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What do monkeys know about others' knowledge?

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A R T I C L E I N F O

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A B S T R A C T

Recently, comparative psychologists have suggested that primates represent others' knowledge states. Evidence for this claim comes from studies demonstrating that primates expect others to maintain representations of objects when those objects are not currently visible. However, little work has explored whether nonhuman primates expect others to share the more sophisticated kinds of object knowledge that they themselves possess. We therefore investigated whether primates attribute to others knowledge that is acquired through the mental transformation of a static object representation. Specifically, we tested whether rhesus macaques (*Macaca mulatta*) expected a human demonstrator to solve a difficult rotational displacement task. In Experiment 1, monkeys watched a demonstrator hide a piece of fruit in one of two boxes. The monkey and the demonstrator then watched the boxes rotate 180°. We found that monkeys looked longer when the demonstrator reached into the box that did not contain the fruit, indicating that they expected her to be able to track the fruit to its current location. In Experiment 2, we ruled out the possibility that monkeys simply expected the demonstrator to search for the food in its true location. When the demonstrator did not witness the rotation event, monkeys looked equally long at the two reaching outcomes. These results are consistent with the interpretation that rhesus macaques expect others to dynamically update their representations of unseen objects.

1. Introduction

A central feature of human cognition is that people not only know things about the world, but they also attribute this same knowledge to others. Take a simple case of physical understanding like watching a golfer hit a golf ball into a hole. As adult humans, we would not only maintain a static representation of the (now unseen) ball inside the hole, but we would expect others to represent the ball's continued existence as well. We would predict that the golfer would search for his ball in the hole, and would be surprised if he didn't do so. In addition, we know that like ourselves, other people dynamically update their static object representations by imaging potential or actual changes in object attributes. For example, if we saw the golfer hit the ball down the fairway and out of sight, we could imagine the trajectory of the ball and would have some idea of where to search for it. We would expect the golfer to make similar inferences about the trajectory of the ball, and would be surprised if he came to radically different conclusions about where the ball was likely to be. This capacity to attribute to others both the static and dynamic object information that we ourselves represent is an important part of our so-called *theory of mind* capacity. Indeed, attributing a simple knowledge of objects to others is essential for normal social functioning as it facilitates complex forms of cooperation, communication through language, and many other uniquely human behaviors (Apperly, 2010).

In order to understand the specific role that a theory of mind played over the course of human evolution, psychologists have examined the possibility that nonhuman primates (hereafter, primates) also represent the knowledge that others have about objects and their motions. Comparative psychologists have generated a considerable amount of evidence that primates expect others to maintain static representations of objects when those objects are not currently visible (e.g., Hare, Call, & Tomasello, 2001; Kaminski, Call, & Tomasello, 2008; MacLean & Hare, 2012; Marticorena, Ruiz, Mukerji, Goddu, & Santos, 2011). However, little work has explored whether primates expect others to share the more dynamic object knowledge that they themselves possess. This is an important question, because to date primates have only demonstrated the ability to represent what others do and do not know in a very limited range of contexts. If primates only attribute static object representations to others, then this would constitute an important representational limitation on primate theory of mind capacities. In addition, showing that primates are able to track what others have seen across a range of scenarios would provide important confirmatory evidence that primates' performance in theory of mind tasks actually involves representations of what others have seen rather than simpler mechanisms that might explain performance (e.g., Heyes, 2015; Penn & Povinelli, 2007). We therefore investigated whether

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primates attribute to others knowledge that is acquired through the mental transformation of static object representations.

Before turning to what primates understand about others' object knowledge though, it's important to first better understand what primates *themselves* know about objects and their trajectories. After all, primates will likely attribute to others only those representations that they themselves have about the world. Conveniently, comparative psychologists have learned much about how primates represent objects and their motions. One of the most relevant aspects of physical objects is the fact that they typically exist as *static* permanent entities. Primates seem to recognize this as well; they know that objects do not randomly enter into and out of existence (Beran, 2004; Call, 2001; de Blois & Novak, 1994; de Blois, Novak, & Bond, 1998; Deppe, Wright, & Szelistowski, 2009; Flombaum, Junge, & Hauser, 2005; Jolly, 1964; Mathieu, Bouchard, Granger, & Herscovitch, 1976; Mendes & Huber, 2004; Menzel, 1973; Neiworth et al., 2003; Rosati & Hare, 2012; Santos, Barnes, & Mahajan, 2005; Santos, Sulkowski, Spaepen, & Hauser, 2002; Schino, Spinozzi, & Berlinger, 1990; Schneider, 1992; Uller, Hauser, & Carey, 2001; Vaughter, Smotherman, & Ordy, 1972; Wise, Wise, & Zimmerman, 1974; Wood, Moriarty, Gardner, & Gardner, 1980). For example, experiments based on Piagetian search paradigms have demonstrated that primates will search for food that they have seen hidden under or behind an occluder (e.g. Call, 2001; de Blois & Novak, 1994; Mendes & Huber, 2004; Neiworth et al., 2003). Looking time tasks assessing primate numerical competencies have also shown that primates are able to detect a mismatch between the number of objects that are placed behind an occluder and the number of objects that are subsequently revealed behind that occluder (e.g. Beran, 2004; Flombaum et al., 2005; Santos et al., 2005; Uller et al., 2001). Finally, naturalistic foraging tasks have confirmed that primates are able to recall the location of hidden food items, sometimes even after substantial delays (e.g. Menzel, 1973; Rosati & Hare, 2012; Santos et al., 2002).

In sum, there is a large body of work showing that primates themselves maintain static object representations. But do primates attribute these same static object representations to others? Much theory of mind work to date has focused on this question. Previous work using at least three kinds of tasks has shown that primates expect others to recall where specific objects are located in space. In a study involving food competition, Hare et al. (2001) showed that chimpanzees (*Pan troglodytes*) were able to use information about what a more dominant chimpanzee knew to strategically acquire food items that had recently been hidden in a central testing room. Subject chimpanzees targeted the food that the dominant had not seen hidden and avoided the food that the dominant had seen hidden (see also Kaminski et al., 2008). Likewise, looking time studies have observed that primates successfully track what others know about the location of hidden food items. In Marticorena et al. (2011), rhesus monkeys watched a human experimenter observe a lemon move into one of two differently colored opaque boxes. The experimenter either reached into the box where she had just seen the lemon go or into the alternative box. Rhesus monkeys looked longer when the experimenter reached into the box that did not contain the lemon, indicating that they were surprised that she did not act on the basis on her knowledge. Finally, gaze following tasks have explored whether primates follow gaze flexibly based on what a particular individual has recently seen. MacLean and Hare (2012) allowed chimpanzees to watch as an experimenter vocalized emotively while looking at an object several meters away. When the experimenter had previously seen the object in that location, chimpanzees looked in the direction of the experimenter's gaze past the object, as if searching for an alternative object. Taken together, the results of these studies provide converging evidence that primates expect others to maintain representations of where objects are and expect those representations to influence agents' subsequent behaviors (Call & Tomasello, 2008; Rosati, Hare, & Santos, 2009; Whiten, 2013; but see Heyes, 2015; Penn & Povinelli, 2007).

Interestingly, although primates attribute static object representations to others across different experimental contexts, it is unclear whether primates can successfully predict how another agent will behave when the agent's representation of the static object is based on outdated or inaccurate information (see review in Martin & Santos, 2016). Specifically, there is evidence that primates often fail to make positive predictions about the behavior of an agent who lacks an accurate static object representation. Marticorena et al. (2011) tested where monkeys expected an experimenter to search for a hidden food item when she had a false belief about the food's location. In this experiment, rhesus monkeys again watched a human experimenter observe a lemon move into one of two different colored opaque boxes. Next, an occluder was raised preventing the experimenter from seeing the stage. With the occluder raised, the lemon moved into the alternative box. The experimenter then reached either into the box where she believed the lemon to be, or in the box where the lemon was actually located. In this case, monkeys looked *equally* long at the two reaching outcomes. This suggests that monkeys neither expected the experimenter to search for the lemon in its true location, nor did they expect the experimenter to search for the lemon on the basis of her false belief about its location. Instead, monkeys appeared to have no expectation regarding where the experimenter would search for the lemon.

Kaminski et al. (2008) observed a similar pattern of performance in great apes (but see Krupenye, Kano, Hirata, Call, & Tomasello, 2016). In their study, subject chimpanzees played a competitive food retrieval game with a competitor chimpanzee who either did or did not see a high-quality reward hidden in one of several possible locations. Subjects could then choose between this high-quality reward and a safer low-quality reward after the competitor made his own choice. Critically however, the subject could not see which food item the competitor chose. Thus, the subject had to infer what the competitor was likely to have done by tracking what the competitor did and did not know about the location of the rewards. Overall, chimpanzee subjects tended to choose the high-quality reward both when the competitor had not seen that reward being hidden—that is, when the competitor was *ignorant* of the reward. However, subject chimpanzees also chose the high-quality reward when, after hiding the high-quality reward in presence of the competitor, the experimenter simply revealed the high-quality reward and *placed it back into the same container* when the competitor was not looking. That is, even when the competitor had a true belief about the location of the food, chimpanzees failed to make a positive prediction that the partner would search for the food on the basis of this belief. Thus, primate's' representations of others knowledge seem to be disrupted as soon as the competitor's representation of the static object no longer obtains.

But primates themselves do more than merely reasoning about static representations of objects. In addition to thinking about static objects, primates are also able to dynamically *transform* static object representations (Call, 2000). Whereas maintaining static representations allows an organism to recall the location of an object, transforming static representations allows an organism to imagine potential or actual changes in an object's location. Continually updating an object's location when it is not currently visible is likely to be more cognitively demanding then simply recalling the location of a stationary object. Nonetheless, primates are able to dynamically update their representations of an object's location in some contexts (e.g. Barborica & Ferrera, 2004; Barth & Call, 2006; Beran & Minahan, 2000; Call, 2003; Collier-Baker & Suddendorf, 2006; Hughes & Santos, 2012; Iversen & Matsuzawa, 2003; Natale, Antinucci, Spinozzi, & Potí, 1986). For example, primates are able to visually anticipate the reappearance of a target that momentarily disappears behind an occluder, taking into account the direction and speed of the hidden target (e.g. Barborica & Ferrera, 2004; Iversen & Matsuzawa, 2003). Primates are also able to infer the location of objects following invisible displacements (e.g. Collier-Baker & Suddendorf, 2006; de Blois et al., 1998;

Natale et al., 1986), which suggests that they are able to mentally recreate the possible trajectory of the hidden object. Primates are also are also able to locate an object following a rotation displacement, an ability that requires them to track an object hidden inside one of several containers while the substrate supporting the containers is rotated (e.g. Barth & Call, 2006; Call, 2003; Hughes & Santos, 2012). For example, Hughes and Santos (2012) used a looking time measure to demonstrate that rhesus macaques (*Macaca mulatta*) were able to successfully track visually displaced objects. Monkeys first saw two differently colored boxes sitting on a rotating platform. They then watched a human experimenter place a piece of food inside one of the boxes. Next the monkeys watched as the platform rotated 180°. The boxes were then opened again, revealing that the fruit was either in the correct or incorrect location. Adult monkeys, but not juvenile monkeys, looked longer at the display when the food appeared in the incorrect location following the rotation, suggesting that they were able to track the food as the platform rotated. In contrast, when the monkeys were prevented from witnessing the rotation event, they did not infer that a rotation had occurred based only based on the change in the position of the different colored boxes.

Unfortunately, although much work has tested whether primates extend their representations of static objects to others, little work has explored whether nonhuman primates expect others to share the ability to transform static object representations dynamically in space and time. We therefore investigated whether primates attribute knowledge to others when this knowledge requires the mental transformation of static object representations, expanding on previous work, which has demonstrated that primates attribute knowledge to others in situations involving the maintenance of static object representations. Specifically, we tested whether rhesus macaques expected another agent to succeed on a rotational displacement task. As mentioned previously, rotational displacement tasks require participants to track an object hidden inside one of several containers while the substrate supporting that object and containers rotates. The participant then has to identify the current location of the hidden object. Note that success on this task requires the representation of the location of the hidden object to be constantly updated throughout the rotation. In other words, it involves a mental transformation of the represented object. Given that primates themselves succeed on these tasks when they watch the rotation, do they expect other individuals to do the same?

To test whether rhesus monkeys expected another agent to succeed on a rotational displacement task, we used the same general design as Hughes and Santos (2012). Recall that in this previous set of studies, monkeys were presented with two different colored boxes on a rotating platform. After seeing that the food was in one of the two boxes, the monkey watched as the platform supporting the boxes was rotated 180°. The boxes were then opened, revealing that the fruit was either in the correct location or the incorrect location. Monkeys looked longer at the display when the fruit was revealed in the incorrect location, suggesting they were able to track the fruit during the rotation event. However, there are several caveats to this finding that informed the methods and predictions of our own experiments. First, only adult monkeys showed this pattern of looking, suggesting that younger monkeys are not able to solve this task. Second, adult monkeys only showed this pattern of looking when the two boxes were different colors *and* when the they had witnessed the rotation. If the monkeys witnessed the rotation but the two boxes were the same color, or if the boxes were different colors but the monkeys did not witness the rotation, monkeys were not able to locate the hidden food item following the rotation. Instead, in both of these cases they looked equally when the fruit was revealed in the correct box and the incorrect box.

In our first experiment, we therefore tested whether adult monkeys would expect another agent to correctly locate a food item following a rotational displacement under the same conditions—that is, when the boxes were two different colors and when the agent had witnessed the rotation. Subject monkeys were shown a display with two boxes on top of a rotating platform. They then watched a human demonstrator place a piece of food inside one of the boxes. Next, both the demonstrator and the subject monkey watched the platform rotate 180°. To examine whether the monkeys expected the experimenter to update her own representation of the location of the object following the rotation event, the demonstrator reached either into the box that contained the food or into the alternative box. We predicted that if the monkeys expected the experimenter to know the current location of the food, they should look longer at the display when she searched for food in the empty box.

2. Experiment 1

2.1. Methods

2.1.1. Subjects

We tested 81 free-ranging rhesus macaques living on the island of Cayo Santiago, Puerto Rico (Rawlins & Kessler, 1986). Monkeys in this population are well habituated to the presence of human experimenters and have shown reliable results in previous looking time studies (e.g., Hughes & Santos, 2012; Marticorena et al., 2011; Martin & Santos, 2014). Individual monkeys can be identified by the presence of unique chest tattoos. All monkeys included in the sample were at least four years of age[1] ($M = 9.04$ years, $SD = 4.48$). We only included monkeys that were four or older because previous work has shown that younger rhesus macaques cannot reliably solve rotational displacement tasks (Hughes & Santos, 2012). An additional 36 monkeys were approached but testing and/or video processing was not completed due to subject inattention, subject approaching the apparatus, or secondary interference from another monkey. Another 30 sessions were not analyzed because we confirmed after testing that the subject had previously completed a testing session.[2] Note that this rate of aborted sessions is similar to (or lower than) that of previous looking time studies conducted with this population (e.g., Marticorena et al., 2011; Martin & Santos, 2014).

2.1.2. Procedure

We used an expectancy-violation looking time method to test whether rhesus monkeys expected another agent to have the same object knowledge as they themselves possess. Two experimenters—a demonstrator and a cameraperson—conducted all testing sessions. The demonstrator presented the stimuli to the monkey and the cameraperson filmed the subject's face so that his looking behavior could be examined later. At the start of each session, the demonstrator knelt down about 2 meters in front of the subject with the apparatus placed in front of her. The cameraperson remained standing about a meter behind the demonstrator.

The apparatus was a white foam-core stage that consisted of a base (61 cm × 43 cm), two side walls (15 cm × 43 cm), and a back wall (61 cm × 48 cm). A hinged occluder (61 cm × 51 cm) was attached to the front of the stage so that objects on the stage could be concealed from the subject monkey prior to the start of the session. A second hinged occluder (61 cm × 35.5 cm) was attached to the back wall of the stage. This occluder could be raised to cover the face of the demonstrator (note that this hinged occluder was only used in Experiment 2). A circular platform (48 cm diameter) supported by a square base (7.5 cm × 40 cm × 40 cm) was fixed to the stage. The demonstrator could surreptitiously rotate the platform while kneeling behind the apparatus. One yellow box and one purple box (each 10 cm^3) were located on opposite sides of the platform. Boxes were different colors because previous work has shown that monkeys are only able to

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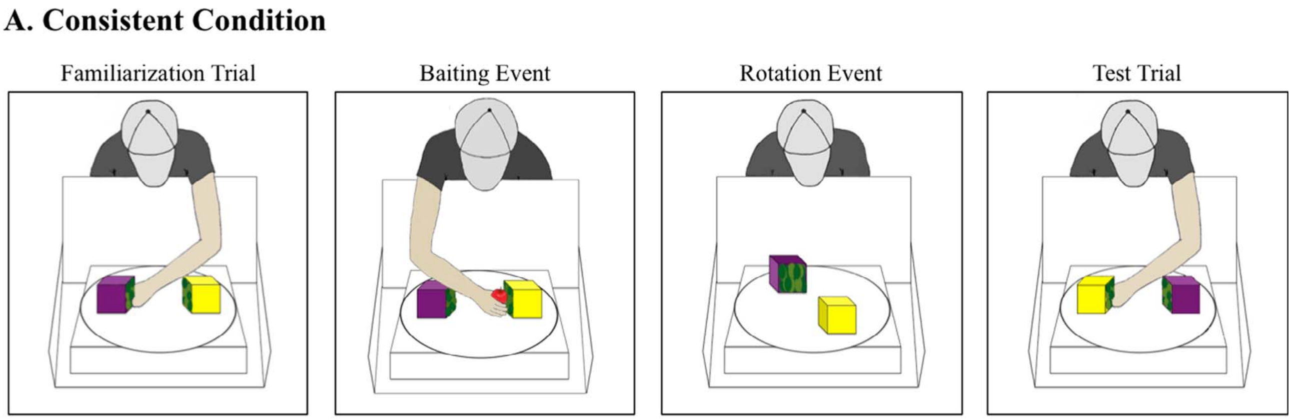
[1] Monkeys' age was calculated based on birth season.

[2] Data for Experiment 1 and Experiment 2 were collected simultaneously and monkeys were only allowed to participate in a single experiment. Therefore, some of the monkeys were excluded from Experiment 1 because they had participated in Experiment 2 rather than because they had already participated in Experiment 1.



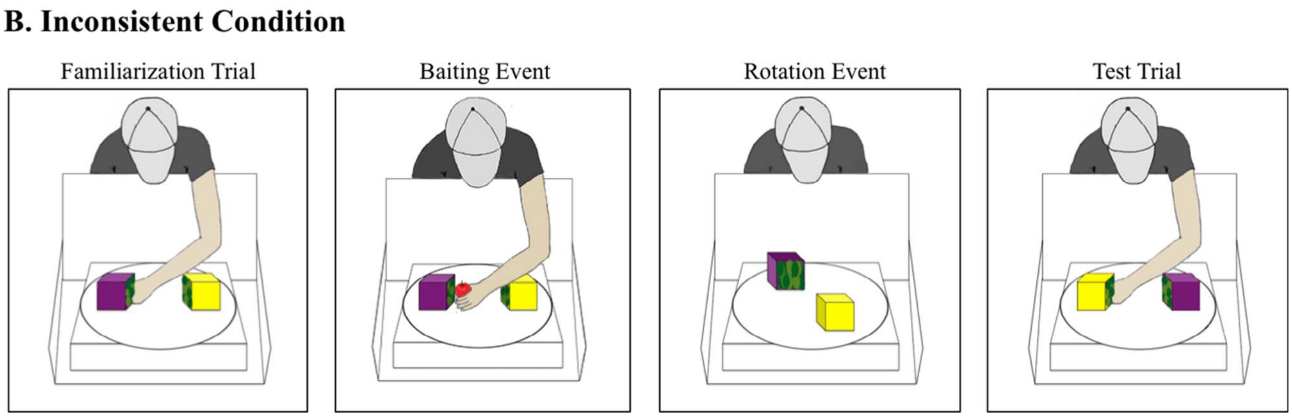


Fig. 1. Depiction of the procedures across the different conditions in Experiment 1.

successfully track objects during rotational displacements when the containers are different colors (Hughes & Santos, 2012). Each box was open on one side so that food could be placed inside. The opening was covered with leaves so that food could no longer be seen once it was inside the box.

Each session consisted of one *familiarization trial*, a *baiting event*, a *rotation event*, and a *test trial* (see Fig. 1). The purpose of the familiarization trial was to familiarize subjects with the contents of the stage and with the fact that the demonstrator might reach into one of the boxes. In addition, it allowed us to obtain a baseline measurement of interest for each monkey. In the familiarization trial, the demonstrator obtained the subject monkey's attention, dropped the front occluder to reveal the contents of the stage, and then reached into the box on the left (from the perspective of the monkey) as if attempting to obtain an object from inside that box. The color of the box was counterbalanced across sessions. As soon as the demonstrator reached into the box she said "now" and remained stationary for 10-s while the cameraperson recorded the monkey's looking behavior. After 10-s, the demonstrator closed the front occluder, obscuring the contents of the stage from the subject.

Immediately after the familiarization trial, the cameraperson announced the condition to the demonstrator using a numerical code. Monkeys were assigned to either the *consistent reach* condition or the *inconsistent reach* condition (described below). The cameraperson did not know which number corresponded to which condition, allowing the cameraperson to remain blind to the condition throughout the duration of the session. After finding out the condition, the demonstrator began the baiting event. During the baiting event, the demonstrator again dropped the front occluder. She then showed the subject a piece of realistic-looking artificial fruit and placed it inside one of the boxes. If the monkey was assigned to the consistent reach condition she placed the fruit in the right box (from the perspective of the monkey). If the monkey was assigned to the inconsistent reach condition she placed the fruit inside the left box (from the perspective of the monkey). Immediately after placing the fruit inside one of the boxes the rotation event began. During the rotation event, both the demonstrator and the subject watched the stage as the apparatus rotated 180° so that the box on the right side of the apparatus was now on the left side of the apparatus and visa versa.

After the rotation was completed, the demonstrator performed the test trial. During the test trial, the demonstrator reached into the box to the monkey's left, just as she had done in the familiarization trial. As soon as the demonstrator reached into the box she said "now" and remained stationary for 10-s while the cameraperson recorded the monkey's looking behavior. Critically, in the consistent reach condition the box on the left now contained the fruit, since the fruit had originally been placed in the right box and the platform was subsequently rotated 180°. In the inconsistent reach condition, the box on the left did not contain the fruit, since the fruit had originally been placed in the left side box prior to the rotation. We predicted that if monkeys understood that the demonstrator was able to track the rotating food item despite not having direct perceptual access to it then they would look longer at the stage when the demonstrator reached inside the box that did not contain food.

2.1.3. *Video coding and analysis*

All videos were assessed by two coders. The two coders independently measured the monkey's looking behavior during the familiarization trial and the test trial using the program MPEG Streamclip. Videos were trimmed so that coders were blind to condition when viewing the videos. Videos were examined frame by frame (30 frames/s) for the 10-s immediately following the onset of the demonstrator's "now" cue to determine how long the subject spent looking at the stage. Inter-rater reliability between the coders was high

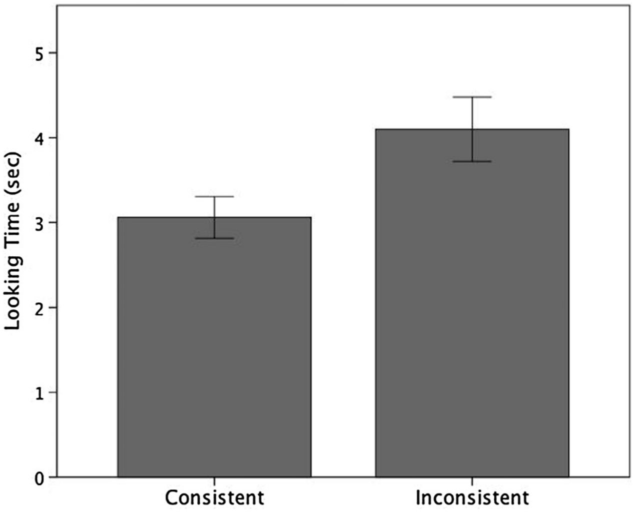


Fig. 2. Mean looking time (in sec) ± SEM across monkeys in the test trial of Experiment 1.

(Pearson's $R = 0.937$) and so only a single coder's data was analyzed. All statistical tests are two-tailed.

2.2. Results and discussion

We compared monkeys' total looking time during the test trial in the consistent and inconsistent reach condition using an independent samples *t*-test. Monkeys showed a reliable difference in looking duration between the two conditions ($t(79) = 2.274$, $p = .026$; Fig. 2). As predicted, monkeys who saw the demonstrator reach into the box that did not contain the fruit looked longer at the stage ($M = 4.098$) than did monkeys who saw her reach into the box that contained the fruit ($M = 3.059$). This suggests that the monkeys expected the demonstrator to know the correct location of the fruit after the rotation event, and consequently were surprised when she did not search for the fruit in its updated location.

We also confirmed that monkeys assigned to the inconsistent reach condition did not look any longer at the stage during the familiarization trial than did monkeys assigned to the consistent reach condition ($t(79) = -0.807$, $p = .422$; consistent condition: $M = 5.100$; inconsistent condition: $M = 4.689$). This allows us to rule out the possibility that monkeys in the inconsistent condition were simply more interested in the events on the stage in general. In addition, we confirmed that monkeys assigned to the different conditions did not differ in age ($t(79) = -0.223$, $p = .824$; consistent condition: $M = 9.150$; inconsistent condition: $M = 8.927$). This suggests that the difference in looking time on the test trial was not because monkeys in the consistent condition were themselves less likely to know where the fruit was located after the rotation. Finally, we confirmed that the color of the box that the experimenter reached into did not affect monkeys' looking times on either the familiarization trial or the test trial ($ps > 0.42$).

These results suggest that monkeys not only expect others to maintain static representations of hidden objects, but also expect others to dynamically update these object representations. However, one alterative explanation for these data is that monkeys expected the demonstrator to search for the food in its updated location not because they attributed knowledge to the demonstrator, but rather because they expected the demonstrator to look for the food where they themselves knew it to be. In other words, monkeys could have been demonstrating a curse of knowledge. We thought this was unlikely to be the explanation for monkeys' performance as previous experiments have successfully ruled out this particular alternative (e.g. Marticorena et al., 2011). Thus, we had strong a priori reasons to suspect that monkeys' performance could not be explained by a curse of knowledge bias. Nevertheless, to rule out this possibility we conducted a second experiment in which the demonstrator had *inaccurate* information regarding the location of the fruit. Specifically, after baiting one of the boxes with the fruit, an occluder was raised which prevented the experimenter from witnessing the rotation event. We predicted that if the experimenter did not actually see the rotation (and thus was not "knowledgeable"), rhesus monkeys would look equally long regardless of where she reached on the test trial, just as they did in Marticorena et al. (2011). In other words, the monkeys would treat the experimenter as "ignorant" of the location of the hidden food.

Of course, using this method, it is possible that the monkeys would expect the experimenter to *infer* that the platform had rotated even though she did not see the rotation directly because the two boxes on the platform were different colors. However, recall that monkeys themselves cannot correctly locate the food if they do not witness the rotation event, even when featural cues are present (such as box color) that would help them do so. Instead, when monkeys simply see that the two colored boxes have switched places, they look equally long at the stage when the food is revealed in either of the two boxes, suggesting that they are uncertain as to where the food is located. Thus, monkeys own pattern of performance suggests that they would not expect the experimenter infer the correct location of the food, nor would they expect the experimenter to search for food on the side of the stage where is was originally hidden. Instead, they should look equally long at the two reaching outcomes, as they and other primates have done other studies where an another agent has inaccurate information about the location of a hidden reward (e.g., Kaminski et al., 2008; Marticorena et al., 2011).

3. Experiment 2

3.1. Methods

3.1.1. Subjects

We tested 85 rhesus macaques living on Cayo Santiago. As in Experiment 1, all subjects were at least four years old ($M = 8.91$ years, $SD = 4.23$). An additional 61 monkeys were approached but testing and/or video analysis was not completed due to subject inattention, subject approaching the apparatus, or secondary interference from another monkey. Five additional sessions were not included due to a camera or experimenter error (n = 3), because we were not able to successfully identify the monkey (n = 1), or because the monkey was younger than four (n = 1). A final 19 sessions were not analyzed because the subject had previously completed a testing session.

3.1.2. Procedure

Experiment 2 followed the same procedure as the first experiment except that only the subject monkey saw the rotation event (see Fig. 3). After placing the fruit in one of the two boxes on the stage, the demonstrator raised the hinged occluder attached to the back wall of the apparatus, obscuring her view of the platform and the boxes. With the demonstrator behind occluder, the monkey watched the platform rotate 180°. As soon as the rotation was complete, the hinged occluder was dropped so that the demonstrator could again see the stage. The demonstrator then performed the test trial by reaching into one of the two boxes.

3.1.3. Video coding and analysis

Videos were processed and coded in the same manner as in Experiment 1. Inter-rater reliability was again high (Pearson's $R = 0.925$).

3.2. Results and discussion

In contrast to Experiment 1, monkeys did not look longer at the display in the inconsistent condition compared to the consistent

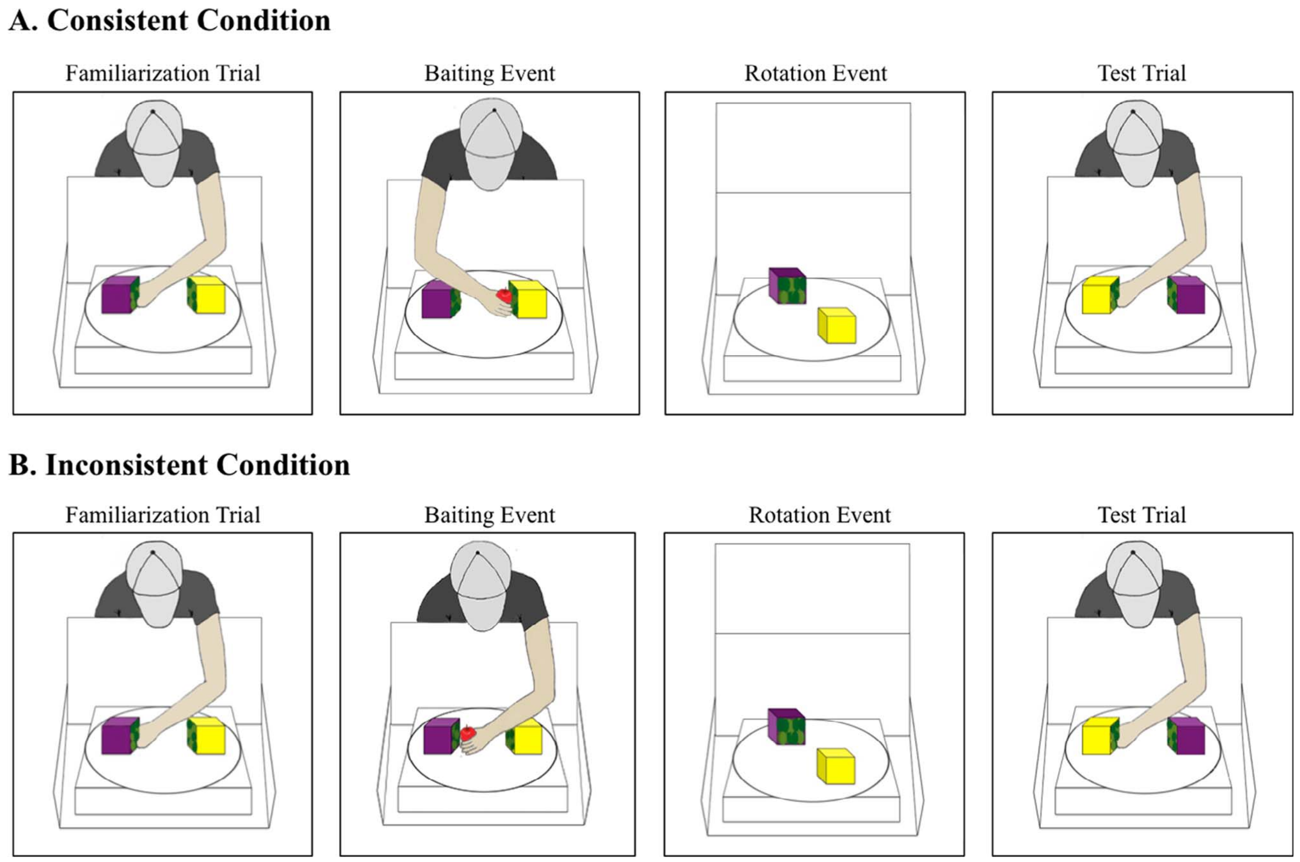


Fig. 3. Depiction of the procedures across the different conditions in Experiment 2.

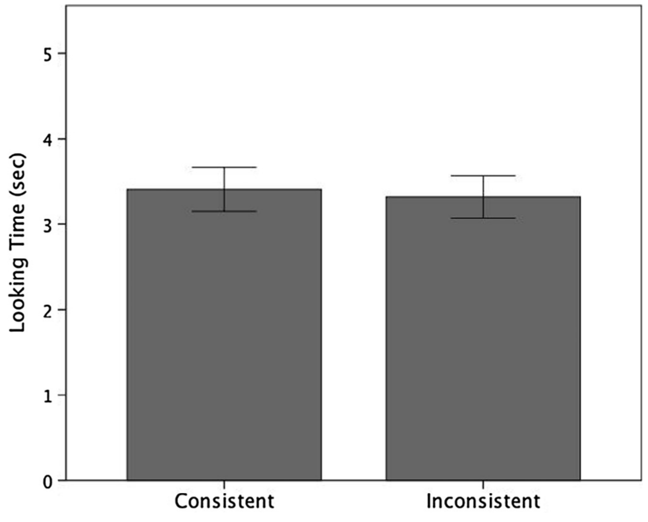


Fig. 4. Mean looking time (in sec) ± SEM across monkeys in the test trial of Experiment 2.

condition ($t(83) = -0.239$, $p = .812$; Fig. 4). Monkeys who saw the demonstrator reach into to the box that contained the food ($M = 3.407$) looked just as long at the display as monkeys who saw the demonstrator reach into the box that did not contain the food ($M = 3.321$). In other words, the monkeys did not expect the demonstrator to search for the food in its actual location when she did not see the platform rotate. As in Experiment 1, we also confirmed that monkeys in the two conditions looked equally long during the familiarization trial ($t(83) = -0.274$, $p = .785$; consistent condition: $M = 5.041$; inconsistent condition: $M = 5.182$), and that they did not differ in age ($t(83) = -1.041$, $p = .301$; consistent condition: $M = 9.415$; inconsistent condition: $M = 8.455$). Once again, the color of the box did not affect monkeys' looking times on either the familiarization trial or the test trial ($ps > 0.31$).

These data suggest that monkeys were not exhibiting a curse of knowledge bias in Experiment 1. If this had been the case, they should have been surprised to see the demonstrator look for the food in the box where it was not located, but this is not the pattern of looking we observed. Instead, monkeys looked equally long at the two outcomes suggesting that they did not have any expectation regarding where the demonstrator would look for the food when she did not have accurate knowledge regarding the food's location. These data also suggest that the monkeys did not expect the experimenter to infer the correct location of the hidden food item by using box color to infer that a rotation event had occurred. However, this is unsurprising because monkeys themselves are uncertain as to where food is located when they do not witness the rotation event (see Hughes & Santos, 2012).

One might be concerned that the monkeys were distracted by the occluder being raised and lowered in the experiment, and that this impacted their performance on the task. However, previous looking time studies using similar methods with the rhesus macaques on Cayo Santiago have specifically ruled out the possibility that an occluder being raised and lowered interferes with performance on theory of mind tasks (Marticorena et al., 2011).

4. General discussion

The results of Experiment 1 show that monkeys expect an experimenter to know the final location of a dynamically displaced object when the experimenter has witnessed the displacement. These results are consistent with those of previous studies demonstrating that primates expect others to maintain representations of objects even when those objects are not currently visible (Hare et al., 2001; Kaminski et al., 2008; MacLean & Hare, 2012; Marticorena et al., 2011). The present findings also extend previous results in that success on our task required monkeys to attribute more sophisticated object knowledge to another agent. Specifically, our results show that monkeys not only expect others to maintain static representations of hidden objects, but also expect others to dynamically update these object representations during a rotation event. Monkeys attributed knowledge of an object's location to another agent when this knowledge required the mental transformation of a static object representation. Our findings are therefore significant in that they show greater flexibility in primates' knowledge representations than has previously been demonstrated. Importantly, in Experiment 2 we ruled out the possibility that monkeys simply expected the demonstrator to search for the food in its true location. When the demonstrator did not witness the rotation event, monkeys looked equally long at the two reaching outcomes.

Monkeys' behavior in our study can help address an important theoretical question about primates' mental state attributions: how is the ease with which knowledge is acquired related to the ease with which that same knowledge is attributed to another agent? The experiments presented here show that primates are able (at least in some cases) to attribute knowledge that manifests relatively late in development to another agent. Recall that Hughes and Santos (2012) tested whether different age cohorts of rhesus macaques would be able to solve a rotational displacement. They found that monkeys older than four showed reliable differences in looking at the expected and unexpected outcomes, whereas infant and juvenile monkeys were not able to successfully track the object during the rotation. Other studies have reported similar developmental delays in other species. For example, Barth and Call (2006) administered a series of object displacement tasks to great apes and 30-month-old human children, they found that both populations performed better on classic A-not-B Piagetian error tasks and transposition tasks than on rotations tasks. Our results suggest that once primates are themselves able to represent the updated location of the object, they also readily attribute this knowledge to others.

Our findings are also consistent with a recent theory concerning the kinds of representations supporting primates' mentalizing abilities. Martin and Santos (2016) proposed that primates succeed on some theory of mind tasks because they are able to attribute awareness relations between different agents and information about the world that primates themselves already represent as true of reality. Awareness relations differ from representational relations— such as a representation of someone else's belief— in that there is no separate mental content that is attributed to the other agent (although for recent evidence that great apes may reason about others' behavior using representational relations, see Krupenye et al., 2016). When representing an agent's awareness relations, a primate merely thinks of other agents as having access to a particular representation that the primate himself holds, or as not having access to that representation. Given this proposal, it makes sense that rhesus macaques would expect other agents to share their ability to transform static object representations; once a primate is able to form a particular representation of the world, he simply has to represent whether the other agent has access to that representation or not; thus, whatever the complexity of the representation, this complexity is not reflected in the attribution of the awareness relation to another agent.

Of course, in many ways our studies required primates to attribute the same kind of conceptual knowledge as previous theory of mind studies: the knowledge that objects are permanent entities that persist in time and space. Although the ability to locate an object following a rotational displacement takes longer to develop than does the ability to locate an object following a visible displacement, the same core object knowledge may support both expectations (for a detailed discussion of core object knowledge, see Carey, 2000; Spelke & Kinzler, 2007). Thus, rotational displacement tasks may not be more difficult because they require qualitatively different conceptual knowledge, but rather because of differing task demands. For example, during rotational displacements the hidden object, containers, and platform supporting the containers all move at the same time. Tracking the movements of all of these parts may require more attentional resources than merely tracking the movement of one or two of the parts. It may be that these attentional resource take longer to develop, and this is why primates solve rotational displacements only relatively late in development.

Regardless, both our study and previous theory of mind studies leave open the question of whether primates are able to attribute object representations to others that have content *other than* spatiotemporal information (e.g., kind information, feature information, etc.). Interestingly, there is reason to suspect that the spatiotemporal features of objects might be particularly easy to represent. For example, humans appear to prioritize spatiotemporal information about objects over other kinds of object attributes, such as property or kind information (for a review, see Flombaum, Scholl, & Santos, 2009). There is evidence that a similar bias towards spatiotemporal information may exist in primate object representations as well. Flombaum et al. (2005) demonstrated that rhesus macaques detect inconsistencies in the spatiotemporal attributes of objects more readily than other kinds of inconsistencies. It is possible, then, that rhesus macaques attribute spatiotemporal knowledge representations to others more easily than representations of other object attributes. Alternatively, primates may attribute to others *any* knowledge about an object that is a direct reflection of the underlying machinery involved in perception. Primates themselves represent a number of different attributes of objects, including shape, color, and kind information (e.g., Beran, Smith, & Perdue, 2013; Menzel, 1973; Phillips & Santos, 2007; Santos et al., 2002). It may therefore be interesting to test whether primates expect agents to represent these aspects of objects.

Moreover, studies have found that primates represent *that* others see objects (Bräuer, Call, & Tomasello, 2007; Flombaum et al., 2005; Hare, Call, Agnetta, & Tomasello, 2000) but not *how* others see objects (Karg, Schmelz, Call, & Tomasello, 2016). That is, primates are capable of level-1 perspective taking but not level-2 perspective taking. On the surface, the studies reported here seem to support the hypothesis that spatiotemporal information is privileged when making knowledge attributions. However, most level-2 perspective taking tasks require that the subject understands not just how the partner sees the object, but that the partner sees the object *differently* from the subject himself. It may be that primates are not capable of representing how a partner sees an object when that partner sees the object different then they themselves do, but that they do attribute featural object knowledge to a partner when they partner does see the object in the same way that they do. This remains an important question for future research.

To summarize, our data support and extend previous work exploring primates' knowledge attributions. Not only did rhesus monkeys expect others to maintain static representations of hidden objects, they also expected others to dynamically update these object representations during a rotation event. While more studies are needed to best understand the boundary conditions of primates' knowledge attributes, our results suggest that primates expect others to have a fairly sophisticated understanding of how objects move in space.

Supplementary material

Please see https://osf.io/9bqcr/g for data files.

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Conflict of interest

The authors declare no conflict of interest.

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