesis; see also Rizzolatti et al., 2001). Interpreted from this perspective, action prediction reflects the "direct" activation of a motor program, which includes—in addition to understanding the goal of the action—task-specific instructions to the oculomotor system to direct the eyes toward the goal (Flanagan & Johansson, 2003). According to an alternative view (Csibra, 2007; Southgate, 2013), action prediction follows action understanding. This view argues that goal encoding must precede motor simulation; thus, this theory proposes that motor activation and the consequent predictive eye movements reflect the observer's reenactment of achieving the goal, as though the observer had executed the action. Here, this theory is referred to as the *reenactment account*.

Notably, both of the above views argue for a role of the motor system, and they cannot be disentangled easily based on the current evidence. Arguably, however, the behavioral experiments can provide circumstantial evidence against the reenactment account. We know from other work (not related to predictive eye movements) that infants and adults can attribute a goal to the actions of an "agent" that lacks all similarity to the human body (Gergely & Csibra, 2003). However, when observing self-propelled "agents" move without the interaction of an actor's hand, predictive eye movements seldom occur (Eshuis et al., 2009; Falck-Ytter, 2010; Falck-Ytter et al., 2006; Kochukhova & Gredebäck, 2010). The reenactment

version of the embodied account cannot readily account for this finding, because it predicts that, once a goal is identified, the observer should be able to reenact the action; thus, the predictive processes associated with the action should be activated, irrespective of the morphological characteristics of the agent.

### ***The roles of prior knowledge, statistical regularity, and goal salience***

As described above, when one observes events that lack a clear correspondence with something in the motor repertoire of the observer, the gaze is typically reactive. However, several studies have shown that when one observes an action that corresponds to an action that one can perform, the action prediction is influenced by prior knowledge, statistical regularity (e.g., the mean result of a repeated action), and the saliency of the goal (Ambrosini, Costantini, & Sinigaglia, 2011; Eshuis et al., 2009; Green, Li, Lockman, & Gredebäck, in press; Henrichs et al., 2014; Rotman et al., 2006). The most extreme influences of this kind can be observed in infancy. At that stage, action predictions occur primarily when the goal is highly salient and when the observed agent consistently reaches for the same (as opposed to a different) object (Henrichs et al., 2012; Henrichs et al., 2014). Finally, recent work has demonstrated cultural influences on action prediction. Green et al. (in press) demonstrated that 8-month-old infants in Sweden and China both predicted that eating actions would go to the mouth. However, this was true only for eating actions performed with a spoon among Swedish infants and only for eating actions performed with chopsticks among Chinese infants.

Together, the results show that embodied processes dedicated to action prediction do not work in isolation; instead, these processes account for other types of information that can be used to predict future states. In other words, although action prediction may be fundamentally an embodied process, the tendency to predict is modulated by broad scope of ancillary functions that either enhance the activation within the motor system of the observer or, more generally, facilitate attention. For example, the effect of goal saliency might be related to attention. When the goal is highly salient, it may be easier to inhibit the initial fixation on the ongoing action and facilitate a saccade to the goal object, which would accelerate the gaze shift to the predicted goal. In a similar manner, the effect of statistical regularity, or repetition, might boost the activation of one's own motor plans through priming. In infants, whose motor plans are less developed, this boost might be necessary to activate the motor system to the threshold required to initiate a predictive saccade.

Finally, it is worth noting that, in addition to modulating action prediction after the embodied system is established, statistical learning may also contribute to the development of the system. Specifically, it has been suggested that embodied systems for action understanding acquire their mirroring properties through Hebbian learning (see, e.g., Heyes, 2010; Keysers & Gazzola, 2014; Keysers & Perrett, 2004).

### ***Prediction in other contexts***

The above evidence relates primarily to the ability to predict in rather simplified contexts (e.g., a hand reaching for an object), but it should be noted that predictive gaze shifts to goals also occur when observing actions embedded in social interactions between people (Fawcett & Gredebäck, 2013, 2015; Senju et al., 2011; Southgate et al., 2007). How embodied and other processes interact in such situations is currently not well understood. It is also notable that infants and adults can predict the future state of certain nonsocial events. For example, predictive eye movements are systematically directed to the future location of non-animate moving balls that temporarily disappear behind a barrier (Gredebäck & von Hofsten, 2004; Johnson, Amso, & Slemmer, 2003; Kochukhova & Gredebäck, 2007; for a review, see Gredebäck & von Hofsten, 2007). Clearly, the embodied account cannot explain predictive gaze shifts in all contexts.

### **Conclusion**

Prediction is a fundamental component of our interactions with the world, including interactions with other people. When you view someone else reach for an object, you anticipate what is going to happen by moving your gaze to the object before the arrival of the other person's hand. As shown in this review, this predictive capacity—which is likely to be a key component of social perception, cognition, and interaction, both in competitive and collaborative contexts—builds upon the activation of one's own motor system (Costantini et al., 2013; Elsner et al., 2013). This hypothesis was proposed over 10 years ago by Flanagan and Johansson (2003), but the lack of brain-based evidence rendered it speculative at that time. Following in the footsteps of the Flanagan and Johansson study, over 30 articles have provided direct evidence for the embodied account of predictive eye movements, and additionally, several studies have shed important new light on the development of action prediction. This body of work has shown that infants possess the impressive capacity to predict other people's action goals and that this capacity develops hand in hand with the infant's own action capacities.

## Future Directions

This review has highlighted key areas for future investigation, including the relationship between action prediction and action understanding and the roles of general factors, such as prior knowledge, statistical regularity, and goal salience, in embodied processes.

The ontogenetic development of the mirror-neuron system and related networks of action understanding in infancy is a matter of current controversy and debate (Heyes, 2013). The infant studies described above, which focused on action predictions early in life, provided a way to illuminate these questions, and those types of studies should be exploited and developed further.

In everyday social interactions, action understanding is never complete; rather, one must constantly revisit current assumptions about other people's actions in light of new information. Therefore, future studies should focus on the role of the predictive gaze in the action understanding *process*—for example, in checking, validating, and updating assumptions and beliefs about other people's goals. This would entail, among other things, going beyond repetitive video presentations of simple manual actions and acknowledging the intricate dynamics of embodied and other processes (Gredebäck & Daum, 2015).

Determining the importance of action predictions in dynamic social interactions requires implementing future-oriented processes in artificial systems designed for real-world interactions (Vernon, Fadiga, & von Hofsten, 2011; and see, e.g., Metta et al., 2010). Initial steps have been taken to integrate action prediction into developmental robotics platforms (Sciutti et al., 2012). In turn, simulations of the action-prediction system may provide useful ways to test putative mechanisms that underlie action predictions. However, much work remains to be completed before this goal can be realized.

To test the proposed theories and demonstrate the clinical relevance of developmental studies, one could test infants with deteriorated motor-control functions or who have been born without hands or arms but with otherwise intact cognitive capacities. Such studies could provide important new evidence for the role of active experience in socio-cognitive development, and they may reveal potential compensatory processes.

Finally, testing action prediction in infants at risk for autism may provide a means to test the hypothesis that disruptions in systems involved in (embodied) action understanding may represent a causal link between genetic/molecular risk factors and a later diagnosis (Cattaneo et al., 2007; Iacoboni & Dapretto, 2006). In general, the identification and study of groups that fail, early in life, to predict other people's action goals would provide a means to test a core assumption presented in this article—namely, that action prediction is a necessary foundation for social cognition and interaction.

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The authors declared that they had no conflicts of interest with respect to their authorship or the publication of this article.

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