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Infants predict other people's action goals

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Do infants come to understand other people's actions through a mirror neuron system that maps an observed action onto motor representations of that action? We demonstrate that a specialized system for action perception guides proactive goal-directed eye movements in 12-month-old but not in 6-month-old infants, providing direct support for this view. The activation of this system requires observing an interaction between the hand of the agent and an object.

Neurophysiological[1,2] and brain-imaging[3] studies indicate that a mirror neuron system (MNS) mediates action understanding in human adults and monkeys. Mirror neurons were first discovered in the premotor area (F5) of the macaque, and they respond both when the animal performs a particular object-related action and when the animal observes another individual perform a similar action. Thus, mirror neurons mediate a direct matching process, in which observed actions are mapped onto motor representations of that action[4,5].

When performing visually guided actions, action plans encode proactive goal-directed eye movements, which are crucial for planning and control[6,7]. Adults also perform such eye movements when the observed actions are performed by others[8], indicating that action plans guide the oculomotor system when people are observing others' actions as well. As the MNS mediates such matching processes[1,3,4], there is a direct link between MNS activity and proactive goal-directed eye movements during action observation[8].

Recently, a strong claim has been presented about the role of the MNS in human ontogeny. According to the MNS hypothesis of social cognition, the MNS constitutes a basis for important social competences such as imitation, 'theory of mind' and communication by means of gesture and language[4,9]. If this hypothesis is correct, the MNS should be functional simultaneous with or before the infant's development of such competencies, which emerge around 8–12 months of life[10]. Furthermore, according to the MNS theory, proactive goal-directed eye movements during the observation of actions reflect the fact that the observer maps the observed actions onto the motor representations of those actions[8]. This implies that the development of such eye movements is dependent on action development. Therefore, infants are not expected to predict others' action goals before they can perform the actions themselves. Infants begin to master the action shown in our study at around 7–9 months of life[11]. Thus, if the MNS is a basis of early social cognition, proactive goal-directed eye movements should be present at 12 but not at 6 months.

Although habituation studies indicate that young infants distinguish between means and ends when observing actions[12,13], no one has tested the critical question of when infants come to predict the goals of others' actions. Using a gaze-recording technique, we tested the MNS hypothesis by comparing the eye movements of adults (n = 11), 12-month-old infants (n = 11) and 6-month-old infants (n = 11) during video presentations showing nine identical trials in which three toys were moved by an actor's hand into a bucket (Test 1). We compared gaze behavior, consisting of (i) timing (ms) of gaze arrival at the goal (the bucket) relative to the arrival of the moving target and (ii) ratio of looking time in the goal area to total looking time in combined goal and trajectory areas during object movement (see **Supplementary Methods** online and **Fig. 1a**).

In adults, the MNS is only activated when someone is seeing an agent perform actions, not when objects move alone[8]. However, according to the teleological stance theory[14], seeing a human agent is not necessary for infants to ascribe goal-directedness to observed events. This theory states that objects that are clearly directed toward a goal and move rationally within the constraints of the situation are perceived as goal-directed by 12-month-old infants. This implies that seeing an interaction between the actor's hand and the toys is not necessary for eliciting proactive, goal-directed eye movements. By comparing the gaze performance of adults (n = 33) and 12-month-olds (n = 33) in three conditions, we evaluated this alternative hypothesis (Test 2). The first condition, 'human agent', was identical to the one in Test 1 (same data used in both tests). In the 'self-propelled' condition (**Fig. 1a**), the motion was identical to that in the human agent condition except that no hand moved the toys. We also included a 'mechanical motion'

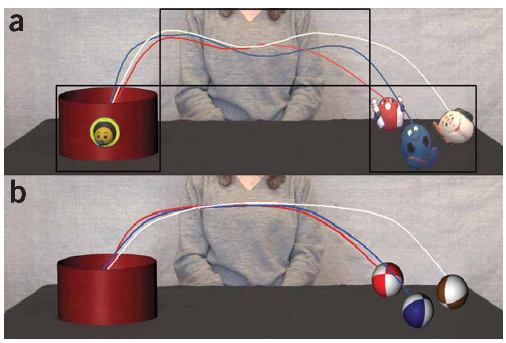

Figure 1 Sample pictures of stimulus videos. (**a**) Stimulus in the human agent and self-propelled conditions with areas of interest (AOIs; black rectangles) and trajectories for each object (colored lines) superimposed. Left AOI was labeled "goal AOI," right AOI was labeled "object AOI," and upper AOI was labeled "trajectory AOI." (**b**) Stimulus in the mechanical motion condition.

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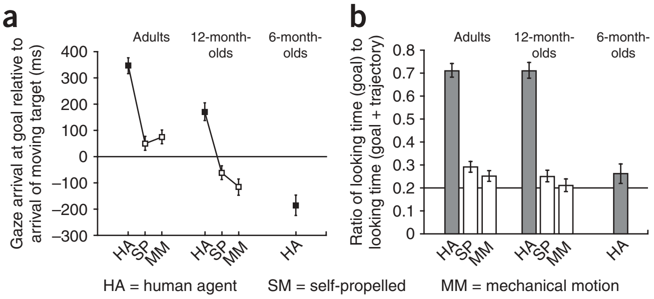

Figure 2 Gaze performance during observation of actions and moving objects. Statistics (means and s.e.m.) are based on all data points for adults (left), 12-month-old infants (middle) and 6-month-old infants (right), respectively. (**a**) Timing (ms) of gaze arrival at the goal relative to the arrival of the moving target. Target arrival is represented by the horizontal line at 0 ms. Positive values correspond to early arrival of gaze at the goal area. (**b**) Ratios of looking time at the goal area to total looking time in both goal and trajectory areas during object movement. The horizontal line at 0.2 represents the ratio expected if subjects tracked the moving target.

condition (**Fig. 1b**). We assigned subjects randomly to the conditions, and sample sizes were equal.

Parents and adult subjects provided written consent according to the guidelines specified by the Ethical Committee at Uppsala University, and the study was conducted in accordance with the standards specified in the 1964 Declaration of Helsinki. Preliminary analyses of the data distributions confirmed normality and homogeneity of variance. We used statistical tests (one-way ANOVAs and single-sample t-tests) with two-tailed probabilities ($\alpha = 0.05$) unless otherwise stated.

In Test 1, we found that in the human agent condition, there was a strong effect of age on predictive eye movements to the action goal ($F_{2,30} = 19.845$, $P < 0.001$; **Fig. 2a** and **Supplementary Table 1** online). Post hoc testing (Bonferroni) showed that there was no significant difference between the adults and the 12-month-olds, whereas the differences between both these groups and the 6-month-olds were significant ($P < 0.001$). Furthermore, both adults ($t_{10} = 5.498$, $P < 0.001$) and 12-month-olds ($t_{10} = 2.425$, $P = 0.036$) shifted their gaze to the goal of the action before the hand arrived, whereas 6-month-olds shifted their gaze to the goal after the hand arrived ($t_{10} = 3.165$, $P = 0.01$). The two predictive groups were further analyzed to check for learning effects using Bonferroni corrected paired-samples t-tests. There was no effect of trial number ($n = 9$) on timing. From the first to the second action of each trial, gaze lead times increased from 247 to 465 ms in adults ($t_{10} = 3.186$, $P = 0.01$) and from –18 to 334 ms in 12-month-olds ($t_{10} = 3.516$, $P = 0.006$; for further details see **Supplementary Table 2** online).

In the human agent condition, the subjects in the different age groups distributed their fixations differently across the movement trajectory ($F_{2,30} = 12.015$, $P < 0.001$; **Fig. 2b** and **Supplementary Table 3** online). Post hoc testing (Bonferroni) showed that there was no significant difference between the adults and the 12-month-olds, whereas both these groups differed from the 6-month-olds ($P < 0.001$). Adults ($t_{10} = 8.073$, $P < 0.001$) and 12-month-olds ($t_{10} = 8.625$, $P < 0.001$) looked significantly longer at the goal area during target movement than would be expected if subjects tracked the target, whereas the 6-month-olds did not (see **Supplementary Methods** online).

In Test 2, we found that in adults and 12-month-olds, predictive eye movements were only activated by a human hand moving the objects ($F_{2,30} = 7.637$, $P = 0.002$ and $F_{2,30} = 7.180$, $P = 0.003$, respectively; **Fig. 2a**). Post hoc testing (Bonferroni) showed that for adults, the human agent condition was significantly different from the self-propelled ($P = 0.004$) and mechanical motion ($P = 0.009$) conditions. 12-month-olds showed the same pattern ($P = 0.019$ and 0.004, respectively). Gaze did not arrive significantly ahead of the moving object in the two control conditions for adults and in the self-propelled condition for the 12-month-olds. The gaze of the 12-month-olds arrived at the goal significantly after the object in the mechanical motion condition ($t_{10} = 4.253$, $P = 0.002$).

Spatial distribution of fixations was different between the conditions (**Fig. 2b**) in both adults ($F_{2,30} = 17.782$, $P < 0.001$) and 12-month-olds ($F_{2,30} = 36.055$, $P < 0.001$). Post hoc testing (Bonferroni) showed that both adults and 12-month-olds were more goal-directed in the human agent condition than in the self-propelled and mechanical motion conditions ($P < 0.001$ in all cases). Furthermore, in the two control conditions, the distributions of fixations for both adults and 12-month-olds did not differ significantly from what would be expected if subjects tracked the objects.

The present study supports the view that action understanding in adults results from a mirror neuron system that maps an observed action onto motor representations of that action[1,3,5,8]. More importantly, we have demonstrated that when observing actions, 12-month-old infants focus on goals in the same way as adults do, whereas 6-month-olds do not (Test 1). The performance of the 6-month-olds cannot originate from a general inability to predict future events with their gaze, because 6-month-olds predict the reappearance of temporarily occluded objects[15]. Finally, in terms of proactive goal-directed eye movements, we found no support for the teleological stance theory claiming that 12-month-old infants perceive self-propelled objects as goal-directed (Test 2).

In conclusion, proactive goal-directed eye movements seem to require observing an interaction between the hand of an agent and an object, supporting the mirror neuron account in general. Furthermore, infants develop such gaze behavior during the very limited time frame derived from the MNS hypothesis of social cognition. During the second half of their first year, infants come to predict others' actions. The mirror neuron system is likely to mediate this process.

Note: Supplementary information is available on the Nature Neuroscience website.

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COMPETING INTERESTS STATEMENT

The authors declare that they have no competing financial interests.

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