

This article was downloaded by:[Wood, Justin N.]
On: 12 October 2007
Access Details: [subscription number 782996181]
Publisher: Psychology Press
Informa Ltd Registered in England and Wales Registered Number: 1072954
Registered office: Mortimer House, 37-41 Mortimer Street, London W1T 3JH, UK



Social Neuroscience

Publication details, including instructions for authors and subscription information:
<http://www.informaworld.com/smpp/title~content=t741771143>

Rhesus monkeys' understanding of actions and goals

Justin N. Wood ^a; David D. Glynn ^a; Marc D. Hauser ^a
^a Harvard University, Cambridge, Massachusetts, USA

Online Publication Date: 01 January 2007

To cite this Article: Wood, Justin N., Glynn, David D. and Hauser, Marc D. (2007)
'Rhesus monkeys' understanding of actions and goals', *Social Neuroscience*, 1 - 9

To link to this article: DOI: 10.1080/17470910701563442

URL: <http://dx.doi.org/10.1080/17470910701563442>

PLEASE SCROLL DOWN FOR ARTICLE

Full terms and conditions of use: <http://www.informaworld.com/terms-and-conditions-of-access.pdf>

This article maybe used for research, teaching and private study purposes. Any substantial or systematic reproduction, re-distribution, re-selling, loan or sub-licensing, systematic supply or distribution in any form to anyone is expressly forbidden.

The publisher does not give any warranty express or implied or make any representation that the contents will be complete or accurate or up to date. The accuracy of any instructions, formulae and drug doses should be independently verified with primary sources. The publisher shall not be liable for any loss, actions, claims, proceedings, demand or costs or damages whatsoever or howsoever caused arising directly or indirectly in connection with or arising out of the use of this material.

Rhesus monkeys' understanding of actions and goals

Justin N. Wood, David D. Glynn, and Marc D. Hauser
Harvard University, Cambridge, Massachusetts, USA

A forced-choice social foraging method was used to explore how free-ranging rhesus monkeys make inferences about other individuals' goals and intentions. Subjects saw an experimenter perform an action towards one of two potential food sources, then were allowed to approach and choose one of those sources. Results showed that subjects selectively picked the food source targeted by the experimenter's action only when the action was within the rhesus' motor repertoire. Further studies explored the extent to which rhesus attend to the details of the goal as well as the means by which the goal was obtained, with results paralleling those obtained from cellular recordings of macaque mirror neurons. Monkeys' pattern of success and failure supports the hypothesis that motor areas play a functionally significant role in event parsing and action understanding.

Social organization depends on the ability to reason about the behavior of other individuals. Recent studies show that nonhuman animals are capable of making inferences about the mental states of other individuals, reasoning about what others can and cannot see, in the service of competitive and cooperative interactions (Dally, Emery, & Clayton, 2006; Flombaum & Santos, 2005; Hare, Call, Agnetta, & Tomasello, 2000). Here, we explored a related psychological component of social understanding, investigating how rhesus monkeys make spontaneous inferences about the actions of others toward particular goals.

A substantial set of physiological studies provided the theoretical and methodological background for the present set of experiments. In particular, the relevant physiological evidence comes from cellular recordings of neurons in

area F5 of the macaque premotor cortex. Some neurons in this area activate both when an individual observes an experimenter act on an object and when the individual acts in the same way. 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* (see Rizzolatti, Fogassi, & Gallese, 2001). Of particular relevance both conceptually and methodologically for the present studies is that these neurons are highly sensitive to the details of an event, and 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 same neurons do not fire when a set of pliers grasps the same object (Rizzolatti, Fadiga, Gallese, & Fogassi,

Correspondence should be addressed to: Justin N. Wood, Harvard University, Department of Psychology, 33 Kirkland Street, Cambridge, MA 02138, USA. E-mail: jwood@wjh.harvard.edu

This publication was made possible by Grant Number CM-5-P40RR003640–13 from the National Center for Research Resources (NCRR), a component of the National Institutes of Health (NIH). Its contents are solely the responsibility of the authors and do not necessarily represent the official views of NCRR or NIH. Further support comes from a fellowship from the NIH (NRSA) awarded to JW and by an NSF-ROLE grant awarded to MH.

We thank Jonathan Beier, Fiery Cushman, Pierre Jacob, and Rebecca Saxe for helpful comments on an earlier version of this manuscript, and Melissa Gerald for facilitating our research on Cayo Santiago. This research adheres to the Animal Behavior Society Guidelines for the Use of Animals in Research, the legal requirements of the country in which the work was carried out and all institutional guidelines.

1996; Rizzolatti et al., 2001). This, together with several other findings, suggests that the mirror neuron system maintains a functional library of the animal's gestural repertoire. Based on these activation patterns, theorists have suggested that an organism comprehends the actions of others through its own actions (simulation theory), mapping a visual representation of an observed action onto its own motor system (Gallese & Goldman, 1998; Goldman, 1989; Gordon, 1986; Heal, 1986; Iacoboni et al., 1999; Rizzolatti et al., 2001). Thus, under this model, observed actions are perceived as intentional only in contexts in which the individual's own behavior would be intentional when performing the same action.

Despite the wealth of neurophysiological data, there is little behavioral evidence investigating how animals make spontaneous inferences about the actions of others. Call, Hare, Carpenter, and Tomasello (2004) showed that captive chimpanzees distinguish between an experimenter that is unable to give food versus an experimenter that is unwilling to do so, and Santos and Hauser (1999) used an expectancy violation measure to show that cotton-top tamarins were able to form an expectation about where an experimenter would reach based on where they were looking. However, there have been no behavioral studies investigating whether, and in what capacity, nonhuman animals parse actions into relevant component dimensions, attending to the details of agents' actions, goals, and the means by which the goals were obtained, leaving considerable debate regarding the cognitive and neural mechanisms underlying action understanding, and especially its evolutionary ancestry.

Here, we present a series of experiments aimed at understanding how macaques parse actions, and specifically whether they are sensitive to details of the agent's goals, as well as the means of achieving such goals. Specifically, the present study had two goals. First, we wanted to develop a new naturalistic, ecologically valid method that could be used to measure subjects' spontaneous responses to different details of an event when observing others perform goal-directed behaviors. Second, we wanted to test subjects using the same properties that have been explored extensively in physiological investigations, thereby providing both insights into the neural bases of action understanding, and potentially a new method

for marrying physiological recordings with detailed, spontaneous, behavioral assays.

EXPERIMENT 1

In Experiment 1, we modified the forced-choice measure used previously to study rhesus monkeys' spontaneous numerical representations (Hauser, Carey, & Hauser, 2000) as well as their capacity to identify edible objects (Santos, Hauser, & Spelke, 2001). In the latter studies, when a human experimenter ate one of two novel food items and then gave rhesus a choice between these two, rhesus selectively approached the food consumed, using color as opposed to shape to mediate their choice. In the present experiments, an experimenter presented two potential food sources (coconut shells) to a monkey subject, acted on one of the shells, and then walked away, allowing the subject to selectively approach. Although coconuts are native to the island of Cayo Santiago, rhesus macaques cannot open the hard outer shells themselves and therefore only obtain the desired inner fruit when the coconuts crack open naturally or have been opened and discarded by a human. We therefore reasoned that when subjects perceive the experimenter's actions as goal-directed toward one of the two coconut shells, then they should more readily approach this coconut.

Methods

Participants

We tested rhesus monkeys living on the island of Cayo Santiago, Puerto Rico (see Rawlins & Kessler, 1987, for details concerning this population). In each condition we successfully tested 16 adult male and female rhesus monkeys; no subject appeared more than once in any condition. With a two-option, forced-choice method, approximately 60% of trials were aborted because of failure to approach (40%), interference from another monkey (15%), or lack of attention to the presentation (5%).

Procedure

We first collected observational data of monkeys acting towards food in order to determine food-related actions within their behavioral repertoire. Rhesus spontaneously grasp objects

with their hand, a pointer finger and thumb precision grip, and their feet. Based on these observations, we tested whether monkeys would preferentially inspect the coconut that was the target of these actions when performed by a human experimenter.

An experimenter set out to find a lone adult subject, not engaged in any distracting activity, such as eating, grooming, or fighting. The experimenter placed two wooden platforms (30 × 30 cm) containing nearly identical looking coconut shells on the ground in front of the subject, 2 meters apart and 2–5 meters from the test subject. The experimenter attracted the attention of the subject and then looked at and performed an action towards one of the two coconuts, maintaining contact for 5 s. He then stood up, turned 180 degrees, and walked away at an even pace, allowing the monkey to approach and inspect one of the coconuts (see Figure 1). We defined a choice as the first coconut approached and touched. We aborted trials when the test subject: (1) failed to watch any part of the presentation; (2) was distracted by another individual during the presentation or choice period; or (3) failed to choose one of the coconuts within 10 s. For each action type, we counterbalanced the targeted side (left versus right).

Description of action types

Grasp. The experimenter reached directly for and grasped the coconut (see Figure 1).

Grip. The experimenter gripped the coconut using a pointer finger and thumb precision grip, with the middle, ring, and little finger extended outwards.

Foot grasp. The experimenter moved his foot directly towards the coconut and then curled his foot around it.

Results and discussion

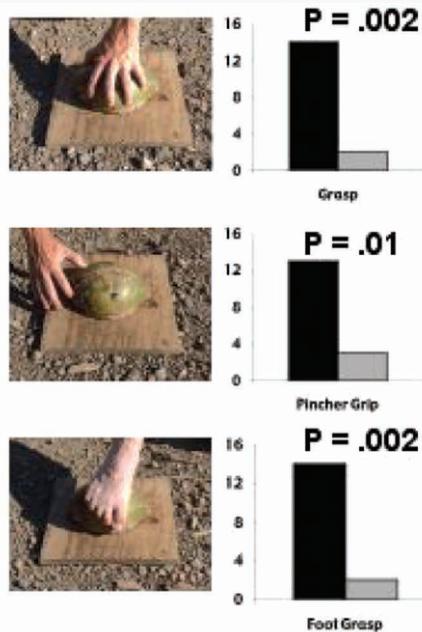
Pooling across all three action types, subjects were more likely to approach the coconut that the experimenter acted towards compared to chance (50%) performance, $\chi^2(1, N = 48) = 13.77, P < .001$ (see Figure 2). Further tests revealed significant, above chance performance for all tested actions: hand grasp (14/16 subjects, binomial probability: $P = .002$), precision grip (13/16 subjects, $P = .01$), and foot grasp (14/16 subjects, $P = .002$). These results show that monkeys preferred to approach an object towards which an experimenter acted.

Monkeys could have approached the contacted coconut shell either because they used the experimenter's actions to locate potential food (the inner coconut fruit), or because they prefer to inspect objects handled by a human experimenter without making the inference that the experimenter was reaching for the coconut containing hidden food. If the former hypothesis is correct, then monkeys should disregard the experimenter's action if both choices clearly contain food, because they would no longer need to use this information as a cue to locate food. In contrast, if monkeys simply prefer to inspect objects that have been touched by an experimenter, then they should continue to show this preference even when presented with unambiguous food objects. In two further studies, we found that monkeys did not selectively approach the contacted shell when the experimenter grasped one of two large carrot wedges in which food was directly available (6/16 subjects, $P = .23$) or one of two coconut shells that were placed so that the subject could see before approaching that both shells contained fruit (9/16 subjects, $P = .40$).



Figure 1. Sample frames from the subject's point of view for the hand-grasp action from Experiment 1. The experimenter approached two coconut shells (Frame 1), reached for and grasped one of the shells (Frames 2–3), and then walked away (Frame 4), allowing the subject to selectively approach.

Actions Within Behavioral Repertoire



 = Contacted coconut
 = Non-contacted coconut

Actions Not Within Behavioral Repertoire

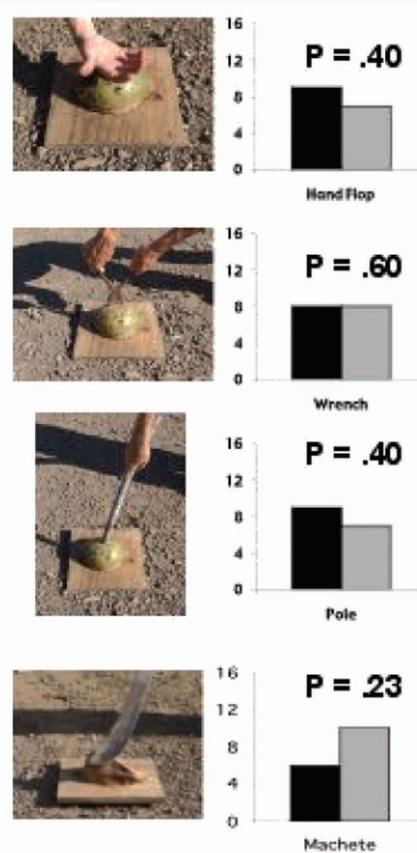


Figure 2. Results from Experiments 1 and 2. Depiction of food-related actions that rhesus monkeys produce (left) and those they do not (right), along with the corresponding results showing the number of subjects that selectively inspected the coconut that the experimenter acted towards (black bars) versus the coconut that the experimenter did not act towards (grey bars). *P*-values represent binomial probabilities with an alpha-level set to .05 (1-tailed prediction).

Rhesus therefore appear to use the experimenter's actions to locate potential food, rather than simply preferring handled objects more generally.

EXPERIMENT 2

Experiment 1 showed that rhesus preferentially inspected the coconut targeted by an action that was part of their behavioral repertoire; moreover, the pattern observed cannot be explained by a general preference to approach contacted objects as rhesus failed to show a selective approach when food was directly visible and accessible. In Experiment 2, we asked whether

the observed preference extends to actions that fall outside of their species-typical motor repertoire. Simulation theory predicts that subjects should understand an action only when the action is part of their motor repertoire, because intentions are computed by simulating actions within the individual's motor system.

We tested monkeys' response to four action types. Over the course of our observations, beginning in 1987, we have never observed any instance of rhesus acting on food with another object such as a tool, or dropping their hand on an object with their palm facing upwards in a goal-directed manner. Thus, we asked whether monkeys would prefer to inspect the coconut that was touched

with a pole, touched with a machete, grasped with pliers, or contacted with the back of the hand.

Methods

Experiment 2 was identical to Experiment 1, except for the actions tested. The tested actions were the following:

Hand flop. The experimenter dropped his hand onto the coconut with his palm facing upwards in a manner that appeared, from a human perspective, unintentional and non-goal directed (Woodward, 1999). This action was designed as a contrast with the intentional grasp of Experiment 1.

Pliers. The experimenter grasped the object with a pair of pliers, holding each arm of the pliers with one of his hands. This action was designed as a contrast to the pincer grip presented in Experiment 1.

Pole. The experimenter touched the object with a steel pole (30°cm in length). This action was designed to extend the logic of the pliers condition to another object, but with minimal contact and action at the coconut itself.

Machete. The experimenter touched the object with a large machete (90°cm in length), the type of tool used to open coconuts on the island, typically in full view of the monkeys. This action was designed to compliment both the pliers and the pole action types, and also to explore the role of perceptual familiarity and previous experience with tools and the objects they target.

Results and discussion

Pooling across action conditions, there was no evidence of a statistically significant pattern of approach based on the experimenter's actions leading to contact with one coconut, $\chi^2(1, N = 64) = 1, P = 0$ (see Figure 1). Further tests revealed non-significant effects for all tested actions: touching the object with the back of the hand (9/16 subjects, $P = .40$), pliers grasp (8/16 subjects, $P = .60$), pole touch (9/16 subjects, $P = .40$), and machete touch (6/16 subjects, $P = .23$).

Across Experiments 1 and 2, subjects were more likely to approach the coconut that the

experimenter acted towards when it was an action that rhesus monkeys perform themselves when engaged in food-directed behavior, $\chi^2(1, N = 112) = 15.16, P < .001$.

Experiments 1 and 2 provided evidence that, at least in this context, monkeys' capacity to reason about the actions of others depends on their own ability to produce those actions. If monkeys watch a human experimenter perform an action towards one of two potential food sources, then they are more likely to inspect that food source if the observed action is part of their motor repertoire, and if it is goal-directed. The present results cannot be accounted for by familiarity with how objects are typically handled. The individuals within this population have experience of observing humans using tools, yet they did not preferentially inspect the object targeted by these actions. This is especially the case for the action involving the machete, because coconuts are opened on the island by using machetes, often in full view of the monkeys. However, these individuals have little to no experience of humans grasping objects with their feet, yet they nevertheless inspected the coconut targeted by this action. Thus, monkeys' own capacity to produce an action, rather than their acquired experience of others performing actions, best predicts whether they will inspect the goal of these actions in this social foraging context.

EXPERIMENT 3

In Experiment 3, we tested whether performance changes depending on whether subjects can observe all parts of the action (object, hand, movement, hand-object interaction) compared to only parts of the action (hand and movement only). Physiological studies show that mirror neurons activate both when observing a complete action as well as when all of the elements that compose the action are not present (Umiltà et al., 2001). If this characteristic of mirror neuron activation also applies when rhesus make inferences about others' goals, then our subjects should continue to perceive actions as goal-directed even when part of the action occurs out of view.

Methods

We successfully tested 16 subjects. Experiments 3 was identical to Experiment 1, except in the

following ways. The experimenter first showed the subject the coconuts on the platforms, and then turned the platforms 90 degrees so that the coconuts were hidden behind occluders (15 × 15 cm). He then reached directly for and grasped one of the coconuts.

Results and discussion

Monkeys selectively inspected the coconut that the experimenter grasped behind an occluder (13/16 subjects, $P = .01$; see Figure 3, *top*). Together, Experiments 1–3 suggest that the meaning of an action can be computed from a full visual

description of an action as well as from the mental representation of that action. Moreover, these results provide evidence for an additional parallel between the activation patterns of mirror neurons and rhesus' spontaneous capacity to perceive observed actions as goal-directed in the wild.

EXPERIMENTS 4 AND 5

In Experiments 4 and 5, we investigated two additional properties of how nonhuman primates reason about the actions of others. Specifically, we tested monkeys' response to details of actions

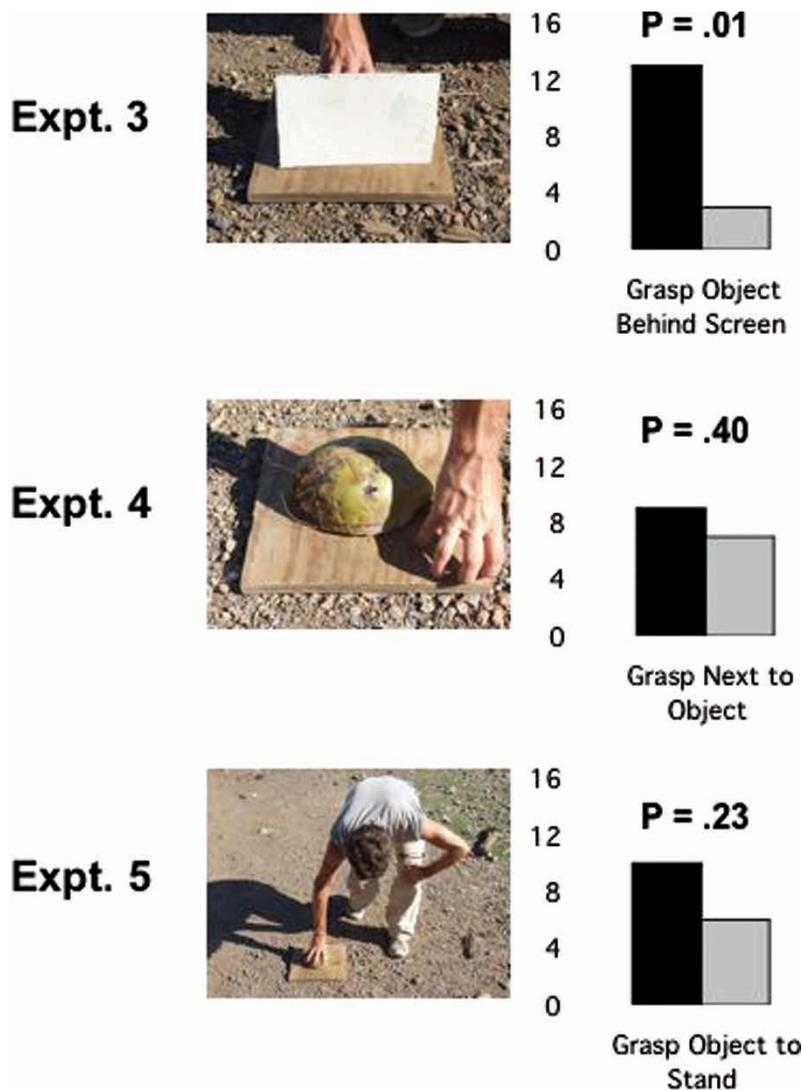


Figure 3. Results from Experiments 3–5. *Top*, results of approaching behavior when the monkey could not see the final part of the action. *Middle*, results of monkeys' approaching behavior when the experimenter performed a grasping action that was not object-directed. *Bottom*, results of approaching behavior when the experimenter placed his hand on the coconut to support his balance while standing up.

that have been previously shown to influence the activation of mirror neurons. First, 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; Rizzolatti et al., 2001). Similarly, Experiment 4 asked whether monkeys would selectively approach when the experimenter reached next to, rather than directly for, the coconut. If rhesus perceive actions as goal-directed towards an object only when observing or inferring hand-object interactions, then they should not prefer either coconut in this condition. In contrast, if monkeys perceive the experimenter's actions as goal-directed to locations in space, for instance, then they should selectively approach the coconut nearest to the experimenter's reach.

Second, 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 action (e.g., eating versus placing), suggesting that these neurons code the agent's intention (Fogassi et al., 2005). Similarly, Experiment 5 asked whether rhesus monkeys code the experimenter's intentions for the smaller acts that compose the action (the grasping act itself) or for the broader action (grasping to obtain food versus grasping to stand). If rhesus code intentions at the level of the act, then they should continue to approach the grasped coconut even when the experimenter appears to grasp the coconut for balance rather than for obtaining food. In contrast, if monkeys code the intention of the broader action, then monkeys should not selectively approach the grasped coconut shell because the intent of the experimenter was to use the coconut for balance.

Methods

We successfully tested 16 subjects in each experiment. Experiments 4 and 5 were identical to Experiment 1, except for the actions tested. The tested actions were the following:

Grasp next to object. The experimenter reached next to, rather than directly for, the coconut.

Grasp object to stand. The experimenter placed his hand on the coconut to support his balance

while standing up, as if the primary purpose of grasping the coconut was support rather than obtaining food. The experimenter maintained contact with the object for 2 s.

Results and discussion

Grasp next to object. When the experimenter reached directly next to the coconut, subjects did not selectively inspect either object (9/16 subjects, $P = .40$), compared to when the experimenter grasped the coconut directly in the grasping condition from Experiment 1, $\chi^2(1, N = 32) = 3.87, P = .025$, 1-tailed prediction (see Figure 3, *middle*).

Grasp object to stand. When the experimenter placed his hand on the coconut to support his balance while standing up, monkeys did not selectively inspect either object (10/16 subjects, $P = .23$), compared to when the experimenter grasped the coconut in the grasping condition from Experiment 1, $\chi^2(1, N = 32) = 2.67, P = .05$, 1-tailed prediction. To ensure that 2 s was sufficient for encoding the target of the action, we tested monkeys with the grasping action from Experiment 1 but where the experimenter maintained contact with the object for only 1 s. Monkeys preferred to inspect the grasped coconut when the experimenter maintained contact for 1 s (13/16 subjects, $P = .01$), showing that monkeys' failure to approach the contacted coconut in Experiment 5 could not have been due to insufficient encoding time (see Figure 3, *bottom*).

In summary, Experiment 4 showed that rhesus do not perceive actions as goal-directed towards an object when the agent reaches directly next to an object, and Experiment 5 showed that rhesus code intentions at the level of broader actions rather than at the level of the action units that compose them.

GENERAL DISCUSSION

The present studies were designed to explore how rhesus monkeys make spontaneous inferences about other individuals' actions, using an ecologically valid task. Our results support at least two primary conclusions. First, rhesus monkeys appear to understand, at least to some extent, the behavior of other individuals through a simulation-based mechanism, such that individuals perceive others' actions as goal-directed provided

that they observe actions that are within their own motor system. Rhesus selectively inspected the coconut that an experimenter acted towards after observing actions within their motor repertoire (hand grasp, pincher grip, foot grasp), but not after observing actions that they do not spontaneously produce themselves when engaged in goal-directed behavior (dropping the back of the hand on the object, touching the object with a pole or machete, grasping the object with pliers). Thus, monkeys may have failed to process the meaning of the actions in Experiment 2 because they were unable to simulate actions that fell outside of their motor repertoire.

Familiarity with the objects and actions cannot explain the pattern of results. Although rhesus have no experience of seeing humans use their feet to grasp objects, they do have some experience of seeing humans use a machete to open coconuts. If rhesus use familiar actions and means of contact to determine object selection, then they should have preferentially approached the coconut contacted by a machete, but shown no preference for the coconut grasped by the experimenter's foot. We found exactly the opposite. Similarly, although grasping an object as a means of support is something that rhesus both do themselves, and witness others doing, they failed to use the experimenter's grasp-for-support action as a relevant cue for approach.

Second, these findings shed light on the neural bases of event parsing and action comprehension. Physiologists have described a set of properties that characterize the activation of mirror neurons during the perception of goal-directed actions. Similarly, on the behavioral level, our results describe a set of properties that trigger attributions of goal-directed behavior. Experiments 1 and 2 show that rhesus' spontaneous foraging behavior depends on the same link between action perception and production that is the defining characteristic of mirror neurons, and Experiment 3 shows that representations of goal-directed behavior can be constructed even in the absence of a full visual description of the action, analogous to F5 mirror neurons that activate when a completed action is directly observed as well as when it is inferred based on the trajectory of a hand behind an occluder (Umiltà et al., 2001). The results from Experiment 4 show that like mirror neurons that do not activate when a monkey observes intransitive gestures, our subjects did not inspect the food source nearest to an action that was not object-

directed. Finally, results from Experiment 5 show that like mirror neurons in the inferior parietal lobe, which show differential patterns of activation to the same act presented in different event contexts, our subjects showed different approach behavior to the same act (grasping the coconut) presented in different event contexts (directed grasp versus grasp for support). Although the convergence between these independently collected data sets do not license the claim that mirror neurons underlie the pattern of behaviors discussed here, they do suggest that this system plays a role in the guidance of functionally parallel behavioral distinctions.

What is the specific role of motor knowledge in action perception? Our results are consistent with at least two possibilities. First, as suggested by Rizzolatti and colleagues (2001), action understanding may consist of an automatic mapping between the visual characteristics of an action and the observer's own motor system. Under this account, actions are automatically perceived as goal-directed when the animal's own behavior would have been goal-directed while performing that same action.

Second, motor knowledge may operate within a more broadly defined system of goal attribution. Gergely and Csibra (2003) have shown that human infants engage in teleological reasoning, where the outcome of an action may, or may not, be seen as a goal, depending on whether the outcome is perceived to justify the action given the environmental constraints faced by the agent. Motor knowledge may be one of many types of information used to evaluate whether an action is rational, conjoining with information processed in non-motor neural substrates (see Perrett, Mistlin, Harries, & Chitty, 1990). Support for this claim comes from studies showing that human infants are capable of perceiving actions as goal-directed when performed by hands (Woodward, 1998), people (Kamewari, Kato, Kanda, Ishiguro, & Hiraki, 2005; Sodian, Schoepner, & Metz, 2004), robots (Kamewari et al., 2005), puppets (Sodian et al., 2004), and geometric shapes performing simple motion trajectories (Csibra, Bíró, Koós, & Gergely, 2003; Gergely, Nadasdy, Csibra, & Bíró, 1995; Wager & Carey, 2005). Thus, motor simulation cannot fully account for these findings, because even though many of these agents were not human or did not have similar body types as human infants, infants were still able to evaluate their actions as goal-directed. Current studies are investigating the nature, and

relation, between motor simulation and information concerning the environmental constraints that guide rational action.

In summary, these studies show that rhesus macaques, and presumably other animals, use their own motor system, in at least some capacity, to make inferences about others' intentions and goals, using the correspondence between action perception and production to guide functionally adaptive, goal-directed behavior. These results therefore provide a crucial link between physiological and psychological mechanisms, while enriching understanding of our evolutionary history.

Manuscript received 28 August 2006

Manuscript accepted 21 July 2007

First published online day/month/year

REFERENCES

- Call, J., Hare, B., Carpenter, M., & Tomasello, M. (2004). "Unwilling" versus "unable": Chimpanzees' understanding of human intentional action. *Developmental Science*, 7(4), 488–498.
- Csibra, G., Bíró, S., Koós, S., & Gergely, G. (2003). One-year-old infants use teleological representations of actions productively. *Cognitive Science*, 27, 111–133.
- Dally, J. M., Emery, N. J., & Clayton, N. S. (2006). Food-caching western scrub-jays keep track of who was watching when. *Science*, 312, 1662–1665.
- Flombaum, J. I., & Santos, L. R. (2005). Rhesus monkeys attribute perceptions to others. *Current Biology*, 15, 447–452.
- Fogassi, L., Ferrari, P. F., Gesierich, B., Rozzi, S., Chersi, F., & Rizzolatti, G. (2005). Parietal lobe: from action organization to intentional understanding. *Science*, 308(5722), 662–667.
- Gallese, V., & Goldman, A. (1998). Mirror neurons and the simulation theory of mind-reading. *Trends in Cognitive Sciences*, 12, 493–501.
- Gergely, G., & Csibra, G. (2003). Teleological reasoning in infancy: The naïve theory of rational action. *Trends in Cognitive Sciences*, 7, 287–292.
- Gergely, G., Nadasdy, Z., Csibra, G., & Bíró, S. (1995). Taking the intentional stance at 12 months of age. *Cognition*, 56(2), 165–193.
- Goldman, A. (1989). Interpretation psychologized. *Mind and Language*, 4, 161–185.
- Gordon, R. (1986). Folk psychology as simulation. *Mind and Language*, 1, 158–171.
- Hare, B., Call, J., Agnetta, B., & Tomasello, M. (2000). Chimpanzees know what conspecifics do and do not see. *Animal Behaviour*, 59, 771–786.
- Hauser, M. D., Carey, S., & Hauser, L. B. (2000). Spontaneous number representation in semi-free ranging rhesus monkeys. *Proceedings of the Royal Society of London*, 267, 829–833.
- Heal, J. (1986). Replication and functionalism. In J. Butterfield (Ed.), *Language, mind, and logic* (pp. 135–150). Cambridge, UK: Cambridge University Press.
- Iacoboni, M., Woods, R. P., Brass, M., Bekkering, H., Mazziotta, J. C., & Rizzolatti, G. (1999). Cortical mechanisms of human imitation. *Science*, 286, 2526–2528.
- Kamewari, K., Kato, M., Kanda, T., Ishiguro, H., & Hiraki, K. (2005). Six-and-a-half-month-old children positively attribute goals to human action and to humanoid-robot motion. *Cognitive Development*, 20, 303–320.
- Perrett, D. I., Mistlin, A. J., Harries, M. H., & Chitty, A. J. (1990). Understanding the visual appearance and consequences of hand actions. In M. Goodale (Ed.), *Vision and action: The control of grasping* (pp. 163–342). Norwood, NJ: Ablex.
- Rawlins, R. G., & Kessler, M. G. (1987). *The Cayo Santiago macaques: History, behavior, and biology*. Albany, NY: SUNY Press.
- Rizzolatti, G., Fadiga, L., Gallese, V., & Fogassi, L. (1996). Premotor cortex and the recognition of motor actions. *Cognitive Brain Research*, 3, 131–141.
- Rizzolatti, G., Fogassi, L., & Gallese, V. (2001). Neurophysiological mechanisms underlying the understanding and imitation of action. *Nature Reviews Neuroscience*, 2, 661–670.
- Santos, L. R., & Hauser, M. D. (1999). How monkeys see the eyes: Cotton-top tamarins' reaction to changes in visual attention and action. *Animal Cognition*, 2, 35–41.
- Santos, L. R., Hauser, M. D., & Spelke, E. S. (2001). Representations of food kinds in the rhesus macaques (*Macaca mulatta*): An unexplored domain of knowledge. *Cognition*, 82, 127–155.
- Sodian, B., Schoeppner, B., & Metz, U. (2004). Do infants apply the principle of rational action to human agents? *Infant Behavior and Development*, 27, 31–41.
- Umiltà, M. A., Kohler, E., Gallese, V., Fogassi, L., Fadiga, L., Keysers, C., et al. (2001). I know what you are doing: A neurophysiological study. *Neuron*, 31, 155–165.
- Wagner, L., & Carey, S. (2005). 12-month-olds represent probable endings of motion events. *Infancy*, 7(1), 73–83.
- Woodward, A. L. (1998). Infants selectively encode the goal object of an actor's reach. *Cognition*, 69, 1–34.
- Woodward, A. L. (1999). Infants' ability to distinguish between purposeful and non-purposeful behaviors. *Infant Behavior and Development*, 22, 145–160.