

Predictive Eye Movements Are Driven by Goals, Not by the Mirror Neuron System

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The importance of a mirror neuron system (MNS) as a mechanism for understanding the actions of others has been established (e.g., Rizzolatti, Fadiga, Gallese, & Fogassi, 1996). Neurons in the primate premotor cortex fire both when a monkey performs an action (e.g., grasping) and when the monkey observes someone else performing the same action. It has also been proposed that the MNS is the starting point for understanding the intentions and goal-directed behavior of others (Fogassi et al., 2005; Gallese & Goldman, 1998). Consistent with this view, Falck-Ytter, Gredebäck, and von Hofsten (2006) argued that the MNS is implicated in proactive goal-directed (predictive) eye movements. In a series of eye-tracking studies, participants observed a toy object moving along a trajectory toward a container. Adults and 1-year-old infants looked ahead of the toy and toward the goal container only when a hand was observed moving the toy (the human-agent condition). Proactive goal-directed eye movements were not found in two further conditions: a self-propelled condition, in which a toy with rudimentary facial features moved along the trajectory by itself, or a mechanical motion condition, in which a ball with no distinctive features moved along the trajectory. Falck-Ytter et al. interpreted these data as evidence that the MNS is necessary for proactive goal-directed eye movements. Moreover, the absence of proactive goal-directed eye movements in 6-month-old infants (who are too young to perform the actions themselves) is taken as further support for the MNS account.

These claims are premature. The conditions run by Falck-Ytter et al. (2006) do not discriminate between predicted human motion tied to intention and predicted agent goals tied to intention consistent with the mirror neuron hypothesis, movement of the hand may necessarily involve the simulation of motion via the MNS, and proactive goal-directed eye movements may therefore only occur when a hand is shown to move the object. Alternatively, a hand moving an object involves the intention of an agent to place the object in the goal container, and the expectation that the agent intends for the object to end up in a goal location may cause the proactive eye movements (consistent with teleological stance theory; Gergely & Csibra, 2003). To arbitrate between these accounts, it is necessary to run a human-agent condition without human movement.

Therefore, we set out to test the claims of Falck-Ytter, et al. (2006), but with the addition of a new critical condition missing in the original study. We ran three movement conditions: the human-agent condition, in which a human agent was shown moving a toy frog toward a goal container (i.e., [1human agent, 1human motion]); the self-propelled condition, in which no human agent was shown moving the frog (i.e., [_human agent, _human motion]); and the new condition, in which a human agent was shown with hand behind the starting point of the frog, flicking it so as to propel it along a trajectory (as in the game "Tiddlywinks"; i.e., [1human agent, _human motion]; see Fig. 1a). In the latter condition, the human-agent intention is matched to that of the human-agent condition, but human motion is not shown along the trajectory. This allows a clean test of the MNS versus goal-intention explanations for the proactive eye-movement data.

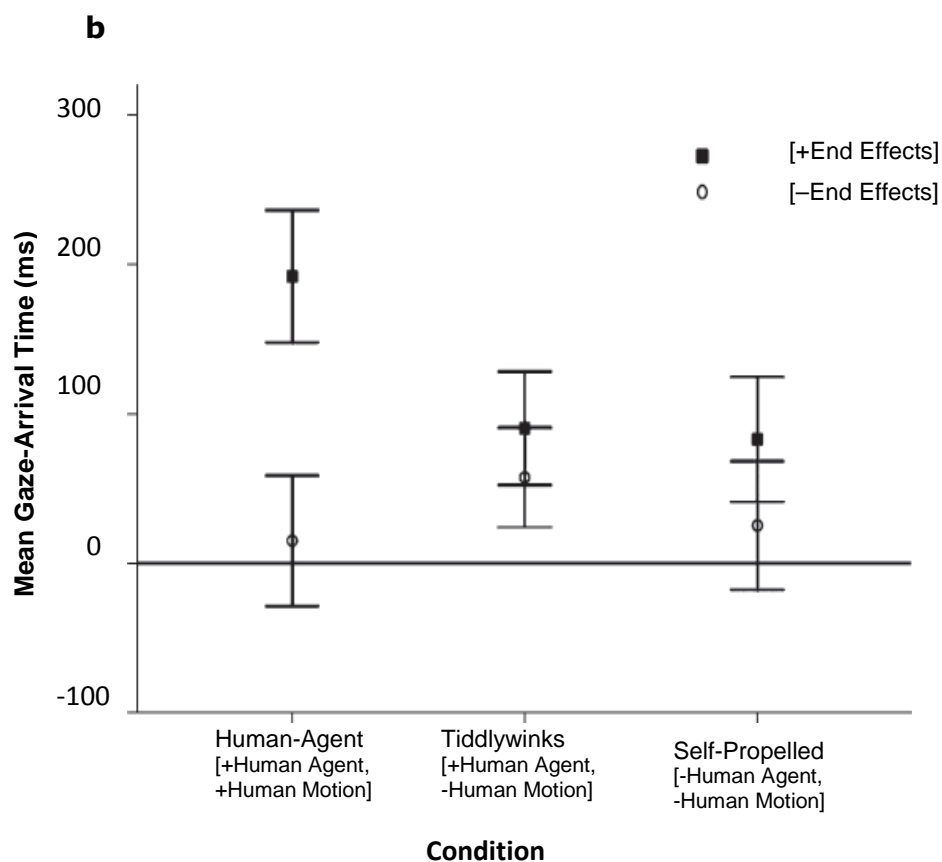
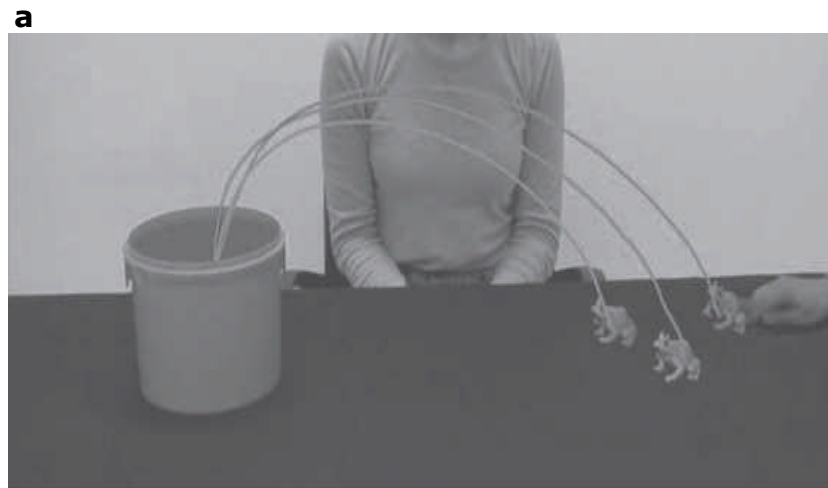


Fig. 1. Example of the video used in the new (Tiddlywinks) condition and experimental results. In the illustration (a), the trajectories traversed by the frogs have been drawn in, but they were not visible during the experiment. The graph (b) shows mean gaze-arrival time relative to the frog's arrival time (time 0; positive values indicate that gaze arrived before the frog) for the human-agent, new (Tiddlywinks), and self-propelled conditions with and without end effects. Error bars indicate ± 1 SEM.

We also ran each condition in two ways. In the original humanagent condition run by Falck-Ytter et al. (2006), when the toy object reached the bucket, a sound was played and a smiley face on the bucket was animated. This could serve to heighten the desirability of the goal state, encouraging proactive eye movements in a manner consistent with teleological stance theory. Therefore, we ran each of the three conditions with and without end effects. For the conditions with end effects, when the toy entered the bucket, water ripples were shown and the sound of a frog croaking was played. In

the conditions without end effects, no animated ripples were seen or sounds were heard when the frog entered the bucket.

The procedures and analyses mirrored those of the original study as closely as possible. Seventy-two adult participants were randomly allocated to one of six conditions: human agent with (i.e., [1human agent, 1human motion, 1end effects]) or without (i.e., [1human agent, 1human motion, _end effects]) end effects, self-propelled with (i.e., [_human agent, _human motion, 1end effects]) or without (i.e., [_human agent, _human motion, _end effects]) end effects, and the new condition with (i.e., [1human agent, _human motion, 1end effects]) or without (i.e., [1human agent, _human motion, _end effects]) end effects. Participants sat in front of the monitor of a Tobii 1750 eye tracker; after the tracker was calibrated, participants were instructed simply to watch the video that followed. The video comprised 27 trials (the same number used by Falck-Ytter et al., 2006).

A 3 (movement) \times 2 (end effects) analysis of variance examining the average gaze-arrival time relative to the arrival time of the frog (Fig. 1b) produced only a significant main effect of end effects on gaze-arrival time, $F(1, 66) = 7.153$, $p = .007$, $\eta^2_p = .10$ (0.98). Gaze-arrival time at goal was earlier for conditions with end effects ($M = 122$ ms) than those without end effects ($M = 133$ ms).

For each condition, we also compared gaze arrival times to the arrival times of the frog. Significant proactive goal-directed eye movements occurred for the human-agent condition with end effects (i.e., [1human agent, 1human motion, 1end effects]), $t(11) = 4.34$, $p = .001$, $d = 1.25$, and the new (Tiddlywinks) condition with end effects (i.e., [1human agent, _human motion, 1end effects]), $t(11) = 2.38$, $p = .028$, $d = 0.69$, but not for any of the other four conditions, all $t(11)s \leq 1.99$, all p s $\geq .05$, all d s ≤ 0.57 . Most notably, predictive eye movements do not occur for the human-agent condition without end effects (i.e., [1human agent, 1human motion, _end effects]), $t(11) = 0.35$, $p = .728$, $d = 0.10$.

These results allow us to tease apart the relative merits of the MNS explanation of proactive goal-directed eye movements compared to an alternative account based on understanding of goals. Proactive eye movements occur as a function of the combination of the intention of an agent to achieve a goal and the desirability of a goal state, and not as a consequence of whether a human agent is seen moving an object. Thus, our results support teleological stance theory, as well as recent accounts claiming that the MNS is a reflection of action understanding rather than the origins of it (Csibra, 2007).

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