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Monkeys represent others' knowledge but not their beliefs

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Abstract

The capacity to reason about the false beliefs of others is classically considered the benchmark for a fully fledged understanding of the mental lives of others. Although much is known about the developmental origins of our understanding of others' beliefs, we still know much less about the evolutionary origins of this capacity. Here, we examine whether non-human primates – specifically, rhesus macaques (Macaca mulatta) – share this developmental achievement. We presented macaques with a looking-time measure of false belief understanding, one that had recently been developed for use with 15-month-old human infants. Like human infants, monkeys look longer when a human experimenter fails to search in the correct location when she has accurate knowledge. In contrast to infants, however, monkeys appear to make no prediction about how a human experimenter will act when she has a false belief. Across three studies, macaques' pattern of results is consistent with the view that monkeys can represent the knowledge and ignorance of others, but not their beliefs. The capacity to represent beliefs may therefore be a unique hallmark of human cognition.

Introduction

It has been over 30 years since Premack and Woodruff (1978) initially asked, 'Does the chimpanzee have a theory of mind?' It is unlikely that these researchers realized at the time exactly how much theoretical and empirical furor the question would inspire. Now, three decades later, interest in our theory of mind capacities has become commonplace in a number of different areas within the developmental sciences. Much of the theoretical debate that ensued following Premack and Woodruff's (1978) paper concerned how to determine whether an organism truly represents the mental states of others. Amidst the debate, one idea gained consensus: in order to represent mental states, one must first recognize that mental states are psychological in nature. Unlike real states of the world, mental states exist inside an individual's mind and, thus, may be incongruent with the genuine state of the world (e.g. Dennett, 1978; Pylshyn, 1978). As such, researchers quickly became interested in the capacity to represent mental states that conflict with real world states – namely, false beliefs.

In the early 1980s, developmental researchers began to explore the time course during which children develop the capacity to reason about the false beliefs of others (see reviews in Flavell, 1999; Wellman, 1990; Wellman, Cross & Watson, 2001). In a typical study (e.g. Wimmer & Perner, 1983), 3- and 4-year-old children are presented with a story in which a character (Sally) hides a toy in one location, and a second character (Anne) surreptitiously moves the toy while the first character is away. The child is then asked where Sally will look for the toy when she returns. Four-year-olds typically reply that Sally will look for the toy in its original location; they recognize that Sally has a false belief about the toy's location and

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that she is likely to act accordingly. In contrast, younger children typically answer incorrectly, thinking that Sally will look for the toy in its current location (e.g. Perner, Leekam & Wimmer, 1987; Wimmer & Perner, 1983).

Historically, much research has supported the view that children undergo an important developmental shift in their understanding of others' beliefs around 4 years of age (see review in Wellman *et al*., 2001). Recent studies using non-verbal methods, however, have hinted that this developmental shift in belief understanding may occur even earlier than previously thought (Kovács, Téglás & Endress, 2010; Onishi & Baillargeon, 2005; Scott & Baillargeon, 2009; Song, Onishi, Baillargeon & Fisher, 2008; Southgate, Senju & Csibra, 2007; Surian, Caldi & Sperber, 2007; see review in Baillargeon, Scott & He, 2010). In the first study to explore these issues, Onishi and Baillargeon (2005) used an expectancy violation method in which 15-month-old infants were presented with a scenario in which an experimenter hid a toy in one of two boxes. In several different test conditions, the experimenter then either possessed a false belief about the toy's location (e.g. the toy moved into the opposite box while the experimenter was out of view) or had a true belief about its correct location (e.g. the toy did not switch places). Infants looked longer when an experimenter failed to act in accord with her true belief (by reaching toward the location opposite to that in which she knew the object to be hidden). When the experimenter had a false belief about the object's location, infants expected her to search where she had last seen the object, looking systematically longer when the experimenter reached to the object's current location. This finding was the first to suggest that infants have some understanding of the knowledge and belief states of others even before 2 years of age (for more recent results, see Scott & Baillargeon, 2009; Song *et al*., 2008; Surian *et al*., 2007). These recent studies on infants' false belief understanding have led to a new debate on the nature and limitations of our early representational understanding (e.g. Baillargeon *et al*., 2010; Csibra & Southgate, 2006; Leslie, 2005; Perner & Ruffman, 2005; Ruffman & Perner, 2005; Song & Baillargeon, 2008; Song *et al*., 2008; Southgate *et al*., 2007; Surian *et al*., 2007; Wellman & Brandone, 2009).

Although developmental psychologists have had much success examining the development of our belief understanding, consensus has not yet emerged regarding the question that Premack and Woodruff originally posed – namely, whether other primates share a human-like capacity to attribute mental states to others. Until recently, primates had consistently produced negative results during experimental tests in which they were required to reason about what another individual sees (e.g. Povinelli & Eddy, 1996) and intends to communicate (e.g. Call, Hare & Tomasello, 1998; see reviews for this early work in Rosati, Hare & Santos, 2009; Tomasello & Call, 1997). Recent studies using more ecologically valid methods, however, suggest that primates do appear to recognize what others see, know, and intend (see Call & Santos, in press; Call & Tomasello, 2008; Rosati *et al*., 2009; Santos, Flombaum & Phillips, 2006; Tomasello, Call & Hare, 2003). In a pioneering series of studies, Hare and colleagues demonstrated that subordinate chimpanzees (*Pan troglodytes*) reliably take food that a dominant chimpanzee cannot see (Hare, Call, Agnetta & Tomasello, 2000) or does not know about (Hare, Call & Tomasello, 2001). Similarly, rhesus monkeys (*Macaca mulatta*) reliably attend to what a human experimenter can see (Flombaum & Santos, 2005) and hear (Santos, Nissen & Ferrugia, 2006) when deciding whether to steal contested pieces of food, even in the absence of training. Finally, both chimpanzees and capuchin monkeys (*Cebus apella*) reason about behavior in terms of goal-directed actions (e.g. Call, Hare, Carpenter & Tomasello, 2004; Phillips, Barnes, Mahajan, Yamaguchi & Santos, 2009).

Despite evidence that primates can reason about what others see and know in competitive tasks (Bräuer, Call & Tomasello, 2007; Flombaum & Santos, 2005; Hare *et al*., 2000; Hare *et al*., 2001; Hirata & Matsuzawa, 2001; Kaminski, Call & Tomasello, 2008; Santos *et al*., 2006), it has to date remained unclear whether primates can represent more than others' knowledge and ignorance, specifically, whether they can recognize that other individuals have *beliefs* about the world that might differ from reality. In an early study, Call and Tomasello (1999) attempted to address this issue. They trained chimpanzees and orangutans (*Pongo pygmaeus*) on a task in which a communicator witnessed the hiding of a food item and informed the subject which hiding place to choose. After a long training phase, subjects received a test in which the communicator had a false belief about the location of the food – the food had been switched from the location in which it was hidden to a new location, unbeknownst to the communicator. All of the apes tested failed this test trial, ignoring the verity of the communicator's beliefs about the location of the food. Kaminski and colleagues (2008), using a competitive paradigm to explore chimpanzees' false belief understanding, found similar negative results. In their study, two chimpanzees took turns competitively searching in buckets for desirable food. In one condition, the subject chimpanzee witnessed the experimenter misleading the competitor chimpanzee about the location of the food (she appeared to put the food in one bucket but actually put it into a different bucket). The question of interest was whether subject chimpanzees could successfully predict the location that the competitor chimpanzee would search based on her false belief about where the food was hidden. In contrast to human children, chimpanzees failed this task; although chimpanzees did successfully reason based on the competitor's ignorance, they did not use information about the competitor's false belief to determine where the competitor would search. These results, at least at first glance, strongly suggest that apes (and, by implication, other primates) may lack the capacity to reason about false beliefs. Unfortunately, the tasks performed to date may have burdened subjects with relatively arduous task demands. In both of the above cases, ape participants were subjected to methods that involved a long training procedure and required understanding complicated scenarios. It is possible that the demands of these tasks may have prevented apes from performing well, regardless of whether they are able to represent beliefs. Indeed, a similar problem with task demands appears to hinder 2-year-old children, who fail on standard elicited response false belief tasks (e.g. Wellman *et al*., 2001) despite their successful performance on violation-of-expectancy measures of false belief understanding (see review in Baillargeon *et al*., 2010).

The goal of the present experiments was to test primates' understanding of beliefs with a behavioral task that relieves the task demand problems of previous methodologies. Specifically, we adapted a version of the expectancy violation false belief test originally developed by Onishi and Baillargeon (2005) for use with human infants. As discussed above, expectancy violation tests appear to tap into human false belief understanding at ages that are developmentally younger than those predicted by other verbal false belief test methodologies (e.g. Wellman *et al*., 2001). We therefore reasoned that such an expectancy violation test could also potentially be used to detect primate capacities that may be masked by other, more complicated, behavioral measures that require elicited responses.

We presented our version of the Onishi and Baillargeon (2005) task to a population of free ranging rhesus monkeys from the Cayo Santiago field site. Previous work has shown that this species can reason about what others see (Flombaum & Santos, 2005), know (Santos *et al*., 2006), and intend (see Rochat, Serra, Fadiga & Gallese, 2008), but to date little work has addressed what this species knows about others' beliefs.

Experiment 1 began by exploring whether rhesus monkeys recognize that a human experimenter should behave accurately when she has a true belief about the state of the world. Specifically, we explored whether monkeys would expect an experimenter who knew about a desired object's position to search for this object in the correct location.

Experiment 1

Method

Subjects—In this and all other experiments, we tested rhesus monkeys from the Cayo Santiago population (see Rawlins & Kessler, 1987). The Cayo Santiago macaques have served as behavioral subjects since the 1930s and are thus well habituated to human experimenters. In addition, monkeys from this population have been successfully tested using similar expectancy violation methods for over a decade (e.g. Cheries, Newman, Santos & Scholl, 2006; Munakata, Santos, Spelke, Hauser & O'Reilly, 2001; Santos & Hauser, 2002; Santos, Miller & Hauser, 2003; Shutts, Condry, Santos & Spelke, 2009). Subjects in this population can be easily identified through ear notches and chest/leg tattoos. In Experiment 1, we successfully tested 62 rhesus monkeys; other monkeys were approached by the experimenters but did not complete testing due to disinterest (defined as interaction with another monkey or inattention to the presentation after it has begun; n = 58), monkey's approach toward the apparatus (3), previous testing (6), or experimenter error (1). The decision to stop testing in all of these cases was made by the cameraperson, who was blind to the testing condition. The sessions of Experiment 1 were interspersed with sessions of Experiment 2 to be sure that these two experimental conditions could be directly compared. Specifically, on each day, individual monkeys were tested on either Experiment 1 or Experiment 2.

Apparatus—In all experiments, we presented monkeys with events that occurred on a stage built from foamcore measuring 45 cm across and 23 cm deep. The stage could be occluded by a screen in the front, which blocked the entire display from the view of the subject. The back of the stage ordinarily rose to a height of approximately 50 cm; attached to the back of the stage was a hinged occluder that could be raised to a height of approximately 91 cm that, as a result, covered the face of the experimenter operating the stage. We placed a small box (10 cm × 10 cm × 10 cm) on each side of the stage; the two boxes were different colors (white and green) to further individuate them. The side of each box facing the center of the stage was left open so that an object moving along the stage could enter it. These openings were concealed with small curtains constructed of artificial leaves, preventing both the subjects and the experimenter from seeing the contents of each box. A track on which a plastic lemon could move was placed along the stage between the two boxes. A handle was attached to the bottom of the lemon so that the experimenter could surreptitiously control the lemon's movement along the track from behind the stage, out of view of the subject.

Procedure—As in previous studies (e.g. Cheries *et al.*, 2006), we opportunistically located subjects by searching the island for individuals separated from other group members; we avoided testing individuals engaged in social interactions or foraging. Two experimenters were involved in running the experiment. One experimenter, the presenter, operated the stage and presented the stimuli to the subject. The second person, the cameraperson, operated the video camera from above the stage and recorded the subject's face and, therefore, the subject's direction of looking using a portable Sony digital video camera. The video record captured the subject but neither the presenter nor her actions on the stage. As a result, the cameraperson had no knowledge of the particular experimental condition being performed. Because the presenter chose the condition randomly at the start of each belief induction event, the cameraperson could serve as a blind judge of the quality of experimental session. After testing, the experimenters noted the subject's identity and checked to be sure that the subject had not previously been tested in this experiment.

We adapted our experimental procedure from the one Onishi and Baillargeon (2005) used to test human infants with a few key differences. Experiment 1 tested monkeys with the true belief (TB) events used in that study. We presented each subject with three *familiarization trials*, one *belief induction event*, and then one *test trial*. In the first familiarization trial (the object trial), the front screen was dropped to reveal the presenter looking down at the motionless lemon at the center of the stage. The presenter called ‘now’ when the screen hit the ground, and the monkey’s looking time was recorded for a 10 second interval, at which point the front screen was raised. In the second familiarization trial, the front screen was dropped to reveal the experimenter reaching into one of the two boxes while the lemon was out of view, simultaneously calling ‘now’. The cameraperson recorded the subject’s looking time for 10 seconds while the presenter remained motionless with her hand still in the box. The screen was raised again upon the trial’s conclusion. The third familiarization trial was identical to the second, except that the presenter reached into the other box. The object trial always occurred first; the order in which the green and white box familiarization trials were presented was counterbalanced across subjects.

After the three familiarization trials, subjects were shown a *belief induction event* (see Figure 1). During these events, the front screen was dropped to reveal the presenter looking down at the stage. The lemon emerged from one of the boxes and the presenter, using exaggerated head and eye movements, watched its movements on the stage. In Experiment 1, the presenter always had a *true belief* about the location of the lemon, as the lemon only moved while it was clearly in view of the presenter. Subjects saw one of two possible belief induction events: (1) same side event: While the presenter watched, the lemon emerged from one of the two boxes, moved to the center of the stage, and then returned to the original box; (2) different side event: While the presenter watched, the lemon emerged from one of the two boxes, moved across the stage and entered the opposite box.

After watching a belief induction event, the screen remained lowered, and subjects were presented with a *test event* in which the presenter reached into one of the two boxes, acting either in accord with or in violation of her belief about the lemon’s location. Upon reaching into one of the boxes during the *test event*, the presenter called ‘now’ and the subject’s looking was recorded for 10 seconds. If monkeys expect a person to act correctly based on her belief, then subjects should look less when the presenter reaches into the box holding the lemon (the expected condition) than when she reaches into the empty box (the unexpected condition).

Video coding—Videotapes were acquired onto a Macintosh laptop and analyzed with MPEG Streamclip software. A video coder, blind to the experimental condition, examined looking time during each frame (30 frames = 1 s) of the 10 s looking period of each trial. A second coder scored 10% of these trials, and inter-observer reliability was high (Pearson’s $R = 0.91$).

Results

We compared monkeys’ duration of looking on expected and unexpected test conditions. Monkeys showed a reliable difference across these two conditions ($t(60) = 2.10$, $p = .04$; Figure 2); monkeys who saw an unexpected event looked longer (Mean = 4.34 s) than those who saw an expected event (Mean = 3.04 s). No such differences were observed in looking times for the familiarization events (Means: expected = 3.70 s, unexpected = 4.55 s; $t(60) = 1.45$, $p = .15$), suggesting that this effect was not due to a general difference between monkeys tested on expected versus unexpected conditions. There was also no effect of box (white vs. green) searched ($t(60) = 0.80$, $p = .43$).

Discussion

When the presenter had a true belief about the location of the lemon, monkeys expected her to search in the correct location, looking reliably longer when the presenter reached into the empty box than when she reached into the box containing the lemon. We interpret this pattern of performance as evidence that monkeys recognized that the human experimenter had knowledge of the lemon's location and expected her to search accordingly. This result is consistent with previous work demonstrating that monkeys in this population recognize others' knowledge states, correctly acting on the basis of another individual's perceptual access and knowledge (Flombaum & Santos, 2005; Santos *et al*., 2006). In addition, monkeys' pattern of performance on Experiment 1 mirrors that of 15-month-old human infants tested in the true belief condition of the Onishi and Baillargeon (2005) task.

In Experiment 2, we explored whether monkeys also make correct predictions when the experimenter should have a false belief. To examine this question, we tested a new group of monkeys on the false belief (FB) condition of Onishi and Baillargeon's study (2005). Monkeys were shown events in which an experimenter was misled about the location of the lemon and then searched for it either where it actually was or where she incorrectly believed it to be. If monkeys have a sophisticated understanding of others' beliefs, then they, like 15-month-old infants, should expect the experimenter to search for the lemon in the location where it was not currently hidden.

Experiment 2

Method

Subjects—We successfully tested 48 monkeys; other monkeys were approached by the experimenters but did not complete testing because of disinterest (*n* = 66), approach to the apparatus (2), previous testing (5), or experimenter error (2). The decision to stop testing in all of these cases was made by the cameraperson, who was blind to the testing condition.

Procedure—The procedure of Experiment 2 was identical to that of Experiment 1 except for the type of belief induction events used. In contrast to Experiment 1, Experiment 2 used events in which the presenter had a false belief about the location of the lemon (Figure 3). In both events, the presenter initially watched as the lemon moved across the stage. After the lemon was completely inside one of the boxes, the back occluder lifted to conceal the presenter. While out of the presenter's view, the lemon moved to the opposite box. In this way, the subject, but not the presenter, could see that the lemon had changed locations. Once the lemon was completely hidden inside the box, the back occluder lowered and the presenter searched for the lemon. Subjects saw one of two events: either the presenter reached into the box where the lemon had been originally (i.e. where the presenter believed it to be, the expected condition) or to the box where the lemon currently was hidden (i.e. where she should not believe it to be, the unexpected condition). If monkeys recognize that the presenter has a false belief, they should expect her to search in the incorrect box, and look longer when she reaches toward the lemon's new location, just as human infants do (Onishi & Baillargeon, 2005).

Results

As in Experiment 2, we found no significant differences in familiarization trial looking time for monkeys tested in the expected and unexpected conditions ($t(46) = 0.39$, $p = .70$; expected = 4.31 s, unexpected = 4.60 s). There was also no effect of box (white vs. green) searched ($t(46) = 0.45$, $p = .66$). In contrast to Experiment 1, however, we also observed no significant differences in looking across expected and unexpected test conditions ($t(46) = 0.33$, $p = .74$; Figure 2). Monkeys showed relatively low levels of looking both when the experimenter reached to the lemon's original location (expected test event: Mean = 3.15 s) and when she reached to the lemon's new location (unexpected test event: Mean = 3.37 s).

Discussion

When a human experimenter had a correct belief about the location of the lemon, as in Experiment 1, monkeys expected her to search in the correct location. Subjects in Experiment 1 looked reliably longer when the presenter reached into the wrong location than when she reached into the box where the lemon was hidden. In contrast, when the presenter had a false belief about the location of the lemon, as she did in Experiment 2, monkeys did not expect her to look in the wrong location (i.e. where she believed it was). In contrast to 15-month-old human infants, monkeys exhibited similar durations of looking regardless of where an experimenter with a false belief searched. Importantly, this pattern of performance suggests that monkeys correctly recognized that the experimenter who had a false belief in Experiment 2 should behave differently from the experimenter who had a correct belief in Experiment 1. In this way, monkeys tested in Experiment 2 successfully recognized that the experimenter who hadn't seen the lemon's movement should behave differently from an experimenter who had. However, even though monkeys in Experiment 2 successfully recognized that this experimenter should behave differently from the first experimenter, they failed to predict how she would act based on her false belief. Indeed, our monkeys' performance in the false belief task is consistent with the view that they expect the experimenter to reach randomly between the two boxes, much like human infants expect random search behavior when an experimenter is completely ignorant of an object's true location (Scott & Baillargeon, 2009; for similar results with toddlers, see He, Bolz & Baillargeon, 2011).

Monkeys' pattern of performance across Experiments 1 and 2 is therefore consistent with the interpretation that rhesus monkeys can represent others' knowledge and ignorance but not their beliefs. Our monkeys show increased looking when a knowledgeable experimenter reaches to the incorrect location (as in Experiment 1), but appear to make no prediction about where an ignorant experimenter will search (as in Experiment 2). In this way, rhesus monkeys' performance radically differs from that of 15-month-old human infants, who show increased looking when a presenter with a false belief searches in the location where the object actually resides. Monkeys seem to realize that an individual can lack the information necessary to know the true location of an object, but they appear unable to utilize information about that person's beliefs to make predictions about how she will act. This distinction between representing others' knowledge versus their beliefs seems to mirror a similar distinction that occurs across human development (see review in Baillargeon *et al.*, 2010). Human infants appear to recognize that other individuals have informational states that are congruent with reality (e.g. perceptual states like seeing and hearing, inferential states like knowledge and ignorance) before they later come to realize that others can have states that are incongruent with reality (e.g. false beliefs, representations of pretense, etc.). In this way, our monkeys appear to possess the ability to represent the mental states that are available to younger infants, but not those reality-incongruent mental states that emerge later in human development after the first year of life.

Unfortunately, there exists at least one alternative interpretation for monkeys' pattern of performance across Experiments 1 and 2. It is possible that monkeys' difference in performance across the two studies resulted not from differences in the nature of the belief induction events used in these two experiments, but instead from differences in task demands. In contrast to Experiment 1, Experiment 2 involved a longer belief induction event and required monkeys to keep track of the lemon's location while the back occluder was lifted and lowered. It is thus possible that monkeys' low durations of looking across expected and unexpected events in Experiment 2 were due to these task demands rather than an inability to understand false beliefs *per se*. To deal with this alternative, Experiment 3 explored whether monkeys could still reason about true belief events that were better equated to the false belief events presented in Experiment 2. Specifically, we presented monkeys with a belief induction event that involved a longer wait and multiple back occluder movements. If monkeys' failure in Experiment 2 was merely due to these task demands, then subjects should perform at chance in Experiment 3 when these demands are equivalent. In contrast, if monkeys' poor performance in Experiment 2 resulted from an inability to understand false beliefs, then monkeys in Experiment 3 should successfully predict how an experimenter with a true belief about an object's location would act even when task demands are more complex.

Experiment 3

Method

Subjects—We successfully tested 54 rhesus monkeys; other monkeys were approached by the experimenters but did not complete testing due to disinterest (*n* = 35), previous testing (5), or experimenter error (1). The decision to stop testing in all of these cases was made by the cameraperson, who was blind to the testing condition. Experiment 3 was run after the completion of Experiments 1 and 2.

Procedure—Experiment 3 used the same procedure as Experiments 1 and 2 except for the belief induction event used. In Experiment 3, the presenter first watched as the lemon moved across the stage. The lemon then moved inside one of the two boxes (either the box from which it emerged or the opposite box, counterbalanced across monkeys) as both the subject and the presenter watched. When the lemon was completely hidden in one of the boxes, the back occluder lifted, concealing the presenter. This occluder then remained in its lifted position for approximately 4 s (the time required to move the lemon from one box to the other in Experiment 2) before lowering again (see Figure 4). Note that this event resulted in the presenter having a correct belief about the lemon's location, even though she could not see the stage for a short period of time. Once the screen was lowered, the presenter reached into either the box with the lemon (expected) or the empty box (unexpected).

Results

We found no significant difference in looking time in familiarization trials across monkeys tested in the expected and unexpected conditions ($t(52) = 0.37$, $p = .71$; Means: expected = 3.73 s, unexpected = 3.52 s). There was also no effect of box (white vs. green) searched ($t(52) = 0.35$, $p = .73$). We did, however, observe significant differences in monkeys' looking on expected and unexpected test trials ($t(52) = 2.83$, $p = .007$; Figure 2). As in Experiment 1, monkeys in Experiment 3 looked significantly longer at the unexpected test event (Mean = 3.69 s) than the expected test event (2.33 s).

Discussion

As in Experiment 1, monkeys in Experiment 3 looked longer at an unexpected event in which an experimenter with a true belief about a lemon's location reached to the incorrect box than at an expected event in which she reached to the correct box. Consistent with the previous studies, monkeys in Experiment 3 succeeded in developing an expectation about how the presenter should act when she knew the lemon's location. Here, however, monkeys succeeded in developing this correct expectation even when the belief induction event included occlusion and a delay. The results of Experiment 3 thus replicate and extend those of Experiment 1, suggesting that monkeys can represent where a knowledgeable person should act even once the objects involved in the display are occluded from her view. More importantly, however, the results of Experiment 3 clarify that monkeys' pattern of results in Experiment 2 resulted less from problems with task demands and more from a real deficit in representing false beliefs.

General discussion

Although monkeys succeeded in making predictions about the behavior of an experimenter with a true belief in Experiment 1, monkeys failed to make specific predictions about how the same experimenter would act based on her false belief. Monkeys presented with false belief events in Experiment 2 demonstrated nearly identical durations of looking to both expected and unexpected events, and the magnitude of their looking on these events best corresponds to their duration of looking in the expected event of Experiment 1. The results of Experiment 3 confirm that this pattern of performance cannot be due to problems with irrelevant task demands, suggesting that the difference in monkeys' performance across the first two experiments results specifically from problems representing beliefs. Taken together, these results suggest that rhesus monkeys represent the actions of others very differently than 15-month-old humans do. While 15-month-olds appear to represent a person's behavior in terms of her beliefs, rhesus monkeys appear to represent behavior only as a function of information states that are consistent with the reality of the situation, such as whether an experimenter is knowledgeable or ignorant. In this way, our results suggest a striking difference between human and non-human theories of others' minds – like humans, macaques appear to represent reality-congruent mental states such as knowledge and ignorance, but, unlike humans, they lack representations of others' beliefs.

Note, however, that even though monkeys are unable to make predictions based on a person's false beliefs, the predictions monkeys do make are not solely based on low-level features of the task. For example, monkeys do not merely expect a person to search where the lemon is actually hidden, in contrast to 3-year-old children tested in elicited response tasks, who expect Sally to look where her toy actually is hidden although she has a false belief that it is elsewhere (e.g. Perner *et al*., 1987; Wimmer & Perner, 1983). In the false belief events of Experiment 2, monkeys find it plausible that the experimenter will search in either box, not just the one where the object is. Throughout these three experiments, monkeys seemed to recognize whether the experimenter possessed knowledge or ignorance of the lemon's movements, and they developed specific expectations about how these states influenced future behaviors. Under this view, monkeys are able to attribute knowledge and ignorance to people based on their perceptions. In doing so, each monkey must attribute to the experimenter an information state that is different from what the monkey himself knows about the world.

Our results appear to fit perfectly with an emerging pattern of performance in this and other primate populations. A growing number of studies now seem to suggest that primates reliably make predictions based on an experimenter's knowledge and ignorance when tested using competitive foraging measures (Flombaum & Santos, 2005; Hare *et al*., 2000; Hare *et al*., 2001; Kaminski *et al*., 2008; Santos *et al*., 2006), but there is little evidence that they can represent others' beliefs (Call & Tomasello, 1999) even when tested in competitive tasks (Kaminski *et al*., 2008). Indeed, Kaminski and colleagues (2008) observed an extremely similar pattern of performance in chimpanzees – like macaques' performance in the present study, Kaminski and colleagues' chimpanzees succeeded in representing others' knowledge and ignorance, but not their beliefs. However, the present results provide an important new step in this line of work, as they reveal that primates' previously reported failures on false belief tasks might not be due to problems with task demands. First, our results indicate that primates fail to represent false beliefs even on a task that is simple enough to demonstrate successful false belief reasoning in humans as young as 15 months of age. However, our monkeys' failures in this looking time task cannot be due to problems with the demands of the task itself, as the same population of monkeys shows successful performance on two other looking time tests (Experiments 1 and 3). Indeed, monkeys performed differently on looking time tests that focus on knowledge and belief even when all possible low-level aspects of the task (e.g. duration, screen movements) were better equated, as in Experiment 3.

In addition to their importance for our understanding of the evolution of theory of mind capacities, our results also have implications for debates regarding the development of false belief understanding in human infants and children. The original publication of Onishi and Baillargeon's (2005) results was met with much controversy (e.g. Leslie, 2005; Perner & Ruffman, 2005; Ruffman & Perner, 2005; Wellman & Brandone, 2009). In the years since this initial finding, researchers have provided a number of deflationary alternative accounts of infants' success in this task, interpreting 15-month-olds' performance not as indicative of false belief understanding but instead as the result of less sophisticated representational capacities, such as associative links between actor, object, and location (Perner & Ruffman, 2005) or representations of knowledge and ignorance (Wellman & Brandone, 2009; see review of such accounts in Baillargeon *et al*., 2010). At least some of these debates (e.g. Perner and Ruffman's behavioral rule alternative, see discussion in Baillargeon *et al*., 2010; Perner & Ruffman, 2005; Ruffman & Perner, 2005) are yet to be resolved, but our macaque results provide a hint that infants' performance on this task might reflect more sophisticated representational abilities than some researchers had originally suggested. As reviewed above, much empirical evidence suggests that monkeys have all the representational capacities needed for success under deflationary accounts of the Onishi and Baillargeon task; rhesus monkeys can represent links between agents, objects, and goal-directed actions (e.g. Rochat *et al*., 2008) and can successfully represent knowledge and ignorance in more complicated mind-reading tasks (Flombaum & Santos, 2005; Santos *et al*., 2006). Most deflationary accounts of infants' performance on the Onishi and Baillargeon (2005) task (e.g. Leslie, 2005; Perner & Ruffman, 2005; Ruffman & Perner, 2005; Wellman & Brandone, 2009) therefore strongly predict that monkeys should have succeeded in our false belief task, performing identically to human infants. In contrast, we have observed striking differences in the performance of rhesus monkeys and 15-month-olds, with only the latter making successful predictions when the experimenter has a false belief. As such, our findings hint that infants' successful performance on this task can not only result from the kinds of mind-reading abilities observed in primates. Indeed, this study suggests that infants succeeded on the Onishi and Baillargeon (2005) task using representational capacities that monkeys have been demonstrated to lack, ones we believe must involve some kind of representation of other individuals' beliefs.

In conclusion, then, rhesus macaques appear to lack a level of representational sophistication that our own species appears to develop by 15 months of age. Although rhesus macaques can distinguish between representational states of knowledge and ignorance, they fail to take the cognitive leap to recognizing others' beliefs. Monkeys' failure to represent others' beliefs in this task may thus reflect an important difference in the theory of mind capabilities of humans and other primate species. The open (and quite difficult) question for future research is how and why the human species is able to acquire this purportedly unique representational capacity.

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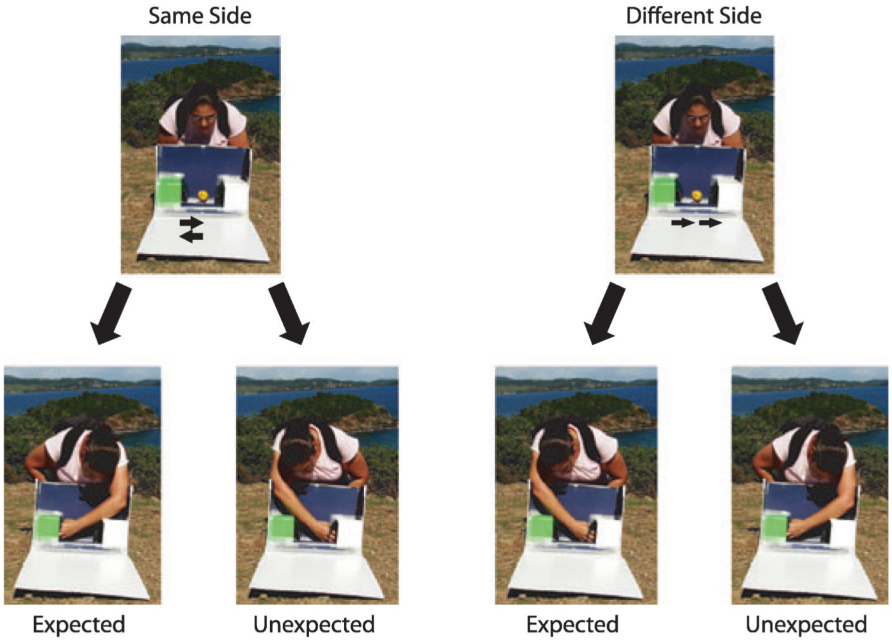

Figure 1.

The belief induction and test events used in Experiment 1. Across two conditions (different side and same side), the experimenter had a true belief about the lemon’s location and should be expected to reach to the box that actually contains the lemon.

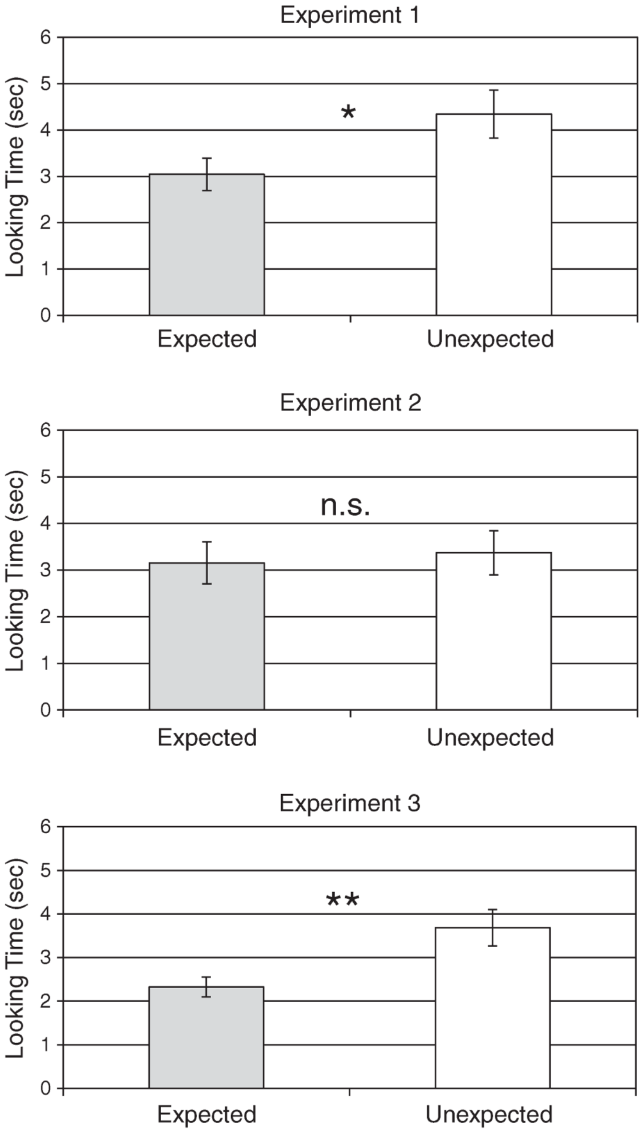

Figure 2.

Mean looking time Expected and Unexpected conditions for all experiments. Brackets show the standard error of the mean. Monkeys looked significantly longer in the Unexpected condition than the Expected condition in Experiments 1 and 3 (*p < *.05*, ** p < .01). There was no significant difference in looking time between conditions in Experiment 2.

Figure 3.

The belief induction and test events used in Experiment 2. Across two conditions (different side and same side), the experimenter had a false belief about the lemon’s location and should be expected to reach to the incorrect box.

Figure 4.

The belief induction and test events used in Experiment 3. Across two conditions (different side and same side), the experimenter knew where the lemon was hidden, but there was a short delay in which the experimenter's view of the stage was occluded before her search action occurred. If the demand of the delay is inconsequential, monkeys should expect the experimenter to reach to the correct box.