Evolving the Capacity to Understand Actions, Intentions, and Goals

Marc Hauser[1,*] and Justin Wood[2]

[1] Departments of Psychology and Human Evolutionary Biology, Harvard University, Cambridge, Massachusetts 02138; email: mdh102559@gmail.com

[2] Department of Psychology, University of Southern California, Los Angeles, California 90089

*Both authors contributed equally to this manuscript.

Key Words

Abstract

We synthesize the contrasting predictions of motor simulation and teleological theories of action comprehension and present evidence from a series of studies showing that monkeys and apes—like humans—extract the meaning of an event by (*a*) going beyond the surface appearance of actions, attributing goals and intentions to the agent; (*b*) using details about the environment to infer when an action is rational or irrational; (*c*) making predictions about an agent's goal and the most probable action to obtain the goal, within the constraints of the situation; (*d*) predicting the most probable outcome of actions even when they are physiologically incapable of producing the actions; and (*e*) combining information about means and outcomes to make decisions about social interactions, some with moral relevance. These studies reveal the limitations of motor simulation theories, especially those that rely on the notion of direct matching and mirror neuron activation. They provide support, however, for a teleological theory, rooted in an inferential process that extracts information about action means, potential goals, and the environmental constraints that limit rational action.

Contents

INTRODUCTION

To understand another's action, it is necessary to go beyond the movement of limbs in space. One must infer that each action is directed toward proximate and ultimate goals, linked to the individual agent. Making this inference enables us to comprehend novel actions, predict future actions, and learn from the prior successes and failures of earlier actions. Further, by probing beneath the surface appearance of actions, we are able to distinguish between intentionally and accidentally caused harms; this capacity is a critical stepping-stone for building a moral agent, an individual who can evaluate both the means and the consequences of actions and then decide what the moral high ground should look like.

Although interest in action comprehension has a long, interdisciplinary history (Davidson 2001, Hart & Honore 1985, Kirsh 1991, Michotte 1962), recent work in the neurosciences and developmental psychology has reinvigorated research, raising new problems, especially in terms of the coordination of action production and perception. For example, although we appear to simulate our own motor production routines when observing the actions of others, damage to motor systems need not diminish perceptual and conceptual comprehension. Further, infants generate rich representations of others' goals and intentions without being able to produce anything comparable (Gallese et al. 2004; Gergely & Csibra 2003; Mahon & Caramazza 2008, 2009).

Recent work on nonhuman animals, especially the monkeys and apes, has entered these debates, allowing further elaboration of at least three different questions that we address here. First, to what extent are the mechanisms subserving action comprehension, especially the capacity to infer goals and intentions, shared across species and implemented in a variety of contexts? Second, to what extent does an animal's motor capacity contribute to action comprehension, and how has the evolution of particular motor capacities in our own species contributed to action comprehension? Third, to what extent do the domain-general mechanisms that support action comprehension (e.g., general processes of visual perception, categorization, and memory) interface with other systems (e.g., folk intuitions about goals and intentions) to support more socially complex interactions that arise in morally relevant situations? In a nutshell, do nonhuman animals have what we might properly consider the precursors or foundations to human morality?

We begin our discussion by providing a succinct review of the dominant theories in the field, starting with simulation/embodiment and

ending with the teleological stance. We then turn to recent behavioral experiments on primates that help adjudicate between these different perspectives and open the door to new predictions and experiments.

Mental Simulation and Embodiment

Since Rizzolatti and colleagues (di Pellegrino et al. 1992; Gallese et al. 1996; Rizzolatti et al. 1996, 1999) made their discovery of mirror neurons in the macaque premotor cortex, the cognitive neurosciences have witnessed an explosion of new studies looking at the relationship between action production and perception systems. Two dominant theories—simulation (Gallese & Goldman 1998) and embodied cognition (Lakoff & Johnson 1999)—suggest that action comprehension relies critically on the capacity to produce the same action. Thus, I understand hair cutting because I can replay the act of holding and cutting hair with scissors, or because my concept of "scissor" entails not only information about the object but also information about what to do with the object (Barsalou et al. 2003, Pulvermuller 2005). However, the observation of motor system activation does not license the conclusion that motor information is necessary or causally involved in action understanding (Mahon & Caramazza 2008). It is equally plausible that action understanding involves purely perceptual, nonmotor processes, and that once an action is understood, it interfaces with the motor system that provides instructions for how to use an object. Thus, we have a concept of "scissor" that includes abstract details of the object (shape, size, material) together with instructions for how to use it. On this view, understanding the meaning of an object or action involves, but does not require, a motor representation. At present, none of the existing data provide definitive evidence in support of one side or the other. Thus, although verbs of action, together with the perception of action, trigger corresponding motor areas (Pulvermuller 2005), these studies can't distinguish between concepts that entail motor information and concepts that do not but that

interface to the motor systems with instructions. Similarly, although apraxic patients can't produce motor-appropriate actions with objects that they semantically comprehend, this doesn't mean that action comprehension is entirely divorced from action production. Specifically, these patients incurred damage in adulthood, after the relevant ontological competence had already been acquired.

The Teleological Stance

Though neither simulation theory nor embodied cognition can provide a complete account of action comprehension, both point to the significant interfaces between action production and perception systems. The teleological stance is one theoretical approach that can account for action comprehension in cases where the observer lacks a motor routine of the observed action (Gergely & Csibra 2003). On this view, interpreting another's actions relies on an inferential process that considers the target goal and the environmental constraints that limit or facilitate goal achievement. Thus, if we witness an agent illuminating a light switch with his knee, while both hands are free, this strikes us as irrational. If this same knee-switch action arises while the agent holds books in his hands, we conclude that the agent is acting in a goal-directed, rational fashion, given constraints on using his hands. Importantly, this theory has been used to argue that infants show great sensitivity to the environmental contexts in which agents act in and on the world, using this information to infer goals (Csibra et al. 1999, 2003; Csibra & Gergely 1998; Gergely et al. 1995, 2002; Gergely & Csibra 2003). Furthermore, a wide variety of animal studies (reviewed below) provide parallel support (Buttlemann et al. 2007, Range et al. 2007, Rochat et al. 2008, Wood et al. 2007b). Finally, when such events are presented to human subjects in a scanner (Brass et al. 2007), the blood-oxygen-level-dependent (BOLD) response reveals selective activation in the superior-temporal sulcus (STS) as opposed to in the mirror neuron system (e.g., inferior frontal gyrus, premotor

cortex); this suggests that the STS is critically involved in the processing of intentionally mediated actions and in the absence of motor input.

Integrating insights from both motor-rich (simulation, embodiment) and motor-poor (teleological) theories of action comprehension is attractive as they provide different angles on the same problem, set up different predictions about the psychological components of action comprehension, and enable a broad comparative approach to understanding how organisms interpret and predict the actions of others.

Action Comprehension in a Comparative Context

We suggest that behavioral studies of non-human primates can enrich the study of action comprehension in unique ways (Wood & Hauser 2008). First, such studies shed light on its evolutionary origins by revealing whether nonhuman primates and human infants and adults recruit similar mechanisms during action comprehension. Many of the studies reviewed here, for example, suggest that some components of action comprehension are shared with species across the animal kingdom; we discuss this topic in more detail below.

Second, much of the evidence in favor of motor simulation comes from physiological studies with macaque monkeys. In a series of now classic experiments, Rizzolatti and colleagues discovered that some neurons in area F5 of the macaque premotor cortex activate both when an individual observes an experimenter act on an object and when the individual acts in the same way (Rizzolatti et al. 1996, 1999, 2001b). Given the parallel pattern of activation for the production of an action and the perception of the same action, these cells have been named mirror neurons. These neurons are highly sensitive to the details of an event, especially the motor patterns underlying reaching and grasping an object considered as a goal. For example, whereas some neurons fire both during the observation and execution of a hand grasping an object with pincer grip

(the thumb and index finger), the same neurons do not fire when a set of pliers grasps the same object (Rizzolatti et al. 1996, 2001b). Despite the wealth of neurophysiological data, however, there is little research connecting the physiological activity of these neurons to behavior, especially social behavior. Filling in this gap is particularly important given that the mirror neuron system in humans has been argued to support imitation, mental state attribution, empathy, and language (see below), processes for which there is either no evidence or very thin evidence in primates. The majority of evidence linking these capacities to the mirror neuron system is correlational (i.e., mirror neurons activate both during action observation and production), making it virtually impossible to determine whether and in what ways the mirror neuron system supports these capacities. With regard to action comprehension, for example, the mirror neuron system might reflect processes that are either necessary or sufficient for computing the intentional state of an actor (Rizzolatti et al. 2001b), or they might reflect processes that are not directly related to action comprehension (Csibra 2007), such as preparation for imitation. Studies of action comprehension in free-ranging animals can provide a unique perspective on this issue by examining whether their spontaneous behavior accords more closely with the predictions of motor simulation, the teleological stance, or some combination of the two. Further, and as discussed in detail below, studies of nonhuman animals can provide causal evidence regarding whether motor capacities are necessary for action comprehension (Wood et al. 2007a).

Third, studies of nonhuman animals allow more control over an individual's experiences, critical for testing the necessary and sufficient processes for action comprehension and enactment. We can teach animals how to perform new actions, use species with restricted motor capacities (e.g., animals vary considerably in their dexterity), and modify an individual's visual experiences (e.g., by restricting their experience of seeing others perform actions). This type of experimental control turns out

to be crucial for distinguishing between motor simulation and the teleological stance with regard to action comprehension because individuals that develop in a normal environment will both have motor experience of their own actions as well as visual experience of seeing others act in motorically familiar ways. Thus, in these animals, it is impossible to distinguish the respective roles of motor and visual experiences in action comprehension. However, when these experiences can be controlled, it becomes possible to isolate their respective roles for action comprehension.

Action Comprehension in Nonhuman Primates

There is a rich comparative literature focusing on how animals respond to different behaviors, including their social interactions and communicative signals. Here we focus on recent behavioral work with macaques (*Macaca*), given that this genus was targeted for the original physiological studies (species *nemestrina* in the case of cellular recordings, *mulatta* in the case of behavior) and that the experiments were explicitly designed to test different aspects of the simulation and teleological hypotheses (Hauser et al. 2007; Wood et al. 2007a,b, 2008).

In a series of studies designed to map out how rhesus monkeys respond to different aspects of an action in the service of drawing inferences about the agent's goals and intentions (Wood et al. 2007b, 2008), an experimenter presented two potential food sources (overturned coconut shells) to a subject, acted on one, and then walked away, allowing the subject to selectively approach. Although coconuts are native to the island on which these animals live, rhesus cannot open the hard outer shells themselves and, therefore, only obtain the desired inner fruit when the coconuts have been opened and discarded by a human. Thus, it logically follows that if rhesus monkeys comprehend the experimenter's action as goal directed, then they should selectively approach the coconut contacted as this maximizes the odds of obtaining food.

Results showed that rhesus selectively approached the targeted container when the experimenter grasped the coconut with his hand, foot, or with a precision grip involving the pointer finger and thumb (**Figure 1**). Control conditions ruled out the possibility that rhesus approached the contacted coconut shell because they preferred to inspect objects handled by a human experimenter without making the inference that the experimenter was acting on a coconut containing hidden food (Wood et al. 2008). These results support the hypothesis that, in the absence of training, rhesus monkeys spontaneously infer the goals and intentions underlying a human experimenter's actions.

Further experiments examined the limits of this ability by testing whether rhesus comprehend the meaning of actions that fall outside of their species-typical motor repertoire. Rhesus do not spontaneously use tools in the wild (although they can be trained to do so in laboratory settings). Thus, for this population of individuals, actions involving tools are not part of the species-specific motor repertoire. Accordingly, Wood et al. (2008) examined whether rhesus comprehend tool-related actions as goal directed in this two-option social foraging context. In striking contrast to their behavior when observing actions that are part of the motor repertoire, rhesus failed to use the tool-related actions as cues to infer the location of hidden food. When the experimenter touched one of the coconuts with a pole or a machete, or grasped the coconut with a pair of pliers—all familiar objects used by personnel on the island—rhesus approached the two coconuts at chance levels (see **Figure 1**). Their failure to perceive the machete action as goal-directed toward hidden food is particularly surprising because coconuts are regularly opened on the island by humans using machetes, often in full view of the monkeys. Nevertheless, rhesus failed to perceive this action as goal directed. However, this same population of monkeys can make other types of inferences about tools, including the importance of their design features in causing particular transformations or achieving

particular outcomes (Hauser & Spaulding 2006, Santos et al. 2003). Thus, the monkeys' failure to perceive tool-related actions as goal directed is not the result of a general inability to reason about actions involving tools; rather, it appears to reflect domain-specific limits on action perception.

How do rhesus monkeys distinguish between intentional and accidental actions? Do they simply differentiate between actions that do, and do not, involve tools, perceiving only the former as goal directed? Or, like human infants and adults, can they make more fine-grained distinctions, such as that between intentional and accidental hand actions? To test this, Wood et al. (2007b, 2008) examined how rhesus monkeys reason about an accidental hand-flop gesture in which the experimenter flopped the back of his hand onto the coconut in a manner that does not appear, from a human perspective, as goal directed (Woodward 1999). In accord with our own comprehension of this action, rhesus also failed to perceive the hand-flop action as goal directed, approaching the two coconuts at chance levels (see **Figure 1**).

Together, these studies show that when assessing the meaning of actions, rhesus are highly sensitive to the action means used to achieve a goal. For example, they perceived a hand-grasp action as goal directed but a hand-flop action as accidental, despite the fact that in both conditions, the experimenter's body and eye gaze were directed toward the targeted coconut shell.

Building Bridges Between Natural Foraging Behavior and Patterns of Neural Activation

Neurophysiological studies show that the mirror neuron system activates both when individuals perform an action and when they observe another individual perform a similar action (e.g., Rizzolatti et al. 2001b). Similarly, the experiments reviewed above suggest that rhesus monkeys perceive actions as goal directed toward hidden food only when the

observed actions are part of their species-specific motor repertoire. This raises the possibility that the mirror neuron system is, in some way, connected with rhesus monkeys' behavior in this natural foraging context. If so, then the natural foraging behavior of rhesus should also accord with other signatures of mirror neuron activation. Wood et al. (2008) tested this hypothesis, generating three significant results. First, physiological studies show that mirror neurons activate both when subjects observe a complete action as well as when some of the elements that comprise the action are absent (Umilta et al. 2001). Similarly, rhesus were able to comprehend the meaning of an action both from a full visual description of an action as well as from an incomplete description that arises under occlusion (see **Figure 1**).

Second, mirror neurons activate only when the subject observes object-directed actions; that is, these neurons do not activate when the monkey observes an object alone, an individual mimicking an action, or an individual making intransitive gestures (Rizzolatti et al. 1996, 2001b). Similarly, rhesus did not perceive an action as goal directed toward an object when the experimenter performed an intransitive gesture (i.e., reaching directly next to an object; see **Figure 1**).

Third, mirror neurons in the inferior parietal lobe show different activation patterns to the same act (e.g., grasping) when this act is part of a different event (e.g., eating versus placing the same object; Fogassi 2005). Similarly, when presented with the same act (grasping the coconut) embedded within different contexts ("grasping to obtain food" versus "grasping the coconut for balance while standing"), rhesus evaluated the action by attending to the broader context, perceiving only the former action as goal directed toward food.

These results are exciting because they provide evidence for common signature limits between neurophysiological studies using cellular recordings with restrained animals and behavioral studies of animals in natural, ecologically relevant contexts. In the same way that neurophysiologists have described a set of properties

that characterize the activation of mirror neurons during the perception of goal-directed actions, so too have ethologists described a parallel set of properties that trigger understanding of others' goals. This suggests that mirror neurons are in some way connected with rhesus monkeys' capacity to comprehend the meaning of actions and that they evolved to solve ecologically relevant problems. What is not clear from these results, however, is whether the mirror neuron system plays a functional role in the comprehension of actions, or whether mirror neuron activation, as well as rhesus monkeys' social foraging behavior, depends on an additional teleological mechanism that computes the meaning of an action. That is, the parallel between mirror neuron activation and monkeys' social foraging behavior is correlational.

To explore the role of teleological mechanisms in action comprehension, we tested the limits of the rhesus monkeys' capacity to comprehend actions across three contexts in which the theories of motor simulation and teleological inference make contrasting predictions. First, we examined whether an individual needs an exact motor representation of an action in order to comprehend its meaning. Second, we examined whether motor representations of actions are sufficient for action comprehension. Third, we examined whether event comprehension can occur in the absence of action observation.

ARE EXACT MOTOR REPRESENTATIONS NECESSARY FOR ACTION COMPREHENSION?

Motor simulation and the teleological stance make contrasting predictions regarding the range of actions that can be successfully interpreted by an observer. Under the motor simulation account, the visual properties of an observed action are mapped onto the observer's premotor system. This causes the motor system to "resonate," thereby allowing the observer to understand the goal of the observed action as if she were performing the action herself (see Rizzolatti et al. 2001b). The resonance of the motor system is, therefore, proposed to be causally involved in and, critically, necessary for the comprehension of an action. Thus, if an observer lacks a motor representation that is similar to the one being observed,[1] then she should be unable to comprehend the action. In contrast, the teleological stance proposes that action comprehension is based on a reasoning process that operates over the visual properties of a context, such as the action means, the apparent target goal, and the environmental constraints that limit or facilitate goal achievement. This process does not depend directly on the motor system (see Brass et al. 2007): Although the output of this process may activate motor regions of the brain, action comprehension, including the agent's goal, is computed by nonmotor processes.

On the direct matching hypothesis, action comprehension should fail in situations where the motor action observed is outside the range of physically producible actions. To test this possibility, Wood and colleagues (2007a) explored the capacity of rhesus monkeys to understand the functional consequences of throwing. Humans, but no other animals, have evolved the capacity for accurate, high-momentum throwing, a morphological specialization with significant adaptive consequences in fighting and prey capture. The fact that only humans have the capacity (and underlying motor representations) to perform accurate, high-momentum throwing raises the question of whether they are also the only species with the capacity to comprehend the meaning of throwing actions, a prediction that follows from the motor simulation theory in which comprehension of observed actions occurs through the activation of the observer's own motor representations.

---

[1] It is not entirely clear what the architects of the direct matching hypothesis have in mind when they say that action comprehension relies on motor routines that are in the repertoire. This could either mean actions that the organism typically produces or ones that it can physically produce even if it never does so. Obviously, actions that are in the repertoire can be produced, but those that can be produced need not be.

The rhesus monkeys living on the island of Cayo Santiago provided a unique opportunity to test whether exact motor representations of observed actions are necessary for action comprehension because many of these individuals have observed humans throw objects,[2] but like other monkeys, they don't throw (i.e., throwing is outside of the species-typical repertoire), and due to the lack of relevant musculature, are incapable of throwing (i.e., throwing is outside of the physically possible range of motor actions). Nonetheless, we can ask whether they might comprehend the meaning of throwing by presenting them with a human experimenter performing a throwing action and observing their patterns of response.

The method worked as follows: An experimenter approached a lone monkey and revealed a rock in one hand. He then performed an overhand throw toward the subject but without releasing the rock. The dependent measure was whether the subject moved from its current location, an adaptive response and measure of avoidance in the face of a potential threat.

When rhesus observed the experimenter perform an overhand throw in their direction, 85% of the subjects moved away. This shows that these individuals are able to predict the outcome of a throwing action and interpret it as a potential threat, despite lacking exact motor representations of throwing actions. However, this result can be explained through two very different types of mechanisms. One possibility is that the behavior was based on a general associative learning mechanism, forging an association between some aspect of the throwing motion (e.g., the overhand motion, the rock, or the thrower's eye gaze) and a negative consequence (i.e., a looming object). Alternatively, rhesus might have recruited a more specialized teleological mechanism that evaluates various characteristics of an event, such as the path of

motion, the object involved in the throw, the thrower's attention, and the various environmental constraints that arise when an individual attempts to strike a target goal by throwing. Unlike a general associative mechanism, this interpretive system should demonstrate flexibility in its capacity to generalize knowledge of one kind of action—such as the familiar overhand throw—to related but novel actions.

To distinguish between these competing mechanisms, Wood et al. (2007a) explored how rhesus respond to throwing actions with which they have little to no experience observing (see **Figure 2** for a visual description of the throws and the corresponding results). The associative learning mechanism predicts that rhesus should show an avoidance response whenever the throwing action contains a property, or a collection of properties, associated with the negative outcome—for example, the overhand pattern of movement and/or the presence of the rock. In contrast, the teleological mechanism predicts that rhesus should show the avoidance response only when all of the properties of the observed throw are sufficient to make it a viable threat. Furthermore, this mechanism should be able to generalize knowledge of an overhand throw to novel actions that the subject has little to no experience observing.

When the experimenter performed a novel underhand throwing motion that rhesus had little to no experience observing, they nevertheless showed identical levels of avoidance (85% avoidance response) compared to the overhand throw. In contrast, rhesus showed less avoidance when the experimenter performed throwing actions that lacked all of the kinematic components of an overhand throw (i.e., moving arm backward: 30% avoidance response; rotating shoulder forward: 45% avoidance response; extending forearm forward: 35% avoidance response). Similarly, rhesus showed less avoidance when the throw was performed with an empty hand (15% avoidance response) or with a soft food object rather than a rock (5% avoidance response), at a slower speed (i.e., overhand throw was performed at one-third of normal speed: 35% avoidance response), toward a

---

[2]Because some rhesus monkeys sometimes aggressively approach human experimenters on the island, it is sometimes necessary for the experimenters to pick up rocks and simulate throwing; here, as in the experiments, individuals are never contacted with the rocks, but merely witness the act of throwing, with rocks released away from the animal, if at all.
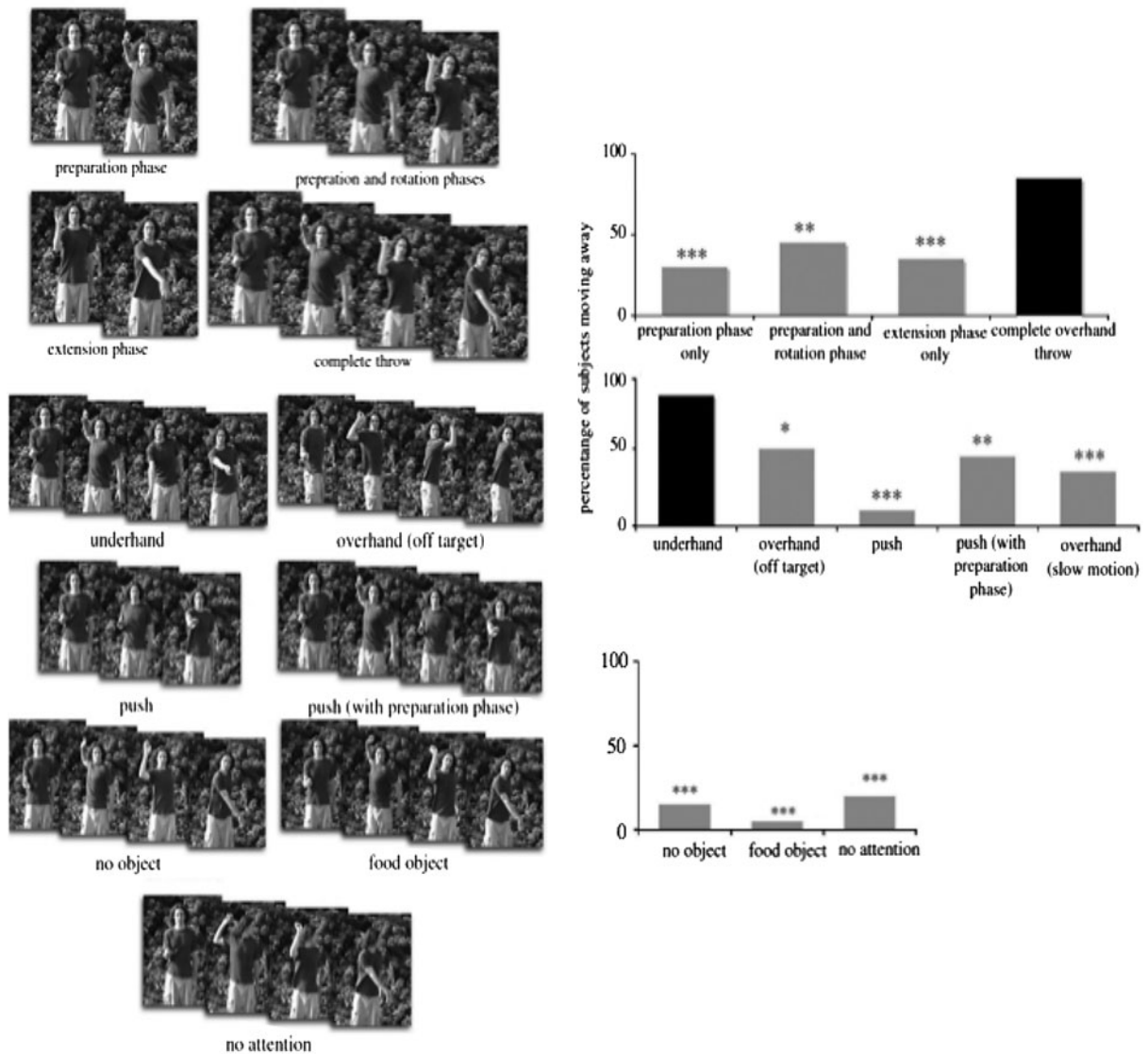
Figure 2

(*left*) Illustration of the key frames of the throwing actions presented to rhesus monkeys. (*right*) Results illustrating the percentage of subjects moving from their current location after observing the throws. Gray bars signify statistically significant differences compared with the complete overhand throw with a rock (chi-square, two-tailed predictions); ***$p < 0.001$, **$p < 0.01$, *$p < 0.05$. Data reported in Wood et al. (2007a).

different direction from the subject (i.e., experimenter looked at, but performed the overhand throw 90° away from, the subject: 50% avoidance response), or with a trajectory that could not produce sufficient torque to serve as a threat (i.e., experimenter moved arm straight toward the subject: 10% avoidance response). Rhesus also showed less avoidance when the experimenters performed the overhand throw but directed their eye gaze 90° in a different direction (20% avoidance rate), indicating that the underlying action-comprehension mechanism

performs an analysis of the kinematics of the motion pattern and combines this with information about the actor's eye gaze.

An associative learning mechanism cannot readily explain this pattern of behavior. Rhesus showed low levels of avoidance in response to the overhand throwing motion when it was performed with an empty hand or a soft food object, or when the action was performed with a rock but the experimenter looked away from the subject. The pattern of motion was identical in all of these cases, and yet rhesus only perceived the throw as a threat when all of the relevant properties were sufficient for the throw to constitute a threat. Similarly, rhesus showed identical levels of avoidance to the overhand and underhand throwing motions, despite their lack of experience with an underhand throw. These results are highly consistent with the hypothesis that individuals reason about actions using a teleological mechanism that evaluates various visual characteristics of an event. This mechanism operates over at least four kinds of information: (*a*) the kinematics of the motor action, (*b*) the object involved in the action, (*c*) the actor's direction of eye gaze, and (*d*) the position of the subject.

These results suggest that exact motor representations of observed actions are unnecessary for comprehension of those actions. This presents a strong challenge to the motor simulation theory of action comprehension and specifically the direct-matching hypothesis. On this view, the visual properties of observed actions (which are initially devoid of meaning; Rizzolatti et al. 2001) acquire their meaning once they have been mapped to the observer's premotor system. Because the input to motor simulation is limited to the visual properties of the action, all actions with identical visual properties should be interpreted in the same way by a direct-matching mechanism. This prediction was not supported by the data. Many of the throwing actions had identical visual properties and yet were interpreted in very different ways. Other characteristics of the event, such as the kind of object involved in the throw and the observer's head and body orientation, had a significant influence on rhesus monkeys' interpretation of throwing events.[3]

ARE MOTOR REPRESENTATIONS SUFFICIENT FOR ACTION COMPREHENSION?

Another approach to distinguishing between motor simulation and the teleological stance is to examine the type of information evaluated within a given context. The teleological stance assigns a goal to an action by evaluating the efficiency of the agent's action with respect to environmental constraints on goal attainment (see Gergely & Csibra 2003). Thus, comprehension of an action involves information about potential goals, the action means, and the environmental constraints limiting the agent's actions. For instance, developmental studies of human infants indicate that individuals read beneath the surface appearance of behavior by referencing each action against a backdrop of environmental constraints. Gergely and colleagues (2002) showed that when 14-month-old infants watched an experimenter use her head to illuminate a box, infants imitated this precise action only if the experimenter's hands were free to move and could have been used to illuminate the box; if the experimenter's hands were occupied, and could not be used, then the infants used their hands. Infants most likely inferred that since the experimenter could have used her hands, but used her head instead, the head must confer some advantage for illuminating the box. This finding converges with others showing that young infants make inferences about actions, goals, and environmental constraints when watching the motions of simple geometric figures (see Gergely & Csibra 2003). For example, 12-month-old infants were habituated to a

---

[3] Studies of mirror neurons in the macaque premotor cortex also show that activation of these neurons depends on contextual properties of an event. Although these results have traditionally been interpreted as consistent with a direct-matching mechanism, they are, in fact, more consistent with a teleological mechanism (see Csibra 2007).

computer-animated event in which a circle approached and contacted another circle by jumping over a barrier that separated them (Gergely et al. 1995). During the test phase, the experimenters changed the constraints of the situation by removing the barrier. Infants then observed the same jumping motion pattern as in the habituation trials or a perceptually novel straight-line approach. Infants looked longer at the jumping pattern, but failed to dishabituate to the perceptually novel straight-line approach. These results suggest that human infants assess whether an agent's actions are rational by evaluating how the intervening environmental circumstances constrain the achievement of a target goal; as such, they infer properties of mental life that are not transparent from the surface appearance of behavior. Is this capacity the product of specifically human evolution or do nonhuman animals also evaluate others' behavior using this same kind of interpretative system?

To investigate this question, Wood and colleagues (2007b) used the two-option social foraging method described above. As noted, rhesus perceive a hand-grasp action as goal directed but perceive a hand-flop action as accidental. What kind of psychological mechanism generated this distinction? One possibility is that rhesus analyzed the actions using their own motor system. Thus, the hand-grasp action was perceived as intentional because this action is part of the rhesus motor repertoire, whereas the hand-flop action was perceived as accidental because rhesus do not produce this action in goal-directed contexts (even though they of course can, motorically speaking, produce the action). An alternative account is that rhesus interpreted these actions in relation to the broader environment in which they occurred. Thus, subjects may have judged the hand flop as accidental because, in this particular situation, the experimenter could have used the more rational grasping action in order to contact the coconut shell.

Do rhesus assess the meaning of actions by evaluating whether an action is rational given the constraints of the situation? Using the two-option approach measure, subjects observed an experimenter perform the same elbow touch action under two contrasting environmental circumstances: in one condition, the experimenter's acting hand was occupied by holding an object, and in the second condition, the experimenter's acting hand was free. If rhesus evaluate actions through direct-matching motor simulation, then they should show the same pattern of searching in both the hand-occupied and hand-empty conditions because the surface properties of the actions—and thus, what will be mapped onto the motor system—are nearly identical. However, if rhesus take into account the environmental constraints facing the experimenter, then only the hand-occupied condition should be perceived as a rational, goal-directed action. Given that the experimenter's acting hand was occupied at the moment of gesturing, his elbow provides an alternative means to contact the target goal. Accordingly, the hand-empty condition would not be perceived as a rational, goal-directed action because at the time, the experimenter could have used his unoccupied acting hand to grasp and indicate the target container, leaving the subject uncertain as to the target goal. Therefore, subjects should not infer that the experimenter's goal was to contact the box with the potentially concealed food.

Results showed that rhesus used the elbow touch as a cue to find the hidden food when the experimenter's acting hand was occupied but not when it was free. A similar pattern of results was found with cotton-top tamarins and chimpanzees (Wood et al. 2007b). Furthermore, other laboratories testing macaques, chimpanzees, and domestic dogs have obtained convergent evidence using a variety of methods, ranging from violation of expectancy looking-time measures (Rochat et al. 2008) to selective imitation (Buttelmann et al. 2007, Range et al. 2007). Buttelmann and colleagues (2007), for example, examined whether chimpanzees evaluate the environmental constraints that limit rational action when imitating others' movements. Chimpanzees observed a human experimenter use an unusual body part to

operate an apparatus (i.e., she pressed it with her forehead). In one condition, the action was performed while the experimenter's hands were occupied, whereas in a second condition, the action was performed while the experimenter's hands were free. If chimpanzees evaluate environmental constraints when imitating others' actions, then they should be more likely to use the unusual body part when the experimenter performed the action while her hands were free and unoccupied. Results support this prediction. Like human infants (Gergely et al. 2002), chimpanzees imitated the unusual action more often when the experimenter performed the action with unoccupied hands (Buttelmann et al. 2007).

Is this capacity unique to nonhuman primates, or do other species also imitate others' actions by evaluating the constraints that limit goal-directed behavior? Remarkably, Range and colleagues (2007) showed that domestic dogs also selectively imitate others' actions. An observer dog watched a demonstrator dog pull a rod using either its paw or its mouth. In one condition, the demonstrator dog performed the action while concurrently carrying a ball in its mouth, whereas in a second condition, the action was performed while the dog's mouth was empty. Thus, in the first condition, the presence of the ball in the demonstrator dog's mouth justified the use of the less preferred paw action because in this particular context, she could not use her mouth to perform the action. In the first trial after observing this action, the observer dogs selectively imitated the less preferred paw action only when the demonstrator dog modeled the action with a ball in its mouth. Thus, dogs, like children and chimpanzees, evaluate the environmental constraints that limit rational goal-directed action when imitating others' movements.

Together, these studies show that nonhuman animals infer the meaning of an action by evaluating action means in relation to the environmental constraints imposed on the agent in relation to a potential goal state. Action comprehension cannot, therefore, depend on a direct-matching motor simulation

mechanism that solely evaluates the properties of the observed action (Rizzolatti et al. 2001b).

Intriguingly, these behavioral studies with nonhuman animals converge with recent functional magnetic resonance imaging data obtained with human adults (Brass et al. 2007). Subjects were presented with actions similar to those presented to human infants (Gergely et al. 2002) and nonhuman animals (Buttelmann et al. 2007, Range et al. 2007, Wood et al. 2007b) while in a scanner. For example, subjects observed an actor operate an apparatus using an unfamiliar body part while her hands were either empty or occupied. The BOLD response revealed that the STS activated differently to the hands-empty and hands-occupied actions, suggesting that this region of the brain supports action-comprehension tasks that require integrating information about environmental constraints with observed movements in order to infer the actor's intention. In contrast, the mirror neuron system activated equally to the hands-empty and hands-occupied actions, suggesting that mirror neurons do not evaluate information about the constraints that limit rational action. Thus, although mirror neurons may activate when observing others' actions, they do not process information that is critical for determining an agent's underlying intention.

Convergent evidence for this conclusion comes from a study showing that the mirror neuron system does not distinguish between animate agents and inanimate objects (Wheatley et al. 2007). Subjects were presented with an identically moving shape that was perceived as either an animate agent (e.g., an ice skater) or an inanimate object (e.g., a spinning top) based on the background scene alone. The BOLD response revealed equal activation in the mirror neuron system regardless of whether the shape was perceived as an agent or an inanimate object. This suggests that although the mirror neuron system may play a role in elucidating the actions of all objects, it does not play a specialized role in evaluating the underlying intentions that motivate the actions of animate agents. In contrast, the STS system was modulated by the perceived animacy of the shape.

ACTION PREDICTION IN THE ABSENCE OF ACTION OBSERVATION

The studies discussed above show that animals use environmental constraints to interpret the actions of others. What happens, however, when there are no actions at all, and subjects must predict an agent's goals based on other features of the environment? Motor simulation predicts that action comprehension occurs when an organism observes an action and then simulates that action within its motor system. It thus logically follows that in a context where an organism does not observe an action at all, then its motor system will not resonate. If event comprehension depends on motor resonance, then monkeys will fail to comprehend an event in the absence of observing an action.

Studies of chimpanzees provide one test of these ideas even though they were not designed for this purpose. In particular, Hare et al. (2000) carried out experiments in which a subordinate and dominant chimpanzee were placed in a competitive situation, sitting in opposite rooms, with a center room containing two bananas. In one test condition, the subordinate could see a banana behind an occluder, but the dominant could not; both subordinate and dominant could, however, see a second banana located in the open. When the door to the subordinate's room was opened first, the subordinate dashed out and grabbed the occluded banana. The subordinate's behavior was thus based on an inference about what the dominant could see, and thus, what the dominant would most likely do. Said differently, subordinate chimpanzees generated an appropriate prediction about the dominant's most likely behavior in the absence of any action at all.

These results are consistent with a teleological mechanism that provides meaning to an event by analyzing the action means, potential goals, and the environmental constraints. As Gergely & Csibra (2003) have shown in their elegant studies of human infants, if individuals are provided with information about two of these three kinds of information, then they can infer the third component. Similarly, when chimpanzees are provided with information about two components of an event, such as potential goals (the food) and environmental constraints (the barrier), they can predict which action the other chimpanzee is most likely to perform and react accordingly.

To conclude this section, evidence from three different contexts reveals that nonhuman primates' capacity for action comprehension accords strongly with predictions of the teleological stance but not with predictions of a motor simulation mechanism.

A SHARED SYSTEM OF ACTION COMPREHENSION: EVOLUTIONARY ROOTS AND ONTOGENETIC BEGINNINGS

A number of developmental studies show that within the first year of life, human infants begin to predict the goals of others' actions. For example, in a now classic study, Woodward (1998) habituated preverbal infants to a human agent who reached for one of two objects that were placed side-by-side on a stage. Following habituation, the experimenter concealed the stage from the infant's view, switched the location of the objects, and then, in view of the subject, reached for either the same object as in the habituation period (goal-consistent trials) or for the other object (goal-inconsistent trials). Infants looked longer during the goal-inconsistent trials, suggesting that they are able to encode the actions of others as goal directed. However, infants failed to show this pattern of looking when an inanimate object touched the target objects or the human agent flopped the back of his hand on the target object in a manner that appeared accidental (Woodward 1999). Recall that rhesus monkeys show a parallel pattern of action understanding, perceiving hand-reaching actions as goal directed, but actions involving inanimate objects and a hand flop as accidental (Wood et al. 2007b, 2008).

Follow-up studies examined the extent to which infants' capacity for action comprehension depends on their own ability to produce

those actions. For example, when tested with the method described above, five-month-old infants, but not three-month-old infants, looked longer during the test trials when the hand reached for the new object in the old location compared to when the hand reached for the old object in the new location. This suggests that at five months of age, infants can infer that agents will perform future actions toward the same object. However, when three-month-old infants were provided with sticky mittens before the experiment—which allowed them to grasp and manipulate objects despite underdeveloped motor dexterity—these infants were able to encode an experimenter's hand-grasp actions as goal directed (Sommerville & Woodward 2005, Sommerville et al. 2005). Similarly, older infants were able to encode means-end actions as goal directed when they were taught how to produce these actions (Sommerville & Woodward 2005).

Human infants acquire the capacity to discriminate intentional from accidental actions during the first year of development (e.g., Gergely & Csibra 2003, Woodward 1999); similarly, adult rhesus monkeys and chimpanzees can make the same kinds of inferences about others' actions (e.g., Buttelmann et al. 2007; Call et al. 2004; Hauser et al. 2007; Wood et al. 2007a,b, 2008). This suggests that human and nonhuman primates share a common system of action comprehension.

ACTION COMPREHENSION AND THE BUILDING BLOCKS OF MORALITY

For socially living species, such as the primates, action comprehension often arises in a social context, including threats from a dominant, requests for coalitionary support, grooming, mating, and the exchange of resources. For observers of these interactions or those directly involved, it is important to assess not only the actual or expected outcomes, but also the means by which they are achieved. Thus, although an individual may obtain food by theft, as a result of another's offering, or by tolerated taking, each

of these modes of attainment, matched for outcome (i.e., food obtained), differs in terms of its social relevance. Theft violates an animal's sense of property or ownership; food offers represent cases of altruism or cooperation; and tolerated taking is either altruistic or possibly accidental depending upon the possessor's attentional state (e.g., if looking away, toleration turns into theft under inattention). In the case of human primates, these events represent morally relevant actions with consequences for the welfare of other group members. For nonhuman primates, they represent the building blocks upon which our own moral sense evolved. Here we explore these foundations further.

Call and colleagues (2004) developed a task for chimpanzees in which a human experimenter presented subjects with an opportunity to reach for and obtain food. Across conditions, the outcome was held constant (the chimpanzees never obtained the food), but the manner of food presentation was manipulated. For example, in the "clumsy" condition, the experimenter repeatedly tried to give food to the chimpanzee through the target hole, but failed, dropping it out of reach. In the "unable" condition, the experimenter tried to give food to the chimpanzee, but the hole was blocked. In the "unwilling" condition, the experimenter placed the food in view, stared at the chimpanzee, but refused to place it in the hole. Finally, in the "tease" condition, the experimenter brought the food toward the opening and as soon as the chimpanzee reached for it, the experimenter pulled it away. Results showed clear patterns of response, suggesting sensitivity to the means underlying the experimenter's actions as opposed to the outcomes. That is, chimpanzees were more likely to leave the test area early and/or bang on the apparatus in the unwilling and tease conditions compared with the clumsy and unable conditions.

Several recent studies have explored the role that inequities play in economic decision making, as such outcomes play a critical role in social interactions. The key issue in this work is whether animals are sensitive to the distribution of rewards and, in particular, the social

consequences of equal as opposed to unequal distributions. In many studies of justice, perceptions of fairness are essential (Hauser 2006, Rawls 1971). As such, studies of how animals compute and act upon fairness serve as an important foundation for thinking about the evolution of human morality and the legal systems that often emerge from it. One of the earliest treatments of this problem was Brosnan & de Waal's (2003) study of brown capuchin monkeys. After subjects were trained to trade tokens for food rewards, they watched a conspecific acquire and eat a high-value food item, and then they were given the opportunity to acquire and eat a lower-value food item. Subjects consistently refused to trade the token for the lower-value food. Brosnan & de Waal (2003) interpreted this result as evidence for inequity aversion and a sense of fairness.

Although the capuchins' response to food distribution suggests that they are sensitive to more than the mere outcome of a transaction, the results are at odds with those obtained in studies of humans, and several important criticisms of this work emerged soon after. In particular, when humans confront inequities, rejections occur only insofar as their actions negatively affect their social partner. In the Brosnan & de Waal (2003) experiments, however, when an individual rejects the lower-quality food, the only cost is to self: that is, rejecting the low-quality food does not affect the paired individual for the trial because this individual maintains access to the high-quality food traded. Several conceptual and experimental follow-ups also pointed to the fact that because rejection rates were comparable in the social and nonsocial condition, it was not possible to rule out the effect of frustration as the driving force behind rejections (Dubreuil et al. 2006; Roma et al. 2006a,b; Wynne 2004). That is, subjects may have rejected unfair offers not because the other individual was getting a better offer but rather because they were frustrated at not being able to obtain the higher-value food item. Though subsequent experiments confirmed the validity of these critiques (Dubreuil et al. 2006, Roma et al. 2006a), Brosnan, de

Waal, and their colleagues have since replicated the original findings with relevant controls and found that their results cannot be explained by frustration (van Wolkenten et al. 2007). Further, there are now parallel findings with chimpanzees (Brosnan et al. 2005) and dogs (Range et al. 2009), though even in these cases the story is not entirely clear (Brauer et al. 2006).

In summary, although there is still much controversy surrounding the results on inequity aversion in animals, it appears that animals are sensitive to the distribution of rewards, in both social and nonsocial contexts, responding negatively when an outcome appears unfair.

A final approach concerns an exploration of the foundations of the Golden Rule, and specifically, the possibility that animals engage in reciprocal altruism. Beginning with the theoretical clarifications by Trivers (1971) concerning the evolution of reciprocity, several studies soon appeared, claiming to find evidence of reciprocal altruism. These studies have failed to replicate, can be interpreted in terms other than reciprocity, or provide only weak support because the requisite conditions are highly artificial and the patterns of exchanges are infrequent and thus relatively insignificant in evolutionary terms. Here, however, we discuss one example because it explicitly explored the relative contribution of outcomes as opposed to means in deciding whether to cooperate.

Hauser and colleagues (2003) ran experiments on cotton-top tamarin monkeys designed to test three properties of a reciprocal relationship: altruistic contingency, reputation tracking, and distinguishing intentional from accidental outcomes. Genetically unrelated tamarins played in four different games, each requiring an actor to decide whether to pull a tool that would deliver food to self, a partner, or both (**Figure 3**). In game 1, individual subjects played against one of two trained confederates, one "nice" cooperative tamarin trained to pull the tool 100% of the time and one "mean" uncooperative tamarin trained to never pull the tool. In this game, pulling the tool resulted in one piece of food for the recipient and no food for the actor, thus, it was considered an
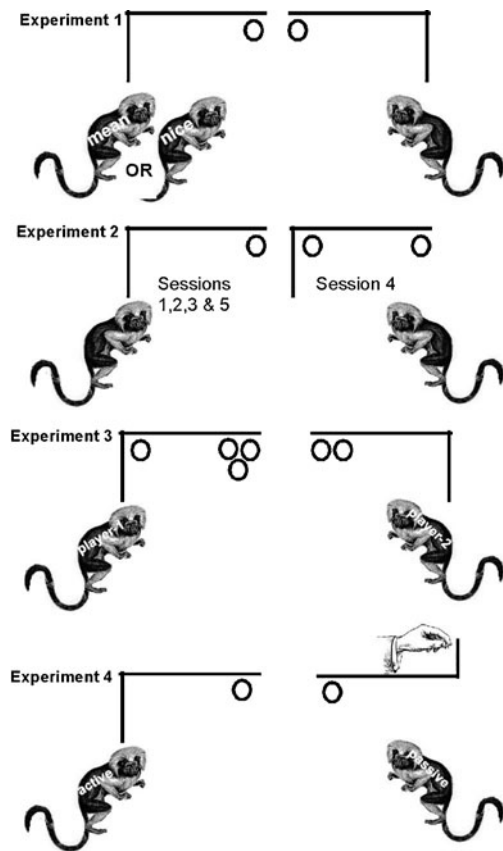
Figure 3

Four different games played by genetically unrelated cotton-top tamarins
(Hauser et al. 2003). In Experiment 1, each subject played alternating sessions
(24 trials; 12 trials each) with either a nice stooge (trained to pull the tool 100%
of the time) or a mean stooge (trained to pull the tool 0% of the time). In
Experiment 2, subjects played a reciprocating altruism game (i.e., no food for
actor but one piece for recipient) for the first three sessions; in the fourth
session a byproduct mutualism game was played (i.e., a piece of food for the
actor and recipient); and in the final session, a reciprocating altruism game was
played. In Experiment 3, one subject was assigned to the player-1 position
(pulling provided one piece to the actor and three pieces to the recipient) and
one subject was assigned to the player-2 position (pulling provided no food for
the actor and two pieces to the recipient). In Experiment 4, the active tamarin
could pull as an altruistic act (no food for self, one for the recipient), while the
passive tamarin had no opportunity to pull; instead, when the tool switched to
the passive tamarin's side, the experimenter pushed the tool on 100% of the
trials, thus mimicking the payoff structure for the nice stooge in Experiment 1.

criticisms immediately arise. First, identifying
cooperators requires an ability to recognize the
partner's motivations—do they incur a cost in
order to cooperate (altruism) or do they only
cooperate when they also benefit (mutualism)?
Experiments 2 and 3 explored this possibility.
Second, subjects may pull more when they
themselves receive food, and this situation
arises most when playing against the nice
confederate who always delivers food. In other
words, the higher rates of pulling when paired
with the nice confederate might be simply a
reflection of the higher rates of reinforcement,
a situation that could just as easily be achieved
by a machine delivering food. Experiment 4
attempted to test this alternative account.

Summarizing across all three experiments,
results show that tamarins are sensitive to the
means by which food is delivered, cooperat-
ing more with those individuals who altruisti-
cally give food than those who deliver food as
an accidental byproduct of an otherwise self-
ish behavior. Further, if a human delivers food
on behalf of a tamarin, this payoff has no im-
pact on the cooperative instincts of a partnered
tamarin. These studies show that cooperation
in tamarins depends on more than the patterns
of reinforcement. A tamarin has to deliver the
payoffs and has to do so on the basis of gen-
uinely altruistic behavior.

Together, these studies suggest that tamarins
are sensitive to some of the important proximal
ingredients that enter into reciprocity, includ-
ing altruistic contingency, reputation tracking,
and distinguishing the means by which out-
comes are obtained. That said, when one ex-
plores the longer-term pattern of cooperation
observed in these experiments together with
studies of a wide variety of other species, it is
clear that tamarins are incapable of sustaining
reciprocity because even a rather brief period
of defection causes the cooperative relation-
ship to unravel. In particular, based on a game
theoretic analysis of the tamarin results from
the nonstooge games, it is clear that after two
consecutive rounds of defection, tamarins stop
pulling in the altruistic condition and never re-
cover the reciprocally cooperative relationship

altruistic act. Here, subjects pulled significantly
more often when paired with the nice stooge
than with the mean stooge. This suggests
that tamarins can distinguish recipients based
on their cooperative tendencies and that
they respond contingently. However, two

(Chen & Hauser 2005). Thus, although tamarins may have some of the cognitive prerequisites for reciprocity, these capacities appear insufficient to sustain reciprocity. Moreover, the reciprocity observed among tamarins only emerges under fairly artificial conditions, including the presentation of discrete packages of food, highly predictable periods of interaction, and with individuals trained to be pure cooperators or defectors.

The most recent entry into the literature on reciprocity in animals comes from an elegant study of chimpanzees by Melis et al. (2008). One reason for its elegance comes from the fact that the design was based on an extensive set of prior and highly relevant experimental findings. Owing to both their natural tendencies to cooperate under a variety of circumstances and their demonstrated skills in captivity, chimpanzees have all of the apparent prerequisites to support reciprocal relationships. Specifically, chimpanzees engage in coalitionary attacks on neighboring communities when there is a significant imbalance of power, usually in the ratio of three to one, use within-community coalitions of two to three individuals (kin and nonkin; Langergraber et al. 2007) to overtake a single dominant, and coordinate individual movement and positioning while hunting for prey and sharing food (Gilby 2006, Muller & Mitani 2005). Chimpanzees show clear evidence of individual recognition (Parr 2003), live in relatively stable communities that enable opportunities for repeated social interactions, have the capacity for numerical quantification (Beran et al. 2008, Boysen et al. 1996, Kawai & Matsuzawa 2000) and the ability to delay gratification beyond that of most other animals and in some cases, even humans (Evans & Beran 2007, Rosati et al. 2007), are sensitive to equitable distributions of resources (Brosnan et al. 2005, 2008), engage in prosocial tendencies in nonfood contexts (Warneken et al. 2007, Warneken & Tomasello 2006), discriminate intentional from accidental outcomes (Call et al. 2004), and use prior reputation to enlist the most likely collaborators in a task requiring joint action (Melis et al. 2006). Together,

these capacities provide the essential ingredients to initiate and sustain reciprocity.

In their experiment, Melis and colleagues (2008) asked whether chimpanzees would preferentially choose to reciprocate an altruistic action toward a previously nice and cooperative stooge over a previously mean and uncooperative stooge. As mentioned above, previous work had already demonstrated that chimpanzees recruit collaborators in a joint action task (i.e., two subjects must work together to obtain a reward; defection by one eliminates the opportunity for either to obtain food) and preferentially select the most collaborative collaborator (Melis et al. 2006). In Experiment 1, subjects first learned that the nice stooge always provided them with access to a rope that, when jointly pulled, provided access to food, whereas the mean stooge never provided access. Once they learned these action contingencies, subjects were then given an opportunity to allow either the nice or mean stooge to join them at the pulling tray. In the first block of trials, 12.5% picked the nice stooge, 62.5% picked the mean stooge, and 25% were indifferent. In the second block of trials, 37.5% picked the nice stooge (only one subject with a strong preference), 37.5% picked the mean stooge, and 25% were indifferent. Although there was a slight increase in the preference for the nice stooge over the baseline period, this effect was only just significant at the $p < 0.05$ level and with a 1-tailed test. Thus, based on analyses of individual preferences, there was, at best, only weak evidence of reciprocity.

In Experiment 2, the nice stooge altruistically opened the door for the subject to get food, whereas the mean stooge opened the door to selfishly get food for himself. Would the chimpanzees assess their partner's prior reputation and use this information to give the nice stooge more frequent access to the pulling tray when compared to the mean stooge? Pooling across individuals, there was no evidence that subjects opened the door more often for the nice than the mean stooge. On an individual level, only 12.5% showed a significant difference between stooges in the predicted direction, opening the

door on every trial for the nice stooge and never for the mean stooge. In summary, and as the authors note, this study provides only weak evidence of reciprocity in chimpanzees.

Although chimpanzees appear to have the cognitive prerequisites to support reciprocal altruism, ultimately, their ability to engage in reciprocity appears to be no better than that of the many other animals that have been tested in either natural conditions or captivity (Hammerstein 2003, Stevens & Hauser 2004). Our suggestion is that although chimpanzees have the capacity to delay gratification, quantify potential payoffs, detect inequities, and punish individuals for norm violations, these ingredients do not combine to create a system for reciprocity. In contrast, from a very young age, human children endowed with similar capacities are able to integrate these into one system that ultimately enables them to develop and sustain reciprocal relationships (Fehr & Fischbacher 2005, Tomasello et al. 2005, Trivers 1971). This integration of different systems is, we believe, one of the distinguishing features of human cognition (see below; Hauser 2009, Rozin 2000).

CONCLUSIONS

The primary goal of this review is to place the study of action comprehension into a broad comparative context and, specifically, to frame the problem in terms of two competing hypotheses that attempt to explain how we and other organisms come to understand the meaning of actions. On the simulation hypothesis, including its neurophysiologically instantiated sister, the direct-matching hypothesis, action comprehension operates by means of personal simulation, with an explicit and necessary recruitment of motor representations. On the alternative, teleological hypothesis, action comprehension operates by drawing inferences from goals, action means, and the environmental constraints that limit rational action. Although the teleological stance doesn't rule out the possibility that motor systems are

involved in action comprehension, they are not necessary.

Our contribution to this work, reviewed here, has been to situate previously published and ongoing studies of nonhuman animal behavior within this rich psychological, neurobiological, and philosophical framework. In particular, we showed that in several studies of nonhuman primates, including studies of macaques (the genus targeted for the original mirror neuron studies), individuals were sensitive to the details of an action vis-à-vis a target goal, both when that goal was explicitly presented (e.g., showing a piece of food disappear into a box) and implicitly inferred (e.g., following a communicative gesture to a box). Many of these behavioral studies show sensitivities that parallel the activation patterns of mirror neurons, which have been characterized in studies carried out by Rizzolatti and his colleagues over the past decade. For example, whereas mirror neurons activate to a pincer grip targeting a piece of food, the same neurons fail to respond when a hand grasps a pair of pliers and uses the pliers—in a pincer grip form—to target a piece of food. Similarly, whereas free-ranging rhesus monkeys selectively approach a coconut shell that is grasped with a pincer grip, they approach the two coconut shells at chance levels when one shell is grasped with a pair of pliers.

Several studies of primate behavior are, however, inconsistent with the simulation theory and more directly consistent with the teleological stance. Thus, studies of apes, monkeys, and dogs indicate that individuals draw inferences about goals based on environmental constraints that dictate considerations of rational as opposed to irrational behavior. Thus, although pointing with an elbow is not within the repertoire of any nonhuman primate, if a human elbow contacts a target box while the actor concurrently holds a board with the acting hand, then this gesture is perceived as a communicative action with a particular goal; the same elbow point is not so perceived when the acting hand is free and, presumably, could be used to

point or grasp the target box. Thus, the same action is interpreted differently depending on context. Stronger evidence against the simulation account comes from the study of throwing. Although rhesus monkeys don't throw and lack the musculature to throw, they analyze in great detail the kinematics of human throwing, showing sensitivity to the position of the arm at the starting point, its trajectory to a termination point, the position of the head and eyes, and the item thrown. With this information, they are able to predict the most probable outcome of a throwing gesture, deciding when to flee versus when to approach. The simulation account, or the direct-matching hypothesis more specifically, cannot explain this finding. These data are, however, highly consistent with the teleological account of action comprehension.

In the final set of studies that we reviewed, we attempted to link the broad topic of action comprehension to the more narrow topic of socially relevant actions and, in particular, actions that may form the substrate for our evolved moral sense. In particular, we argued that in order for a moral system to get off the ground, it must minimally distinguish between means and outcomes, such as the distinction between intended and accidental outcomes (e.g., punching someone has significant moral consequences, whereas accidentally tripping someone does not). In several studies of monkeys and apes, there is evidence that individuals use aspects of an agent's intentions and goals to evaluate the nature of the outcome. Thus, even though chimpanzees may never obtain food from an experimenter holding the food, they show greater signs of frustration when the experimenter teases the individual than when the experimenter is clumsy or unable to provide food. Further, tamarins are more likely to reciprocate with individuals who altruistically provide food than with individuals who deliver food as a byproduct of otherwise selfish behavior.

Much of this work is in its infancy. What we find exciting is that for the first time, studies of action comprehension entail all four of what Tinbergen (1963) described as the essential causal questions to account for a behavior. That is, we are beginning to understand how action comprehension evolved (issues of phylogeny), its adaptive significance (how it contributes to survival and reproductive success), how it develops within individuals, and its underlying neural mechanisms in both humans and nonhuman animals. Many questions remain. For example, although phylogenetic considerations make it clear that humans must have a mirroring system given the neurophysiological data from macaques, the imaging work makes it difficult to establish given the spatial resolution of this technique. For example, although several studies show that areas activated for the perception of action are also activated for the production of the same action (Rizzolatti et al. 2001a), it is possible that these areas consist of discrete populations, some proportion of cells firing in response to perception and a different proportion firing to production. On a functional level, problems also arise. Thus, even if the computational function of mirror neurons in macaques and humans is the same, their role in cognition is clearly different. Thus, the human mirror neuron system appears to play some role in imitation and in the comprehension of disgust. But monkeys don't imitate and do not show a facial expression analogous to disgust. Furthermore, some have argued that mirror neurons play a role in language (Rizzolatti & Arbib 1998), and yet, monkeys clearly don't have language. Thus, we are faced with a situation where mirror neurons may have evolved for some function, and then over evolutionary time and with neural reorganization, may have been co-opted in human brains for a variety of novel cognitive functions. This possibility seems to be generally true of the human brain, with its massive capacity to link cognitive representations across domains and recruit a number of domain-general generative mechanisms to support a finite but highly variable range of potential representations (Hauser 2009).

DISCLOSURE STATEMENT

The authors are not aware of any biases that might be perceived as affecting the objectivity of this review.

LITERATURE CITED

Barsalou LW, Simmons WK, Barbey AK, Wilson CD. 2003. Grounding conceptual knowledge in modality-specific systems. *Trends Cogn. Sci.* 7:84–92

Beran M, Evans T, Harris E. 2008. When in doubt, chimpanzees rely on estimates of past reward amounts. *Proc. R. Soc. London B: Biol. Sci.* 276:309–14

Boysen ST, Berntson GG, Hannan MB, Cacioppo JT. 1996. Quantity-based inference and symbolic representations in chimpanzees (*Pan troglodytes*). *J. Exp. Psychol.: Anim. Behav. Process.* 22:76–86

Brass M, Schmitt RM, Spengler S, Gergeley G. 2007. Investigating action understanding: inferential processes versus action simulation. *Curr. Biol.* 17:2117–21

Brauer J, Call J, Tomasello M. 2006. Are apes really inequity averse? *Proc. R. Soc. London B: Biol. Sci.* 273:3123–28

Brosnan SF, de Waal FBM. 2003. Monkeys reject unequal pay. *Nature* 425:297–99

Brosnan SF, Grady M, Lambeth S, Schapiro S, Beran M, Zak P. 2008. Chimpanzee Autarky. *PLoS ONE* 3:e1518

Brosnan SF, Schiff HC, de Waal FBM. 2005. Tolerance for inequity may increase with social closeness in chimpanzees. *Proc. R. Soc. London B: Biol. Sci.* 272:253–58

Buttelmann D, Carpenter M, Call J, Tomasello M. 2007. Enculturated chimpanzees imitate rationally. *Dev. Sci.* 10:F31–38

Call J, Hare B, Carpenter M, Tomasello M. 2004. "Unwilling" versus "unable": chimpanzees' understanding of human intentional action. *Dev. Sci.* 7:488–98

Chen MK, Hauser M. 2005. Modeling reciprocation and cooperation in primates: evidence for a punishing strategy. *J. Theor. Biol.* 235:5–12

Csibra G. 2007. Action mirroring and action interpretation: an alternative account. In *Sensorimotor Foundations of Higher Cognition. Attention and Performance XXII*, ed. P Haggard, pp. 435–59. Oxford, UK: Oxford Univ. Press

Csibra G, Biro S, Koos O, Gergely G. 2003. One-year-old infants use teleological representations of actions productively. *Cogn. Sci.* 27:111–33

Csibra G, Gergely G. 1998. The teleological origins of mentalistic action explanation: a developmental hypothesis. *Dev. Sci.* 1:255–59

Csibra G, Gergely G, Biro S, Koos D, Brockbank M. 1999. Goal attribution without agency cues: the perception of "pure reason" in infancy. *Cognition* 72:237–67

Davidson D. 2001. *Essays on Actions and Events*. Oxford, UK: Oxford Univ. Press

di Pellegrino G, Fadiga L, Fogassi L, Gallese V, Rizzolatti G. 1992. Understanding motor events: a neurophysiological study. *Exp. Brain Res.* 91:176–80

Dubreuil D, Gentile MS, Visalberghi E. 2006. Are capuchin monkeys (*Cebus apella*) inequity averse? *Proc. R. Soc. London B: Biol. Sci.* 273:1223–28

Evans T, Beran M. 2007. Chimpanzees use self-distraction to cope with impulsivity. *Biol. Lett.* 3:599–602

Fehr E, Fischbacher U. 2005. The economics of strong reciprocity. In *Moral Sentiments and Material Interests*, ed. H Gintis, S Bowles, RT Boyd, E Fehr, pp. 151–92. Cambridge, MA: MIT Press

Fogassi L. 2005. Parietal lobe: from action organization to intention understanding. *Science* 308:662–67

Gallese V, Fadiga L, Fogassi L, Rizzolatti G. 1996. Action recognition in the premotor cortex. *Brain* 119:593–609

Gallese V, Goldman A. 1998. Mirror neurons and the simulation theory of mind-reading. *Trends Cogn. Sci.* 2:493–501

Gallese V, Keysers C, Rizzolatti G. 2004. A unifying view of the basis of social cognition. *Trends Cogn. Sci.* 8:398–403

Gergely G, Bekkering H, Kiraly I. 2002. Rational imitation in preverbal infants. *Nature* 415:755

Gergely G, Csibra G. 2003. Teleological reasoning in infancy: the naive theory of rational action. *Trends Cogn. Sci.* 7:287–92

Gergely G, Nadasdy Z, Csibra G, Biro S. 1995. Taking the intentional stance at 12 months of age. *Cognition* 56:165–93

Gilby IC. 2006. Meat sharing among the Gombe chimpanzees: harassment and reciprocal exchange. *Anim. Behav.* 71:953–63

Hammerstein P. 2003. Why is reciprocity so rare in social animals? A protestant appeal. In *Genetic and Cultural Evolution of Cooperation*, ed. P Hammerstein, pp. 83–94. Cambridge, MA: MIT Press

Hare B, Call J, Agnetta B, Tomasello M. 2000. Chimpanzees know what conspecifics do and do not see. *Anim. Behav.* 59:771–85

Hart HLA, Honore T. 1985. *Causation in the Law*. Oxford, UK: Oxford Univ. Press

Hauser M. 2006. *Moral Minds*. New York: Ecco/Harper Collins

Hauser M, Spaulding B. 2006. Wild rhesus monkeys generate causal inferences about possible and impossible physical transformations in the absence of experience. *Proc. Natl. Acad. Sci. USA* 103:7181–85

Hauser M, Spelke ES. 2004. Evolutionary and developmental foundations of human knowledge: a case study of mathematics. In *The Cognitive Neurosciences, Vol. 3*, ed. M Gazzaniga, pp. 325–41. Cambridge, MA: MIT Press

Hauser M, Wood JN, Glynn DD. 2007. Wild, untrained and nonenculturated rhesus monkeys correctly read the goal-relevant gestures of a human agent. *Proc. R. Soc. London B: Biol. Sci.* 274:1913–18

Hauser MD. 2009. The possibility of impossible cultures. *Nature* 460:190–96

Hauser MD, Chen MK, Chen F, Chuang E. 2003. Give unto others: genetically unrelated cotton-top tamarin monkeys preferentially give food to those who altruistically give food back. *Proc. R. Soc. London B: Biol. Sci.* 270:2363–70

Kawai N, Matsuzawa T. 2000. Numerical memory span in a chimpanzee. *Nature* 403:39–40

Kirsh D. 1991. *Foundations of Artificial Intelligence*. Cambridge, MA: MIT Press

Lakoff G, Johnson M. 1999. *Philosophy in the Flesh: The Embodied Mind and Its Challenge to Western Thought*. New York: Basic Books

Langergraber KE, Mitani JC, Vigilant L. 2007. The limited impact of kinship on cooperation in wild chimpanzees. *Proc. Natl. Acad. Sci. USA* 104:7786–90

Mahon BZ, Caramazza A. 2008. A critical look at the embodied cognition hypothesis and a new proposal for grounding conceptual content. *J. Physiol.* 102:59–70

Melis AP, Hare B, Tomasello M. 2006. Chimpanzees recruit the best collaborators. *Science* 311:1297–300

Melis AP, Hare B, Tomasello M. 2008. Do chimpanzees reciprocate received favours? *Anim. Behav.* 76:951–62

Michotte A. 1962. *The Perception of Causality*. London: Methuen

Muller MN, Mitani JC. 2005. Conflict and cooperation in wild chimpanzees. *Adv. Stud. Behav.* 35:275–331

Parr LA. 2003. The discrimination of faces and their emotional content by chimpanzees (*Pan troglodytes*). *Ann. N. Y. Acad. Sci.* 1000:56–78

Pulvermuller F. 2005. Brain mechanisms linking language and action. *Nat. Rev. Neurosci.* 6:576–82

Range F, Horn LVZ, Huber L. 2009. Absence of reward induced aversion to inequity in dogs. *Proc. Natl. Acad. Sci. USA* 106:340–45

Range F, Viranyi Z, Huber L. 2007. Selective imitation in domestic dogs. *Curr. Biol.* 17:1–5

Rawls J. 1971. *A Theory of Justice*. Cambridge, MA: Harvard Univ. Press

Rizzolatti G, Arbib MA. 1998. Language within our grasp. *Trends Neurosci.* 21:188–94

Rizzolatti G, Fadiga L, Fogassi L, Gallese V. 1999. Resonance behaviors and mirror neurons. *Arch. Ital. Biol.* 137

Rizzolatti G, Fadiga L, Gallese V, Fogassi L. 1996. Premotor cortex and the recognition of motor actions. *Cogn. Brain Res.* 3:131–41

Rizzolatti G, Fogassi L, Gallese V. 2001. Neurophysiological mechanisms underlying the understanding and imitation of action. *Nat. Rev. Neurosci.* 2:661–70

Rochat M, Serra E, Fadiga L, Gallese V. 2008. The evolution of social cognition: goal familiarity shapes monkeys' action understanding. *Curr. Biol.* 18:227–32

Roma PG, Silberberg A, Ruggiero AM, Suomi SJ. 2006a. Capuchin monkeys, inequity aversion, and the frustration effect. *J. Comp. Psychol.* 120:67–73

Roma PG, Silberberg A, Ruggiero AM, Suomi SJ. 2006b. On inequity aversion in nonhuman primates. *J. Comp. Psychol.* 120:76

Rosati A, Stevens J, Hare B, Hauser M. 2007. The evolutionary origins of human patience: temporal preferences in chimpanzees, bonobos, and human adults. *Curr. Biol.* 17:1663–68

Rozin P. 2000. Evolution and adaptation in the understanding of behavior, culture, and mind. *Am. Behav. Sci.* 43(6):970–86

Santos LR, Miller CT, Hauser M. 2003. Representing tools: how two nonhuman primate species distinguish between the functionally relevant and irrelevant features of tools. *Anim. Cogn.* 6:269–81

Sommerville JA, Woodward AL. 2005. Pulling out the intentional structure of human action: the relation between action production and processing in infancy. *Cognition* 95:1–30

Sommerville JA, Woodward AL, Needham A. 2005. Action experience alters 3-month-old infants' perception of others' actions. *Cognition* 96:B1–11

Stevens JR, Hauser MD. 2004. Why be nice? Psychological constraints on the evolution of cooperation. *Trends Cogn. Sci.* 8:60–65

Tinbergen N. 1963. On aims and methods in ethology. *Zeitschrift fur Tierpsychologie* 20:410–33

Tomasello M, Carpenter M, Call J, Behne T, Moll H. 2005. Understanding and sharing intentions: the origins of cultural cognition. *Behav. Brain Sci.* 28:1–17

Trivers RL. 1971. The evolution of reciprocal altruism. *Q. Rev. Biol.* 46:35–57

Umilta MA, Kohler E, Gallese V, Fogassi L, Fadiga L, et al. 2001. I know what you are doing: a neurophysiological study. *Neuron* 31:155–65

van Wolkenten M, Brosnan SF, de Waal FBM. 2007. Inequity responses of monkeys modified by effort. *Proc. Natl. Acad. Sci. USA* 47:18854–59

Warneken F, Hare B, Melis A, Hanus D, Tomasello M. 2007. Spontaneous altruism by chimpanzees and young children. *PLoS Biol.* 5:5–10

Warneken F, Tomasello M. 2006. Altruistic helping in human infants and young chimpanzees. *Science* 311:1301–3

Wheatley T, Milleville SC, Martin A. 2007. Understanding animate agents: distinct roles for the social network and mirror system. *Psychol. Sci.* 18:469–74

Wood JN, Hauser MD. 2008. Action comprehension in nonhuman primates: motor simulation or inferential reasoning? *Trends Cogn. Sci.* 12:461–65

Wood JN, Glynn DD, Hauser MD. 2007a. The uniquely human capacity to throw evolved from a nonthrowing primate: an evolutionary dissociation between action and perception. *Biol. Lett.* 3:360–64

Wood JN, Glynn DD, Phillips BC, Hauser MD. 2007b. The perception of rational, goal-directed action in nonhuman primates. *Science* 317:1402–5

Wood JN, Hauser M, Glynn DD. 2008. Rhesus monkeys' understanding of actions and goals. *Soc. Neurosci.* 3:60–68

Woodward AL. 1998. Infants selectively encode the goal object of an actor's reach. *Cognition* 69:1–34

Woodward AL. 1999. Infants' ability to distinguish between purposeful and nonpurposeful behaviors. *Infant Behav. Dev.* 17:515–21

Wynne CDL. 2004. Fair refusal by capuchin monkeys. *Nature* 428:140
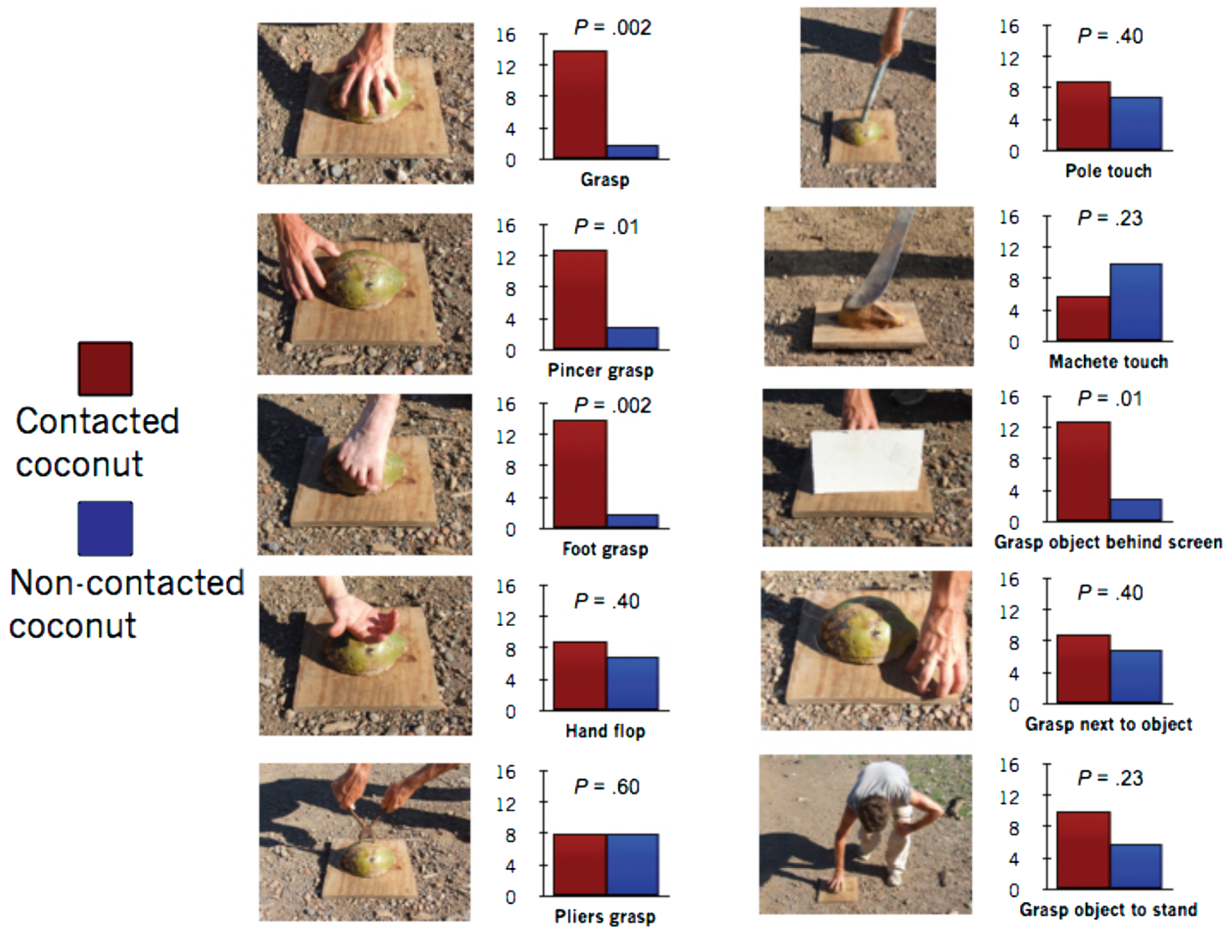
Figure 1

Illustration of the final frame of the actions presented to rhesus monkeys in the two-option forced-choice social foraging method, along with the corresponding results showing the number of subjects that selectively inspected the coconut shell that the experimenter acted toward versus the coconut shell that the experimenter did not act toward. Data reported in Wood et al. (2008).

**Annual Review of
Psychology**

Volume 61, 2010

Contents

Bargaining, Negotiation, Conflict, Social Justice

Personality Development: Stability and Change

Work Motivation

Cognition in Organizations

Work Attitudes (Job Satisfaction, Commitment, Identification)

Human Factors (Machine Information, Person Machine Information, Workplace Conditions)

Learning and Performance in Educational Settings

Personality and Coping Styles

Indexes

Errata

An online log of corrections to *Annual Review of Psychology* articles may be found at
http://psych.annualreviews.org/errata.shtml