Journal of Comparative Psychology
2015, Vol. 129, No. 3, 304–310

0735-7036/15/$12.00 http://dx.doi.org/10.1037/a0039294

Evidence That Monkeys (*Macaca tonkeana* and *Sapajus apella*) Read Moves, but no Evidence That They Read Goals

Morgane Costes-Thiré, Marine Levé, Pierre Uhlrich, and Cristian Pasquaretta
Centre National de la Recherche Scientifique and Université de Strasbourg

Arianna De Marco
Fondazione Ethoikos, Radicondoli, Italy; Parco Faunistico di Piano dell'Abatino, Poggio San Lorenzo, Italy; Istituto di Scienze e Tecnologie della Cognizione, Consiglio Nazionale delle Ricerche, Rome, Italy

Bernard Thierry
Centre National de la Recherche Scientifique and Université de Strasbourg

Whereas most experiments indicate that monkeys have no theory of mind, a study carried out by Wood and collaborators (2007) claimed that they can make inferences about the intentions of another individual. We applied the experimental procedure devised by these authors to investigate whether monkeys can recognize goal-directed actions. We tested 16 Tonkean macaques (*Macaca tonkeana*) and 12 tufted capuchin monkeys (*Sapajus apella*). Each subject was submitted to 24 trials in randomized order. The experimenter presented 2 containers, 1 of which was potentially baited with a food reward. After the experimenter had either intentionally or accidentally made an action on 1 of the containers, the subject was asked to select 1 of them. We found that individuals in both species failed to distinguish between accidental and intentional actions. However, they displayed a significant preference for the container touched by the experimenter in the hand conditions, and not in the elbow conditions. These results do not support those reported by Wood and collaborators, but they are consistent with other studies concluding that monkeys are not capable of mind reading.

Keywords: social cognition, theory of mind, intentionality, Tonkean macaque, capuchin monkey

Being sensitive to the attention of others and making inferences about their behavior allows animals to understand the meaning of the actions of other individuals. Animals can use human directional gestures as cues for finding hidden food (e.g., Emery & Clayton, 2009; Miklósi & Soproni, 2006), and experimental studies have shown that nonhuman primates adjust their own manual requesting gestures to the visual attention of others (Bourjade, Meguerditchian, Maille, Gaunet, & Vauclair, 2014; Liebal & Call, 2012; Maille, Engelhart, Bourjade, & Blois-Heulin, 2012). A main question, however, is whether attendants rely on their partners' intentions or behaviors, that is, whether or not they have a "theory of mind." For great apes such as chimpanzees, convincing evidence exists that they have some comprehension of mental states: They show awareness of what others perceive or know, and they appear able to distinguish between intentional and accidental actions (Call & Tomasello, 2008; Crockford, Wittig, Mundry, & Zuberbühler, 2012). In contrast, monkeys generally fail in tasks requiring them to attribute goals, knowledge or ignorance to partners, and it is generally held that they are not able to attribute intentions to others (Cheney & Seyfarth, 2007; Kummer, Anzenberger, & Hemelrijk, 1996; Suddendorf & Whiten, 2001). In experiments on perspective taking, for instance, chimpanzees (*Pan troglodytes*) take into account what their conspecifics can see, whereas tufted capuchin monkeys (*Sapajus apella*) do not recognize what their partner sees, and only behave on the basis of their partner's actions (Hare, Addessi, Call, Tomasello, & Visalberghi, 2003; Hare, Call, Agnetta, & Tomasello, 2000). Several researchers, however, think that monkeys could be capable of mind reading (Drayton & Santos, 2014; Marticorena, Ruiz, Mukerji, Goddu, & Santos, 2011; Overduin-de Vries, Spruijt, & Sterck, 2014; Phillips, Barnes, Mahajan, Yamaguchi, & Santos, 2009).

This article was published Online First May 25, 2015.

Morgane Costes-Thiré, Marine Levé, Pierre Uhlrich, and Cristian Pasquaretta, Centre National de la Recherche Scientifique, Département Ecologie, Physiologie et Ethologie, Strasbourg, France and Université de Strasbourg, Institut Pluridisciplinaire Hubert Curien, Strasbourg, France; Arianna De Marco, Fondazione Ethoikos, Radicondoli, Italy; Parco Faunistico di Piano dell'Abatino, Poggio San Lorenzo, Italy; and Istituto di Scienze e Tecnologie della Cognizione, Consiglio Nazionale delle Ricerche, Rome, Italy; Bernard Thierry, Centre National de la Recherche Scientifique, Département Ecologie, Physiologie et Ethologie, Strasbourg, France and Université de Strasbourg, Institut Pluridisciplinaire Hubert Curien, Strasbourg, France.

We are grateful to the staff of the *Parco Faunistico di Piano dell'Abatino* of Rieti for their unremitting support, to Elisabetta Visalberghi for her fruitful advice, and to three anonymous reviewers for their constructive comments.

Correspondence concerning this article should be addressed to Bernard Thierry, Département Ecologie, Physiologie et Ethologie, IPHC, CNRS, 23 rue Becquerel, 67087 Strasbourg, France. E-mail: bernard.thierry@iphc.cnrs.f

In this context, an often-quoted study by Wood and collaborators (Wood, Glynn, Phillips, & Hauser, 2007) tested cotton-top tamarins (*Saguinus oedipus*), rhesus macaques (*Macaca mulatta*), and chimpanzees in choice tasks where subjects were presented with two food containers. An experimenter performed an action that was either "intentional" or "accidental" on one of the containers. In all three species, animals selected the container targeted by the intentional action more frequently than that targeted by the accidental action, leading authors to conclude that the monkeys recognized goal-directed gestures. However, these results raise several concerns. Apart from the fact that the validity of the research work carried out by Hauser's team was questioned (Miller, 2010), it appears that the experimental procedure varied from one species to another, and involved different methodological problems. In particular, the training of tamarins prior to experiments involved the experimenter placing rewards in containers using a gesture similar to those qualified as intentional in subsequent trials, and this may have influenced the choices made by subjects during testing. Moreover, experiments in rhesus macaques were conducted in semifree ranging conditions and although they were replicated by Wood and Hauser (2011), the examination of video footage recorded during tests reveals substantial variations in the experimenter's posture and gestures from one trial to another. Since no attempt was made to check them, contrasts between experimental conditions may have been induced by a clever Hans effect due to unconscious experimenter bias.

The above problems prompted us to reproduce the study of Wood and collaborators (2007, 2011) in two further species of primates, tufted capuchin monkeys and Tonkean macaques (*Macaca tonkeana*). With regard to tufted capuchin monkeys and cotton-top tamarins, it is worth mentioning that these two New World species likely differ in their cognitive abilities. Capuchins monkeys generally exhibit higher performance in problem-solving tasks than callitrichid monkeys (Deaner, van Schaik, & Johnson, 2006; Tomasello & Call, 1997). By contrast, no major difference has been reported so far in the cognitive performances of macaque species. Direct comparisons, however, showed that Tonkean macaques were more responsive than rhesus macaques in object exploration tasks (Thierry, Anderson, Demaria, Desportes, & Petit, 1994), and perform better in experiments requiring the use of visual or auditory cues to locate food rewards (Petit, Dufour, Herrenschmidt, De Marco, Sterck, & Call, 2015). Thus, we conservatively assumed that capuchin monkeys and Tonkean macaques should not score less than tamarins and rhesus macaques in the task devised by Wood and collaborators (2007).

Given that nonhuman primates may take into consideration not only the type of action carried out by other individuals, but also the direction of their gaze and movements (Emery & Clayton, 2009; Liebal & Call, 2012; Miklósi & Soproni, 2006; Tomasello, Call, & Hare, 1998), we tested the following three hypotheses: (1) if subjects discriminate between intentional and accidental actions, they should choose the container targeted by the experimenter's intentional action more frequently; (2) if subjects mainly rely on the direction of the experimenter's gaze, they should show a stronger preference for the container the experimenter looks at, regardless of the intentional or accidental nature of her action; (3) if subjects use the experimenter's pointing movement, they should follow directional gestures more than nondirectional gestures.

Method

Subjects

We studied 16 Tonkean macaques and 12 tufted capuchin monkeys maintained in social groups at the Parco Faunistico di Piano dell'Abatino Rescue Centre in Rieti, Italy (Costes-Thiré, Levé, Uhlrich, De Marco, & Thierry, 2015). All subjects were captive-born. Their age and sex are presented in Table 1. Animals were never food deprived. They were fed with commercial diet pellets, fresh fruit and vegetables. Water was available ad libitum. For testing, positive reinforcement was used to temporarily separate subjects from the rest of the group and place them in an individual compartment. The subjects selected for testing were all individuals that willingly entered the compartment and took part in the experiment. The study complied with APA ethical guidelines.

Apparatus

We used two opaque containers, having covered the inside base with foam to avoid noise production when baiting a container with a piece of cake as food reward. The experimenter used a wooden spatula to fill the container or to give the reward to the subject, our aim being to avoid any resemblance between these actions and the gestures performed by the experimenter during testing. When it was necessary to prevent the subjects' visual access to the containers, an opaque screen was placed in front of the apparatus, as

Table 1
Species, Sex, and Age of Subjects

Name	Species	Sex	Age in years
Cho	Capuchin monkey	Male	25
Coc	Capuchin monkey	Male	23
Pil	Capuchin monkey	Male	22
Pim	Capuchin monkey	Female	16
Pic	Capuchin monkey	Male	12
Pet	Capuchin monkey	Female	12
Pao	Capuchin monkey	Female	12
Rav	Capuchin monkey	Male	11
Rel	Capuchin monkey	Male	11
Ros	Capuchin monkey	Female	11
Sam	Capuchin monkey	Male	10
Raj	Capuchin monkey	Male	6
Nat	Tonkean macaque	Male	14
Rim	Tonkean macaque	Male	11
Cha	Tonkean macaque	Male	11
Sib	Tonkean macaque	Female	10
Dan	Tonkean macaque	Female	10
Don	Tonkean macaque	Male	10
Sho	Tonkean macaque	Male	10
Fle	Tonkean macaque	Female	8
Utt	Tonkean macaque	Male	8
Gra	Tonkean macaque	Male	6
Gua	Tonkean macaque	Female	5
Dat	Tonkean macaque	Male	5
Cou	Tonkean macaque	Male	5
Gue	Tonkean macaque	Female	3
Arj	Tonkean macaque	Male	3
Ann	Tonkean macaque	Male	3

detailed below (see Figure 1). This occluder was equipped with a box in the middle of the rear side to allow experimenters to put the reward down without the subject seeing this action. Testing sessions were videotaped using two cameras for later analysis: the first focused on the subjects' choices, whereas the second focused on the experimenter's gestures.

Training Phase

Prior to the testing phase, we trained subjects to point at the container filled with a food reward. The experimenter sat in front of the subject. She repeatedly presented two empty containers placed 30 cm apart on a plate, then baited one container with a reward in full view of subjects. The latter had to touch the filled container or pass a hand through the fence toward it to obtain the reward; in other words, we did not require monkeys to point as a human would, but to use any hand motion to indicate the container they wanted. In a second step, each subject took part in a session of 12 trials to verify its ability to designate the filled container. In each trial the experimenter presented the containers and baited one of them in full view of the subject, as previously described. She then covered both containers with a lid and slid the plate toward the subject, keeping it out of its reach. The subject obtained the reward when pointing at the filled container. The reward was placed in each container six times in a randomized order. We required subjects to succeed in 11 out of 12 trials to be considered ready for testing. If they did not succeed, we repeated the session the next day. Fifteen subjects reached the criterion in one session, 10 needed two sessions, and three needed between three and five sessions.

Testing Procedure

We ran each subject in three daily sessions, each composed of 17 trials: 8 testing trials and 9 reinforcement trials. Testing trials involved an action carried out by the experimenter on one of the containers. Four different actions were performed (see Figure 2): (1) *Hand flop*: the experimenter placed her hand on the container, palm upward, for 3 s; (2) *Hand point*: the experimenter closed her hand by placing her thumb against her fingers and pointed vertically toward the container for 3 s; (3) *Hand empty elbow touch*: the experimenter held a wooden board in one hand and touched the container using the tip of the elbow of her free hand for 3 s; (4) *Hand occupied elbow touch*: the experimenter held a wooden board with both hands and touched the container with the tip of one of her elbows for 3 s. Wood and collaborators (2007) considered Actions 1 and 3 to be "accidental," as they assumed that they were not goal-directed. The same authors called Actions 2 and 4 "intentional" because they assumed that these actions designated a container. The rationale regarding Action 4 was that the elbow made it possible to point at the container when both hands were occupied.

In each trial, the experimenter sat in front of the subject with an assistant beside her. She placed the spatula with the food reward on the plate, and two empty containers placed 8 cm apart (Figure 1*a*). She showed the spatula to the subject, blocked its visual access to

Figure 1. Trial sequence: the experimenter presents the containers and the wooden spatula with the food reward (*a*), shows the spatula to the individual and places the screen in front of the containers (*b*), removes the screen then performs a targeted action toward a container (here the hand flop) (*c*), after which the subject may choose one container (*d*).

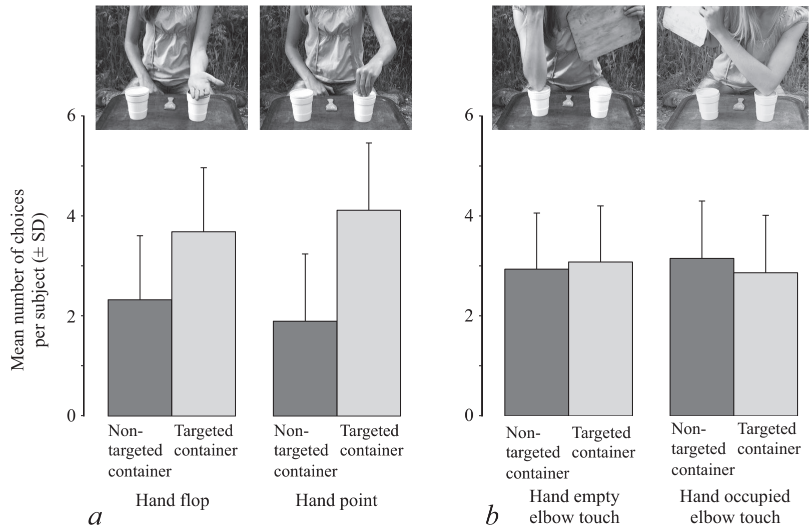

Figure 2. The performance of subjects in choosing targeted and nontargeted containers following "accidental" versus "intentional" action by the experimenter: (*a*) hand flop versus hand point, (*b*) hand empty elbow touch versus hand occupied elbow touch.

containers with the screen (Figure 1*b*), then placed the reward inside the box fixed to the back of the screen, and covered the containers with lids. Next, she removed the screen, performed one of the four targeting actions previously described while looking at the container (Figure 1*c*), and pulled the containers 30 cm apart before sliding the plate toward the subject, looking at a fixed point in the middle of the fence. Once the subject had chosen one container (Figure 1*d*), the plate and the containers were withdrawn and the trial ended. The experimenter waited 20 s before starting a new trial.

Each subject was submitted twice to the same action condition during a session. We randomized both the order of conditions and the side of the targeted container, left or right. To avoid potential learning effects we did not reward subjects during testing trials, so we added reinforcement trials before and after each testing trial to maintain motivation in the subjects. Reinforcement trials were identical to those carried out in the training session, meaning that the experimenter baited a container in full view of the subject, and gave it the reward if the correct response was obtained.

Videotape Analysis

Footage was processed by two collaborators who were uninformed about experimental conditions. One identified container choices from the videotapes of subject responses. The other measured two variables related to the experimenter's actions from the videotapes of her gestures: movement duration (time lapse between beginning of action and container contact) and pause duration (hand or elbow in contact with the container for approximately 3 s).

Statistical Analysis

We first checked for the absence of significant differences in the duration of the experimenter's movements and pauses during hand actions (hand flop vs. hand point) and elbow actions (hand empty vs. hand occupied) using a Kolmogorov–Smirnov test. We then compared how many times subjects chose targeted and nontargeted containers in the intentional and nonintentional conditions for the hand touch (i.e., hand flop vs. hand point), and the elbow touch (i.e., hand empty vs. hand occupied). We used a generalized linear mixed effect models (GLMM) approach following binomial law and logit link function. In order to evaluate possible differences between species within each condition, two more GLMMs for targeted/nontargeted choices were applied, including the species and their interaction with the two accidental/intentional conditions for hand or elbow touch as fixed effects. We used individual identity as random effect in each model to account for repeated measures. The models were implemented using the *glmer* function in the lme4 package of R (Bates, Maechler, Bolker, & Walker, 2014). Note that the GLMM approach represents a more powerful statistical method than the multiple nonparametric tests performed by Wood and collaborators (2007, 2011). Contrary to the latter, who employed one-tailed tests, we applied a two-tailed criterion of significance at the 0.05 level as we saw no justification for using a one-tailed criterion.

Results

We verified that the duration of the experimenter's movement and pause were not significantly different between hand flop and hand point actions (Kolmogorov–Smirnov test: movement, $D = 0.357$, $p = .056$; pause, $D = 0.143$, $p = .937$) or between hand empty and hand occupied elbow touch actions (movement, $D = 0.179$, $p = .764$; pause, $D = 0.179$, $p = .764$).

The GLMM showed that the number of times subjects chose the container targeted by the experimenter did not differ between "intentional" and "accidental" actions for either the hand touch (hand flop vs. hand point: $z = 1.389$, $p = .165$; Figure 2*a*) or for the elbow touch (hand empty vs. hand occupied: $z = -0.655$, $p = .513$; Figure 2*b*). Subjects chose the targeted container more frequently than the nontargeted one for both hand flop and hand point touches (hand flop$_{targeted/nontargeted}$: $z = 2.803$, $p = .005$; hand point$_{targeted/nontargeted}$: $z = 4.163$, $p < .001$; Figure 2*a*). By contrast, no significant differences appeared in the number of times that targeted and nontargeted containers were chosen for both types of elbow touch (hand empty$_{targeted/nontargeted}$: $z = 0.309$, $p = .758$; hand occupied$_{targeted/nontargeted}$: $z = -0.617$, $p = .537$; Figure 2*b*). Nor did we find any significant differences between the two species studied, or any significant interactions between actions for both hand and elbow touches (see Table 2).

Discussion

Our results did not support the hypothesis that monkeys discriminated between intentional and accidental actions. Neither Tonkean macaques nor capuchin monkeys differentiated between hand point and hand flop, or between the two types of elbow actions. These results contrast with those reported by Wood and collaborators (2007) in rhesus macaques and cotton-top tamarins, and also with those of Phillips and collaborators (2009) who found that capuchin monkeys discriminated between intentional and accidental actions. It might be hypothesized that monkeys had learned during training that any type of hand gesture, in contrast to an elbow gesture, could be associated with the 'correct' container. In that case, they would have conflated performing and seeing a performance, which might explain why they did distinguish hand from elbow gestures but did not distinguish the two hand gestures. Such an explanation could, however, also be likely for the subjects trained by Wood and colleagues, but would fail to explain how their subjects could succeed in the same task. Moreover, because we did not give food rewards to our subjects during testing, they could not learn to make an association between a given human gesture and receiving a reward. Note that the difference between the durations of the experimenter's hand flop and hand point actions approached statistical significance. This did not appreciably affect the choices made by subjects, however, as no significant differences were found in their behavior according to hand actions.

A second hypothesis held that the direction of the experimenter's gaze was a main determinant of subjects' choices, in which case the latter should show a preference for the container targeted by the experimenter regardless of her gestures. Actually, the choices made by subjects did not differ between targeted and nontargeted containers for elbow actions. This finding is consistent with results on gaze tracking; whereas nonhuman primates are able to utilize gaze as a cue to look in a given direction, they have difficulties recognizing its target (e.g., Call, Agnetta, & Tomasello, 2000; Kummer et al., 1996; Vick & Anderson, 2000; Vick, Bovet, & Anderson, 2001).

A third hypothesis was that monkeys used the experimenter's movements as a cue, meaning that they should follow directional gestures more than nondirectional ones. Our findings did indeed show that subjects chose the container targeted by the experimenter's hand, regardless of the type of hand gesture. This outcome could have been expected given the abilities of nonhuman primates to understand the human pointing gesture which are quite good when the target is located at a short distance from the experimenter's hand (Emery & Clayton, 2009; Miklósi & Soproni, 2006). In addition, active requests appear to improve the efficiency of gestures compared with passive postural cues (Melis, Warneken, Jensen, Schneider, Call, & Tomasello, 2011; Yamamoto, Humle, & Tanaka, 2012). Accordingly, our subjects did not display any preference for the targeted container when the experimenter performed any type of elbow action. In these actions there was no clear forward arm movement toward a container, and elbow moves were also combined with hand motions; it is therefore likely that such gestures did not make sense for monkeys.

It should be kept in mind that we tested different monkey species to those studied by Wood and collaborators (2007). We currently have no reason to think that the cotton-top tamarins and rhesus macaques studied by this team had better cognitive skills than tufted capuchin monkeys and Tonkean macaques, respectively (see Introduction). It should be added, however, that two other studies have previously found opposite results in the two macaque species. In an experiment where rhesus macaques had to approach an experimenter and choose between two baited boxes, subjects often hid their action from the experimenter's attention by choosing the silent box, which led these authors to conclude that monkeys attribute perceptions to others (Santos, Nissen, & Ferrugia, 2006). We ourselves tested Tonkean macaques in the same task, but did not find any evidence that they took the experimenter's hearing into account (Costes-Thiré et al., 2015).

Table 2
Results of GLMM Models

Terms included in models	Coefficient	*df*	χ^2	*p*
Hand flop vs. hand point model				
Action	0.67 (± .37)	1,335	1.875	0.171
Species	−0.09 (± .33)	1,335	1.965	0.161
Action/species	−0.58 (± .45)	1,335	1.505	0.220
Hand empty vs. hand occupied model				
Action	−0.06 (± .33)	1,335	0.428	0.513
Species	−0.01 (± .31)	1,335	0.168	0.682
Action/species	−0.15 (± .44)	1,335	0.120	0.729

Note. Wald chi-square tests for the significance of terms included in binomial generalized linear mixed effect models (GLMM) models with targeted/non-targeted choices as dependent variables. Action (first model: hand flop vs. hand point; second model: hand empty vs. hand occupied), species (Tonkean macaques vs. capuchin monkeys) and their interactions were used as predictors, and individual identity as random effect to account for repeated measures in the model. For each model, sample size was based on a total of 336 trials distributed over 28 subjects.

It should be emphasized that different views have been expressed on how nonhuman primates could represent the attentional and mental states of others (Call & Santos, 2012). For instance, many authors would agree that chimpanzees can distinguish between accidents and intentions, but that they have no access to the beliefs of others (Call & Tomasello, 2008). Recent studies indicate that monkeys—including capuchin monkeys and Tonkean macaques—do indeed have some understanding of the attentional states of others (Bourjade et al., 2014; Canteloup, Bovet, & Meunier, 2015; Hattori, Kuroshima, & Fujita, 2010; Maille et al., 2012). Mind reading does not necessarily constitute a unitary phenomenon, and could have different levels. Furthermore, as previously said, several researchers even advocate the existence of mind reading in monkeys (Drayton & Santos, 2014; Marticorena et al., 2011; Overduin-de Vries et al., 2014; Phillips et al., 2009). At present, however, it remains that applying the experimental procedure of Wood and collaborators (2007) did not allow us to find evidence that capuchin monkeys and Tonkean macaques recognize others' goals.

References

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2014). lme4: Linear mixed-effects models using Eigen and S4. R package version 10–6. Retrieved from http://CRAN.R-project.org/package=lme4

Bourjade, M., Meguerditchian, A., Maille, A., Gaunet, F., & Vauclair, J. (2014). Olive baboons, *Papio anubis*, adjust their visual and auditory intentional gestures to the visual attention of others. *Animal Behaviour, 87,* 121–128. http://dx.doi.org/10.1016/j.anbehav.2013.10.019

Call, J., Agnetta, B., & Tomasello, M. (2000). Cues that chimpanzees do and do not use to find hidden objects. *Animal Cognition, 3,* 23–34. http://dx.doi.org/10.1007/s100710050047

Call, J., & Santos, L. R. (2012). Understanding other minds. In J. C. Mitani, J. Call, P. M. Kappeler, R. A. Palombit, & J. B. Silk (Eds.), *The evolution of primate societies* (pp. 664–681). Chicago, IL: University of Chicago Press.

Call, J., & Tomasello, M. (2008). Does the chimpanzee have a theory of mind? 30 years later. *Trends in Cognitive Sciences, 12,* 187–192. http://dx.doi.org/10.1016/j.tics.2008.02.010

Canteloup, C., Bovet, D., & Meunier, H. (2015). Do Tonkean macaques (*Macaca tonkeana*) tailor their gestural and visual signals to fit the attentional states of a human partner? *Animal Cognition, 18,* 451–461. http://dx.doi.org/10.1007/s10071-014-0814-4

Cheney, D. L., & Seyfarth, R. M. (2007). *Baboon metaphysics: The evolution of a social mind*. Chicago, IL: University of Chicago Press. http://dx.doi.org/10.7208/chicago/9780226102429.001.0001

Costes-Thiré, M., Levé, M., Uhlrich, P., De Marco, A., & Thierry, B. (2015). Lack of evidence that Tonkean macaques understand what others can hear. *Animal Cognition, 18,* 251–258. http://dx.doi.org/10.1007/s10071-014-0795-3

Crockford, C., Wittig, R. M., Mundry, R., & Zuberbühler, K. (2012). Wild chimpanzees inform ignorant group members of danger. *Current Biology, 22,* 142–146. http://dx.doi.org/10.1016/j.cub.2011.11.053

Deaner, R. O., van Schaik, C. P., & Johnson, V. (2006). Do some taxa have better domain-general cognition than others? A meta-analysis of nonhuman primate studies. *Evolutionary Psychology, 4,* 149–196.

Drayton, L. A., & Santos, L. R. (2014). Capuchins' (*Cebus apella*) sensitivity to others' goal-directed actions in a helping context. *Animal Cognition, 17,* 689–700. http://dx.doi.org/10.1007/s10071-013-0700-5

Emery, N. J., & Clayton, N. S. (2009). Comparative social cognition. *Annual Review of Psychology, 60,* 87–113. http://dx.doi.org/10.1146/annurev.psych.60.110707.163526

Hare, B., Addessi, E., Call, J., Tomasello, M., & Visalberghi, E. (2003). Do capuchin monkeys, *Cebus apella*, know what conspecifics do and do not see? *Animal Behaviour, 65,* 131–142. http://dx.doi.org/10.1006/anbe.2002.2017

Hare, B., Call, J., Agnetta, B., & Tomasello, M. (2000). Chimpanzees know what conspecifics do and do not see. *Animal Behaviour, 59,* 771–785. http://dx.doi.org/10.1006/anbe.1999.1377

Hattori, Y., Kuroshima, H., & Fujita, K. (2010). Tufted capuchin monkeys (*Cebus apella*) show understanding of human attentional states when requesting food held by a human. *Animal Cognition, 13,* 87–92. http://dx.doi.org/10.1007/s10071-009-0248-6

Kummer, H., Anzenberger, G., & Hemelrijk, C. K. (1996). Hiding and perspective taking in long-tailed macaques (*Macaca fascicularis*). *Journal of Comparative Psychology, 110,* 97–102. http://dx.doi.org/10.1037/0735-7036.110.1.97

Liebal, K., & Call, J. (2012). The origins of non-human primates' manual gestures. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences, 367,* 118–128. http://dx.doi.org/10.1098/rstb.2011.0044

Maille, A., Engelhart, L., Bourjade, M., & Blois-Heulin, C. (2012). To beg, or not to beg? That is the question: Mangabeys modify their production of requesting gestures in response to human's attentional states. *PLoS ONE, 7,* e41197. http://dx.doi.org/10.1371/journal.pone.0041197

Marticorena, D. C. W., Ruiz, A. M., Mukerji, C., Goddu, A., & Santos, L. R. (2011). Monkeys represent others' knowledge but not their beliefs. *Proceedings Biological Sciences, 14,* 1406–1416. http://dx.doi.org/10.1111/j.1467-7687.2011.01085.x

Melis, A. P., Warneken, F., Jensen, K., Schneider, A. C., Call, J., & Tomasello, M. (2011). Chimpanzees help conspecifics obtain food and non-food items. *Proceedings Biological Sciences, 278,* 1405–1413. http://dx.doi.org/10.1098/rspb.2010.1735

Miklósi, A., & Soproni, K. (2006). A comparative analysis of animals' understanding of the human pointing gesture. *Animal Cognition, 9,* 81–93. http://dx.doi.org/10.1007/s10071-005-0008-1

Miller, G. (2010). Cognition research. Investigation leaves field in the dark about a colleague's work. *Science, 329,* 890–891. http://dx.doi.org/10.1126/science.329.5994.890-b

Overduin-de Vries, A. M., Spruijt, B. M., & Sterck, E. H. M. (2014). Long-tailed macaques (*Macaca fascicularis*) understand what conspecifics can see in a competitive situation. *Animal Cognition, 17,* 77–84. http://dx.doi.org/10.1007/s10071-013-0639-6

Petit, O., Dufour, V., Herrenschmidt, M., De Marco, A., Sterck, E. H. M., & Call, J. (2015). (in press). Inferences about food location in three cercopithecine species: An insight into the link between sociality and cognition. *Animal Cognition*. Advance online publication. http://dx.doi.org/10.1007/s10071-015-0848-2

Phillips, W., Barnes, J. L., Mahajan, N., Yamaguchi, M., & Santos, L. R. (2009). 'Unwilling' versus 'unable': Capuchin monkeys' (*Cebus apella*) understanding of human intentional action. *Developmental Science, 12,* 938–945. http://dx.doi.org/10.1111/j.1467-7687.2009.00840.x

Santos, L. R., Nissen, A. G., & Ferrugia, J. (2006). Rhesus monkeys, *Macaca mulatta*, know what others can and cannot hear. *Animal Behaviour, 71,* 1175–1181. http://dx.doi.org/10.1016/j.anbehav.2005.10.007

Suddendorf, T., & Whiten, A. (2001). Mental evolution and development: Evidence for secondary representation in children, great ages, and other animals. *Psychological Bulletin, 127,* 629–650. http://dx.doi.org/10.1037/0033-2909.127.5.629

Thierry, B., Anderson, J. R., Demaria, C., Desportes, C., & Petit, O. (1994). Tonkean macaque behaviour from the perspective of the evolution of Sulawesi macaques. In J. J. Roeder, B. Thierry, J. R. Anderson & N. Herrenschmidt (Eds.), *Current primatology, Vol. 2: Social development, learning and behaviour* (pp. 103–117). Strasbourg, France Université Louis Pasteur.

Tomasello, M., & Call, J. (1997). *Primate cognition*. New York: Oxford University Press.

Tomasello, M., Call, J., & Hare, B. (1998). Five primate species follow the visual gaze of conspecifics. *Animal Behaviour, 55,* 1063–1069. http://dx.doi.org/10.1006/anbe.1997.0636

Vick, S. J., & Anderson, J. R. (2000). Learning and limits of use of eye gaze by capuchin monkeys (*Cebus apella*) in an object-choice task. *Journal of Comparative Psychology, 114,* 200–207. http://dx.doi.org/10.1037/0735-7036.114.2.200

Vick, S. J., Bovet, D., & Anderson, J. R. (2001). Gaze discrimination learning in olive baboons (*Papio anubis*). *Animal Cognition, 4,* 1–10. http://dx.doi.org/10.1007/s100710100081

Wood, J. N., Glynn, D. D., Phillips, B. C., & Hauser, M. D. (2007). The perception of rational, goal-directed action in nonhuman primates. *Science, 317,* 1402–1405. http://dx.doi.org/10.1126/science.1144663

Wood, J. N., & Hauser, M. D. (2011). Replication of "The perception of rational, goal-directed action in nonhuman primates". *Science, 332,* 537.

Yamamoto, S., Humle, T., & Tanaka, M. (2012). Chimpanzees' flexible targeted helping based on an understanding of conspecifics' goals. *Proceedings of the National Academy of Sciences, USA of the United States of America, 109,* 3588–3592. http://dx.doi.org/10.1073/pnas.1108517109

Received January 14, 2015
Revision received March 31, 2015
Accepted April 10, 205 ■