

The Evolution of Social Cognition: Goal Familiarity Shapes Monkeys' Action Understanding

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Summary

What is the evolutionary origin of the human ability to understand and predict the behavior of others? Recent studies suggest that human infants' early capacity for understanding others' goal-directed actions relies on nonmentalistic strategies [1–8]. However, there is no consensus about the nature of the mechanisms underpinning these strategies and their evolutionary history. Comparative studies can shed light on these controversial issues. We carried out three preferential looking-time experiments on macaques, modeled on previous work on human infants [1–5], to test whether macaques are sensitive to the functional efficacy of familiar goal-related hand motor acts performed by an experimenter in a given context and to examine to which extent this sensitivity also is present when observing non-goal-related or unusual goal-related motor acts. We demonstrate that macaque monkeys, similar to human infants, do indeed detect action efficacy by gazing longer at less efficient actions. However, they do so only when the observed behavior is directed to a perceptible and familiar goal. Our results show that the direct detection of the functional fitness of action, in relation to goals that have become familiar through previous experience, is the phylogenetic precursor of intentional understanding.

Results and Discussion

The evolutionary origin of the human ability to understand and predict the behavior of others has become a matter of controversy since the apparent inability of nonhuman primates to understand others as intentional agents [9] was recently challenged. In fact, there is evidence that chimps, when engaged in a competitive setting, are able to infer what others know on the basis of where they are looking [10]. Even more impressively, it has been shown that rhesus monkeys can establish a cognitive link between seeing and knowing [11] and hearing and knowing [12]. These results show that nonhuman primates

possess the ability to understand what others know about the world on the basis of observable behavioral cues.

We decided to address the issue of the evolution of human ability to understand the intentional behavior of others by studying how macaque monkeys evaluate the efficacy of the observed motor behavior of a human agent in terms of the adequacy between means and ends in a given context. To that purpose, we carried out three preferential looking-time experiments modeled on Gergely et al.'s previous work with infants [1] and substituted their computer-generated stimuli with real actions performed in front of the monkeys by a human agent. In experiment 1, macaque monkeys were tested to assess their sensitivity to the adequacy between the means (the type of reaching-to-grasp trajectory) and the goal (grasping an object) of observed goal-directed motor acts according to the contextual constraints (presence or absence of an obstacle). In experiment 2, macaque monkeys were tested to evaluate to which extent this sensitivity correlates with the goal relatedness of the monkeys' observed motor acts by showing them non-goal-related movements. Finally, experiment 3 was designed to assess whether the observation of any goal-directed motor act, regardless of whether it is part of the monkeys' behavioral repertoire, would trigger the sensitivity to its means-end adequacy.

In contrast to previous studies [1–7, 13], we introduced quantitative methods to assess the monkeys' gaze by means of an infrared eye-tracking device. We also measured the kinematics components of the actions observed by the monkeys via a high-resolution video motion analysis (see the [Supplemental Data](#)).

Experiment 1

Experiment 1 included two testing sessions (Figure 1). In the experimental session, monkeys (n = 6) were familiarized with a human experimenter who moved her hand above an obstacle to grasp an object (see [Movie S1](#)). In the following two test events, the obstacle was removed. In one test event (motor acts were congruent to the physical context), the experimenter canonically reached and grasped the object by following a novel, straight-line trajectory (see [Movie S2](#)). In the other test event (motor acts were incongruent to the physical context), the experimenter reached up and grasped the object by following a curvilinear path identical to the one executed during the familiarization trial to bypass the obstacle (see [Movie S3](#)).

If during the familiarization trial monkeys interpreted the observed motor act as the shortest path to the goal with respect to the context, a motor act displaying the same curvilinear path to the goal in a context free from any obstacle should have triggered monkeys' attention (expressed by a greater amount of looking time) more often than when observing a motor act that follows a shorter, straight-line path. Alternatively, if monkeys attended to the surface structure of the observed motor act without relating it to the target object or the context, we expected a reverse pattern of gaze behavior during test trials, indicating sensitivity to novel actions.

In the control session, the same monkeys (n = 6) were familiarized with a motor act identical to that used in the

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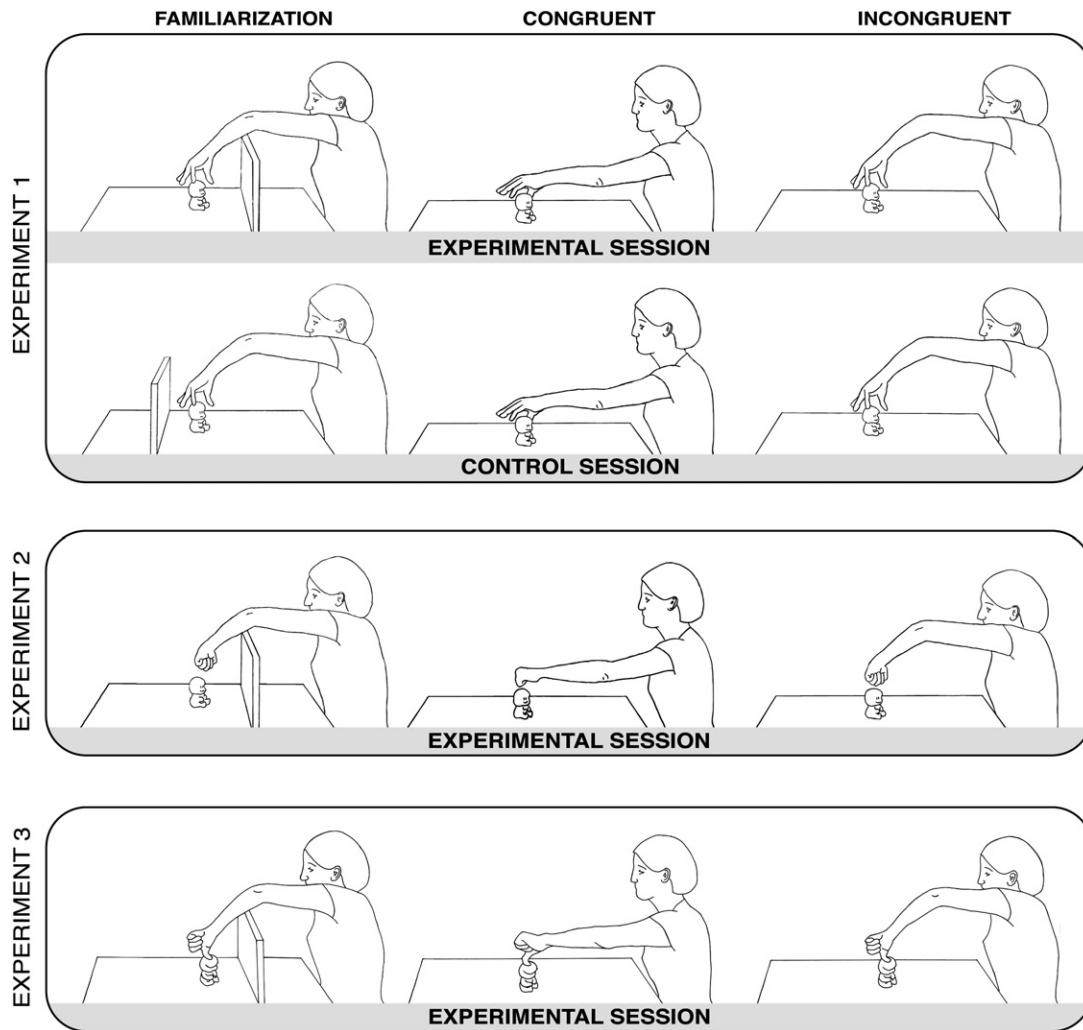


Figure 1. Testing Conditions in Experiments 1, 2, and 3

The top two panels illustrate the familiarization condition followed by the congruent and incongruent test events in both experimental and control sessions in experiment 1. The middle panel shows the familiarization condition followed by the congruent and incongruent test events presented in experiment 2. The bottom panel illustrates the familiarization condition followed by the congruent and incongruent test events presented in experiment 3.

experimental session (curvilinear trajectory, see Figure 1) but executed in a situation where the location of a physical obstacle didn't block the direct access to the target object (see Movie 4). The familiarization trial was then followed by the same two test events presented during the experimental session (see Movies S2 and S3). The rationale was to assess the importance of contextual features during motor-act observation and prediction. First, an analysis of variance (ANOVA) with repeated measures, with session (experimental or control) as the within-subjects variable, was conducted on the normalized (Arcsine transformation) mean looking time for the familiarization events (for further details on the statistical analyses, see the Supplemental Data). Results revealed no session effect on looking time ($F_{(1,5)} = 0.138$, $p = 0.726$). Thus subjects' familiarization with the events was comparable between both sessions.

Second, in order to assess looking-time differences between test events for both sessions and to control for the presentation order of test events, a $2 \times 2 \times 2$ repeated-measures ANOVA was carried out on the normalized mean looking time, with session (experimental or control) and condition

(congruent or incongruent) as within-subjects factors and order (congruent first or incongruent first) as the between-subjects factor. Results revealed no significant main effect or interaction for order (all p values are >0.05). Thus this variable was collapsed in the subsequent analyses. The interaction between the factors session \times condition was significant, $F_{(1,4)} = 28.576$, $p = 0.006$. A separate two-way ANOVA (session \times condition) was therefore performed, followed by Tukey's post-hoc test. The results (Figure 2A) showed that in the experimental session, monkeys looked significantly longer at the incongruent events (mean = $43.26 \pm SD = 10.12$) than at the congruent events (24.76 ± 7.42), $p = 0.001$. A sign test confirmed that all monkeys (100%) behaved the same way ($p = 0.031$). This difference, however, didn't reach significance during the control session, $p = 0.692$; sign test, n.s. (Figure 2B).

Because it is known that monkeys use gaze information as an indicative behavioral cue (see [14] for a review), we compared the amount of time monkeys spent looking at the experimenter's face (see the Supplemental Data) when congruent and incongruent events were observed. Results from the two-way ANOVA (session \times condition) showed that only the

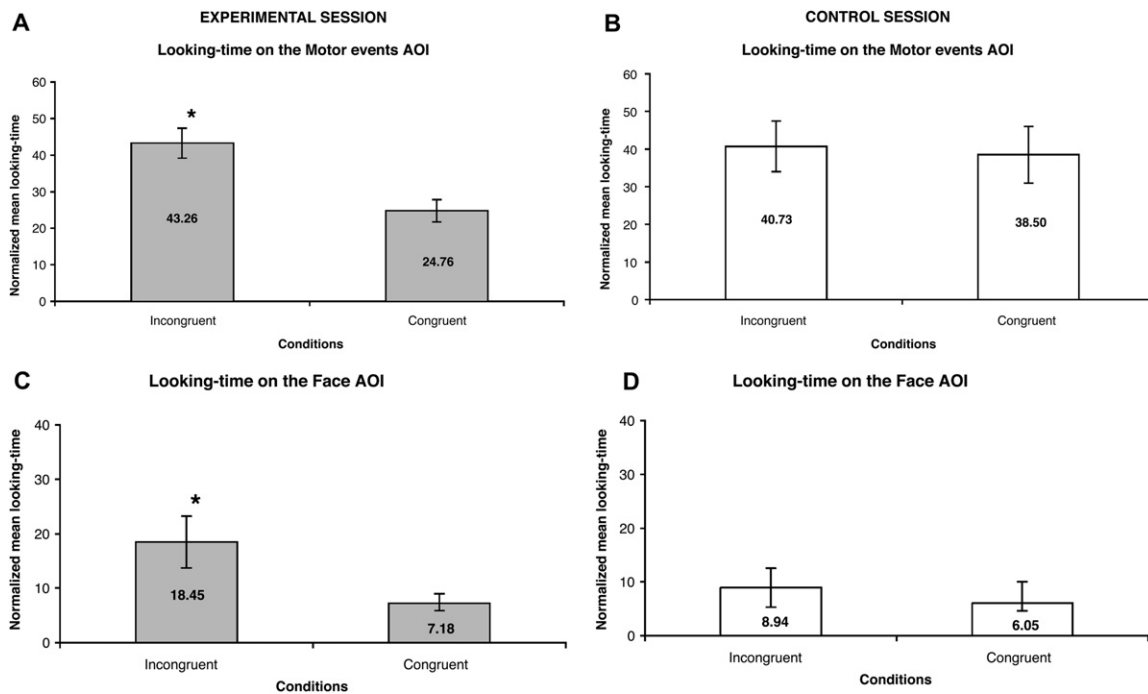


Figure 2. Looking-Time Analysis in Experiment 1

(A and B) Shown are the normalized mean looking-time \pm SEM directed to the motor events area of interest (AOI) in the experimental session (A) and in the control session (B).

(C and D) Shown are the normalized mean looking-time \pm SEM directed to the face AOI in the experimental session (C) and in the control session (D). * $p < 0.05$.

main condition factor was significant, $F_{(1,5)} = 15.222$, $p = 0.011$. Results from Tukey's post-hoc test demonstrated that monkeys looked longer at the experimenter's face during incongruent events than during congruent ones, $p = 0.011$. We further explored the looking time with a sample-paired t-test for both the experimental and control sessions. The results showed that during the experimental session, monkeys explored the experimenter's face significantly more when she performed incongruent actions (18.45 ± 11.65) compared to when she performed congruent actions (7.18 ± 4.47), $t(5) = 3.496$, $p = 0.017$ (Figure 2C). No significant differences emerged during the control session, $t(5) = 1.41576$, $p = 0.216$ (Figure 2D).

Experiment 2

In experiment 2 (Figure 1), we investigated the influence of the goal directedness of the experimenter's movements on the modulation of the monkeys' looking time. To this purpose, we familiarized the monkeys ($n = 6$) to the observation of a non-goal-related curvilinear trajectory of the experimenter's arm in which she brought her hand above the obstacle and stopped it in a fist posture above the target object without touching it (see Movie S5). In the following two test events, the obstacle was removed. In one test event (trajectory congruent with the physical context), the experimenter moved her hand toward the target object by following a novel straight-line trajectory and stopped it in a fist posture without touching it (see Movie S6). In the other test event (trajectory incongruent with the physical context), this movement was executed by following a curvilinear path identical to the one performed during the familiarization trial to bypass the obstacle (see Movie S7). If the monkeys' appreciation of means-ends

adequacy depended on their sensitivity to the goal relatedness of observed movements, the absence of a concrete goal shouldn't evoke any attentional enhancement during the observation of incongruent hand trajectories. A one-way ANOVA showed no difference between the amount of looking-time during the familiarization condition of both experiment 2 and experiment 1 (experimental session) ($F_{(1,10)} = 1.182$, $p = 0.302$). Two separated repeated-measures ANOVAs showed no main effect of condition on the amount of looking time during both test events, $F_{(1,5)} = 3.514$, $p = 0.119$ (Figure 3A) and on the amount of looking time directed to the experimenter's face during test events observation, $F_{(1,5)} = 0.341$, $p = 0.585$ (Figure 3B).

Experiment 3

In experiment 3 (Figure 1), we explored whether the evaluation of the action's efficiency in a certain context is extended to goal-related motor acts the monkeys most likely never observed before and certainly never executed, such as lifting an object with the thumb. To this purpose, monkeys ($n = 5$) observed the actions of a human experimenter who had a piece of Velcro wrapped around the tip of her thumb. They were first familiarized to the observation of the experimenter moving her hand above an obstacle to contact and lift the target object (the same one used in experiment 1) with the thumb (see Movie S8). In the following test events, the obstacle was removed. In one test event, the experimenter contacted and lifted the object by following a novel, straight-line trajectory (see Movie S9), whereas in the other test event the experimenter executed this action by following a curvilinear path identical to the one monkeys had been familiarized with (see Movie S10).

If the observation of any goal-directed motor act automatically triggered a particular sensitivity to its efficiency within

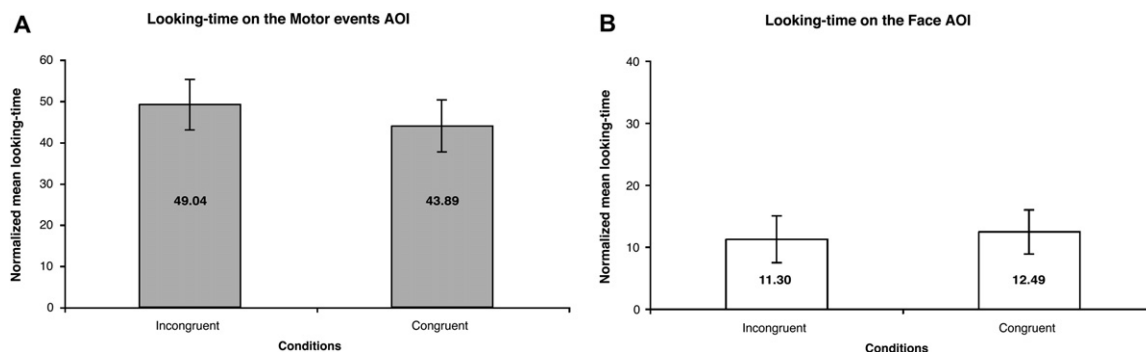


Figure 3. Looking-Time Analysis in Experiment 2

Normalized mean looking time \pm SEM directed to the motor events AOI (A) and to the face AOI (B).

a given context, then watching a human agent achieve her/his goal through an inefficient trajectory should provoke a reliably greater attentional enhancement than would watching her/him following a path congruent to the context (see results of experiment 1). On the other hand, if the appreciation of the means-ends adequacy was restricted to the goal-directed motor acts previously practiced by the monkey, the observation of unfamiliar goal-related motor acts shouldn't evoke any attentional enhancement even when following incongruent trajectories. A one-way ANOVA showed no difference between the amount of looking time during the familiarization condition of experiments 3 and 1 (experimental session), ($F_{(1,9)} = 0.010$, $p = 0.920$). Two separated repeated-measures ANOVAs showed no main effect of condition on the amount of looking time during both test events, $F_{(1,4)} = 6.796$, $p = 0.596$ (Figure 4A) and on the amount of looking time directed to the experimenter's face during test-event observation, $F_{(1,4)} = 0.402$, $p = 0.560$ (Figure 4B).

Finally, in order to compare the results of experiments 1 and 3, a crossexperiment mixed-design ANOVA with experiment (experiment 1, experimental session; experiment 3) as a between-factor and condition (congruent or incongruent) as a within-factor was conducted. Results yielded a significant interaction between experiment and condition, $F_{(1,9)} = 11.565$, $p = 0.008$. Results from Tukey's post-hoc test showed that in experiment 1 (experimental session), monkeys looked significantly longer at the incongruent events than at the congruent ones ($p = 0.0003$), whereas no significant differences occurred between those two conditions in experiment 3, $p = 0.132$.

Conclusions

Results from experiment 1 show that macaque monkeys, similar to 9- to 12-month-old human infants, detect the goal of an observed motor act and, according to the physical characteristics of the context (position of the obstacle), construe expectancies about the most likely action the agent will execute in a given context and therefore react differently to the same goal (object grasping) when accomplished by different means (type of hand trajectory). Monkeys' sensitivity to means-ends adequacy was further corroborated by their longer exploration of the experimenter's face in the experimental incongruent condition. It could be hypothesized that when the experimenter started to execute motor acts that violated the expected means-ends adequacy that monkeys tried to disambiguate the situation by searching for additional cues such as exploring experimenter's gaze direction and/or facial expression.

How do the present data relate to the evidence of Gergely et al. [1] on human infants given that our paradigm was modeled on theirs? Csibra and Gergely [2] proposed that the development in ontogeny of a full-blown, mentalistic intentional stance [15] is preceded by a nonmentalistic teleological stance based on a similar rationality principle applied to factual reality and not on mental states. Teleological reasoning is described as a "normative evaluation of actions based on the principle of rational action, which allows for the assessment of the relative efficiency of the action performed to achieve the goal within the situational constraints given" [16]. According to the teleological hypothesis, revolving around an emerging theory of

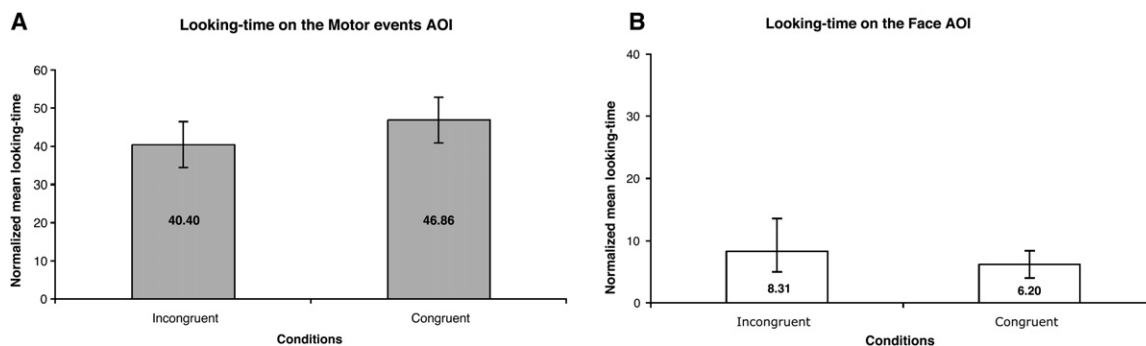


Figure 4. Looking-Time Analysis in Experiment 3

Normalized mean looking time \pm SEM directed to the motor events AOI (A) and to the face AOI (B).

rational action, infants assume that agents pursue their goal in the most efficient manner available given the constraints of reality. Thus, 9- and 12-month-old infants refer to this interpretational system to attribute goals to humans [4] as well as to nonhuman [1–3] agents.

The results of our experiment 1, in spite of the different types of stimuli employed, show an apparent similarity with those obtained by Gergely et al. [1]. Experiment 2 demonstrates that macaque monkeys' evaluation of the action mean employed in a certain context strictly depends upon the achievement of a goal state (e.g., a motor act producing an observable change in the state of reality). Just like 12-month-old human babies observing actions directed to an absent target object [4], our results show that when no interaction exists between effector and target object with the resulting lack of causal effect in reality, the evaluation of the observed motor act's fitness to the physical constraints of its context becomes impossible.

The results of our first two experiments demonstrate that macaque monkeys pay attention to the relation between the observed motor acts and their observable outcome within the constraints of a certain context (see also [17]). The results from experiment 3, though, reveal that the specific sensitivity to means-ends adequacy disappears when the goal-related behavior and its end state are unfamiliar to the observing monkeys. However, given that the action in experiment 3 was both visually unfamiliar and absent from monkeys' action repertoire, our data do not enable us to firmly establish whether the monkeys' failure to see the observed action as goal directed was due to either a lack of motor or perceptual familiarity. Both hypotheses are, in principle, equally possible. The issue of whether motor training or extensive perceptual exposure would allow monkeys to extract the action's goal remains to be assessed through future experiments. Nevertheless, we think that evidence both from monkeys and humans makes it reasonable to propose the "lack of motor expertise" hypothesis as a viable option. Let us see why.

Single neurons recording studies in macaque monkeys revealed the existence of a class of motor neurons (mirror neurons) that discharge during both the execution and the observation of goal-directed motor acts [18, 19]. It has been proposed that the mirror neuron system (MNS), by matching observed, implied, or heard goal-directed motor acts on their motor representation in the observer's motor system, allows a direct form of action understanding through a mechanism of embodied simulation [20].

Recent neurophysiological studies have reported that a particular class of ventral premotor mirror neurons starts to respond to the observation of unfamiliar actions after extensive visual exposure to them [21] or after motor training [22]. The results of both experiments seem to suggest that when an action performed by others becomes familiar, independently from the perceptual or motor source of its familiarization, it is nevertheless always mapped onto the motor representation of a similar goal (to take possession of an object) belonging to the observing individual (on the impact of visual familiarity on motor representations, see also [23, 24]).

A similar MNS involving homolog cortical areas has been discovered in the human brain [18]. Even more strikingly, several brain-imaging studies have shown that the intensity of the MNS activation during action observation depends on the similarity between the observed actions and the participants' action repertoire [25–30]. In particular, one fMRI study [27] focused on the distinction between the relative contribution of

visual and motor experience in processing an observed action. The results revealed greater activation of the MNS when the observed actions were frequently performed with respect to those that were only perceptually familiar but never practiced. Finally, it has been shown that motor familiarity, but not perceptual familiarity, influences the capacity of 3-month-old infants to extract goals from observed actions [5].

Our study does not provide direct evidence about the neural mechanisms underpinning the present results. However, we believe that a plausible explanation could be that macaques evaluate the observed human acts by mapping them on their own motor representation through the activation of the MNS. Furthermore, we propose that the monkeys' experience in programming and executing goal-directed hand motor acts within certain contextual constraints would result in an automatic activation of the very same neural clusters when observing a motor act that reflects a similar adequacy to the context [19]. It is possible that when the monkeys are familiarized with an observed motor act consonant with their motor repertoire (like passing over an obstacle to grasp an object), its resulting embodied simulation automatically drives the perception of the other experimenter as a "like-me" entity [31], thus enabling the observer to predict the trajectories of future actions in different contexts (see congruent and incongruent test events). This, however, appears to be true only to the extent that observed motor acts are familiar to the observer, whereas familiarization with inadequate motor acts (experiment 1, control session), non-goal-related movements (experiment 2), or unfamiliar goal-related motor acts (experiment 3) does not allow any simulation and prediction.

One final point worth discussing is related to the possible different level of complexity of the actions displayed in experiments 1 and 3 as a potential source of the difference in results obtained in these experiments. Yet, if the displayed actions are parsed as a sequence of goal-related motor acts, both of them appear to be composed of two sequentially chained motor acts ("reach-to-grasp" in experiment 1 and "reach-to-lift" in experiment 3), thus showing a similar level of complexity.

Let us finally turn to the relevance of our results to the ontogeny of action understanding. An increasing body of experimental evidence shows that human infants develop early action understanding abilities within the first year of life [32, 33] and that the capacity to detect the goal of another's action is closely related to the infants' prior motor experience [5–8]. Furthermore, a recent study demonstrates that 3-day-old human neonates [34], similar to other species of animals such as chicks [35], show an inborn predisposition to attend to biological motion. Such a mechanism has high evolutionary relevance because it allows the act of recognizing the movement of others in order to make an appropriate response [36]. Although no strong evidence directly links human infants and nonhuman primates' ability to understand others as goal-oriented agents to the natural tendency to attend to biological motion, it seems reasonable to hypothesize that these two abilities are grounded on a common implicit embodied mechanism. Such a mechanism might account for the phylogenetic evolution of goal attribution [37, 38].

Taken together, our results suggest that nonhuman primates and human infants possess a similar ability to recognize and evaluate the adequacy of goal-related behavior, which, however, seems to operate at a broader level in infants. The present evidence shows that perceptual and/or motor expertise are important elements for the evolution of humans' capacity of understanding the intentional behavior of others.

We propose that the direct detection of the functional fitness of action, in relation to goals that have become familiar, is the phylogenetic precursor of intentional understanding.

Supplemental Data

Experimental Procedures, three figures, and ten movies are available online at <http://www.current-biology.com/cgi/content/full/18/3/227/DC1/>.

Acknowledgments

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