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The origins of belief representation: Monkeys fail to automatically represent others' beliefs

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ABSTRACT

Young infants' successful performance on false belief tasks has led several researchers to argue that there may be a core knowledge system for representing the beliefs of other agents, emerging early in human development and constraining automatic belief processing into adulthood. One way to investigate this purported core belief representation system is to examine whether non-human primates share such a system. Although non-human primates have historically performed poorly on false belief tasks that require executive function capacities, little work has explored how primates perform on more automatic measures of belief processing. To get at this issue, we modified Kovács et al. (2010)'s test of automatic belief representation to examine whether one non-human primate species—the rhesus macaque (*Macaca mulatta*)—is automatically influenced by another agent's beliefs when tracking an object's location. Monkeys saw an event in which a human agent watched an apple move back and forth between two boxes and an outcome in which one box was revealed to be empty. By occluding segments of the apple's movement from either the monkey or the agent, we manipulated both the monkeys' belief (true or false) and agent's belief (true or false) about the final location of the apple. We found that monkeys looked longer at events that violated their own beliefs than at events that were consistent with their beliefs. In contrast to human infants, however, monkeys' expectations were not influenced by another agent's beliefs, suggesting that belief representation may be an aspect of core knowledge unique to humans.

1. Introduction

People understand other agents' behaviors not only in terms of their superficial physical properties, but also as the result of a rich repertoire of unobservable mental states. Much debate in developmental psychology has focused on the problem of how we acquire the ability to represent such unobservable mental states, and how we come to recognize that these mental states can be different from our own. Although early research suggested that children begin to represent others' false beliefs only around four years of age (see reviews in Wellman, Cross, & Watson, 2001), more recent work demonstrates that infants show some understanding of others' false beliefs even in the first two years of life (e.g., Buttelmann, Carpenter, & Tomasello, 2009; Knudsen & Liszkowski, 2012; Kovács, Téglás, & Endress, 2010; Luo, 2011; Onishi & Baillargeon, 2005; Poulin-Dubois & Chow, 2009; Scott & Baillargeon, 2009; Scott, Baillargeon, Song, & Leslie, 2010; Song & Baillargeon, 2008; Song, Onishi, Baillargeon, & Fisher, 2008; Southgate, Chevallier, & Csibra, 2010; Southgate, Senju, & Csibra, 2007; Surian, Caldi, & Sperber, 2007; Surian & Geraci, 2012). In a landmark paper, Onishi and Baillargeon (2005) observed that 15-month-old infants look longer when an agent with a false belief searches for an object in its true location than when the agent searches in the spot where she saw it last (see also Surian et al., 2007). Infants around this age are also able to take false beliefs into account when inferring an agent's preferences

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(Luo, 2011), deciding how to help an agent (Buttelmann et al., 2009; Knudsen & Liszkowski, 2012; Tomasello, 2009), and determining the object of an agent's verbal reference (Southgate et al., 2010).

These new infant findings have been used by many researchers to argue that humans may be equipped with an early emerging system for representing others' beliefs (e.g., Apperly & Butterfill, 2009; Baillargeon, Scott, & He, 2010; Butterfill & Apperly, 2011; Leslie, 2005; Luo & Baillargeon, 2010). Although these specific accounts differ in their claims about the development of the complex belief reasoning observed in human adults, the proposal that infants possess an early emerging system for representing others' beliefs fits with recent "core knowledge" accounts of infant development (see reviews in Kinzler & Spelke, 2007; Spelke, 2004). These core knowledge accounts argue that infants begin life endowed with a set of domain-specific systems for making sense of the physical and social world. These core systems are thought to be older cognitive systems, designed to rapidly solve domain-specific learning problems that our ancestors faced over their evolutionary history. Core knowledge systems are thought to be relatively automatic processes that are constrained by specific signature limits and tend to show characteristic breakdowns under certain situations. These features together require that core knowledge systems show a set of empirical quirks. First, such systems should be experience-independent, and therefore should tend to emerge early in human development. Second, the limits posed by core knowledge systems often persist into adulthood, especially in cases of cognitive load. Finally, because core knowledge systems are thought to be phylogenetically ancient, they are likely to be shared by closely related nonhuman primates.

To get a sense of these core knowledge features playing out in a different cognitive domain, consider the case of our core knowledge system for object cognition (see review in Kinzler & Spelke, 2007). Some researchers have proposed that there is a core system for representing inanimate physical objects and their movements (e.g., Spelke, Breinlinger, Macomber, & Jacobson, 1992). In line with this view, there is a rich body of evidence that infants possess a set of principles for reasoning about physical objects within the first few months of life, for instance, that objects maintain consistent paths in time and space and tend to cohere (e.g., Aguiar & Baillargeon, 1999; Baillargeon, Spelke, & Wasserman, 1985; Kellman & Spelke, 1983; Kellman, Spelke, & Short, 1986; Leslie & Keeble, 1987; Slater et al., 1990; Spelke, 1990; Spelke, Kestenbaum, Simons, & Wein, 2011; Valenza, Leo, Gava, & Simion, 2006; von Hofsten & Spelke, 1985). Importantly, such principles also implicitly guide adult object processing. When tested on object-based attention tasks, adult participants fall prey to the limits of this system; people fail to track objects that break apart briefly during motion (Scholl & Pylyshyn, 1999) or fail to cohere (vanMarle & Scholl, 2003). Finally, at least some of these principles seem to guide object reasoning in closely related primates (Cacchione & Call, 2010; Flombaum, Kundey, Santos, & Scholl, 2004; Munakata, Santos, Spelke, Hauser, & O'Reilly, 2001; Santos, 2004). These empirical findings together have been used to argue that object knowledge is one of several early emerging core systems for representing the world (see reviews in Santos & Hood, 2009; Spelke, 2004).

Is there empirical reason to argue that a similar core knowledge system exists for early belief reasoning? First, as reviewed above, there is ample evidence that infants begin representing others' beliefs early in life without the need for much experience (e.g., Luo, 2011; Onishi & Baillargeon, 2005; Surian et al., 2007). Indeed, at least one recent study suggests that belief representation may be present in the first few months of life, which is as early as we see evidence for other core abilities. Kovács and colleagues (2010) tested whether 7-month-old infants automatically represent the beliefs of another agent. Their logic was that infants who represent another agent's belief about the location of an object may experience interference in cases in which that agent's belief differs from their own. To test this, Kovács and colleagues presented four different groups of infants with videos involving a cartoon agent who watched a ball roll along a table and behind an opaque occluder. When the ball moved behind the occluder, neither the infant nor the agent could see it. Although each group of infants saw a different series of events, all infants saw a final test outcome in which the occluder was lowered to reveal that there was no ball behind it. Infants in the *Agent and Infant True Belief* condition (ATB-ITB) saw the agent in the video watch the ball roll behind the occluder, out into the open on the table, and then off the visible part of the video screen. In this case, the final test outcome (no ball behind the occluder) was consistent with both the infants' and agent's beliefs. Infants in the *Agent and Infant False Belief* condition (AFB-IFB), in contrast, saw the agent in the video watch the ball roll behind the occluder without rolling back out. In this condition, the final test outcome was inconsistent with both the infants' and agent's beliefs. Indeed, Kovács and colleagues found that infants looked longer in the AFB-IFB condition than in the ATB-ITB condition. In a third condition, *the Agent True Belief Infant False Belief* condition (ATB-IFB), infants saw the agent watch the ball roll off the video screen. Then, while the agent was not watching, infants saw the ball roll back on screen and behind the occluder. In this condition, the final test outcome was inconsistent with the infants' belief even though it was consistent with the agent's belief. Perhaps unsurprisingly, infants looked longer in this ATB-IFB condition than they did in the ATB-ITB condition. In the final and critical *Agent False Belief Infant True Belief* condition (AFB-ITB), infants saw the agent watch the ball roll behind the occluder. Then, while the agent was not watching, infants saw the ball roll out from behind the occluder and off screen. In this condition, the final test outcome was inconsistent with the agent's belief, even though infants should find it expected. Interestingly, infants looked longer in this AFB-ITB condition than in the ATB-ITB case. This pattern of performance suggests that infants reacted to seeing a test outcome that violated the agent's belief even when that outcome was consistent with their own belief. This finding demonstrates that infants (potentially automatically) compute an agent's false belief, even from as young as seven months of age. In this way, infants are able to represent others' false beliefs at around the same time that they demonstrate core knowledge principles in other domains (e.g., Spelke et al., 1992; Wynn, 1992).

In addition to evidence that infants begin processing others' beliefs in the absence of much experience, there is also work suggesting that adult belief processing is—at least in some situations—constrained in ways that one might predict from a core knowledge account. Using reaction time as a dependent measure, Kovács et al. (2010) presented adult participants with events similar to the ones they showed to seven month-old infants. Adult participants were instructed to respond as quickly as possible when a ball was present behind the occluder. Adults detected the ball just as quickly when they expected the ball to be present behind the occluder as when the agent alone expected the ball to be present behind the occluder. In this way, adults' reaction times were influenced by the agent's false belief in the same way as infants' looking times. Consistent with this result, Samson, Apperly, Braithwaite, Andrews, and Bodley Scott (2010) demonstrated that adults' judgments of their own visual perspective are impaired when their perspective is different from that of another agent. Together, these findings suggest that an early emergent system for belief processing observed in infants may persist into adulthood, as one might expect if this were part of a core knowledge system (for more review of this evidence, see Apperly, 2011).

So far, evidence from human infants and adults is consistent with the view that there may be a core knowledge system for belief representation. Inconsistencies arise, however, when looking at the third line of evidence, namely that from non-human primates. Although there is evidence that non-human primates reason about conspecifics' behavior in ways consistent with an understanding of some unobservable mental states such as seeing (Bräuer, Call, & Tomasello, 2007; Flombaum & Santos, 2005; Hare, Call, Agnetta, & Tomasello, 2000; Hare, Call, & Tomasello, 2001, 2006), hearing (Melis, Call, & Tomasello, 2006; Santos, Nissen, & Ferrugia, 2006), and inference (Schmelz, Call, & Tomasello, 2011), there is no evidence to date that non-human primates understand others' beliefs (see reviews in Call & Santos, 2012; Rosati, Hare, & Santos, 2010). In an early study, Call and Tomasello (1999) found that chimpanzees (*Pan troglodytes*) performed more poorly than human children on a non-verbal false belief test; four-year-old children were able to ignore an experimenter's cue to one location when the experimenter had a false belief about the location of a food reward, but chimpanzees failed to do so despite the motivation of finding food. More recently, researchers found that chimpanzees failed to show an understanding of false beliefs in a competitive task (Kaminski, Call, & Tomasello, 2008; Krachun, Carpenter, Call, & Tomasello, 2009), even though they have shown an understanding of knowledge and ignorance in similar competitive situations (e.g., Hare et al., 2001). In addition, rhesus macaques (*Macaca mulatta*) tested on a version of the Onishi and Baillargeon (2005) looking time task showed evidence of understanding another agent's knowledge and ignorance, but not the agent's beliefs (Marticorena, Ruiz, Mukerji, Goddu, & Santos, 2011). In this experiment, monkeys in the true belief condition saw a human experimenter watch an object move into one of two box hiding locations. Like 15-month-old infants, monkeys in this condition looked longer when the experimenter reached in the incorrect location than when she reached in the correct location. In the false belief condition, monkeys first saw an event in which a human experimenter watched an object move into one of two boxes. The experimenter then turned away as the monkey alone saw the object move from the original box to the second box. In contrast to human infants' performance, monkeys looked for the same duration when the experimenter with a false belief reached to either of the two locations. Non-human primates' failures in false belief tasks are especially striking when viewed in light of the same species' successful performance in tasks that requires representations of other individuals' perceptual access and knowledge. For example, rhesus monkeys selectively steal food from a competitor who cannot see the food, even in cases where the perceptual manipulations involve situations as subtle as slight gaze shifts away from the food (Flombaum & Santos, 2005, see Hare et al., 2000, 2001 for similar results in chimpanzees). Macaques also prefer to steal food from a container that makes noise when opened than from one that is quiet, but do so only when a competitor is not looking (Santos et al., 2006). Taken together, these findings suggest that some non-human primates are able to reason quite flexibly about some mental states of others (perceptions and knowledge) though they may lack an understanding of beliefs.

What are the implications of non-human primates' failures in false belief tasks for core knowledge theories of belief representation? One possibility is that these findings suggest that the human system for belief understanding may not represent a core knowledge system at all; the non-human primate evidence suggests that our human belief representations may not phylogenetically ancient like other core systems, and thus that human belief representation systems may not work like other core knowledge systems. As second possibility, though, is that human belief representations may reflect a different type of core knowledge system, one that has many key features of other core systems but has evolved to solve uniquely human problems. Although the current evidence is consistent with the possibility that belief representation is human-unique, a stronger test of this claim might come from testing non-human primates on a belief understanding task that is simple enough for human infants to succeed on in the first year of life. Although non-human primates fail to perform at the level of 15-month-old infants on the Onishi and Baillargeon (2005) test of false belief understanding (Marticorena et al., 2011), it is unclear how they would perform on a measure of automatic false belief attribution, such as that originally developed by Kovács et al. (2010) for use with very young human infants. To test this prediction, we presented rhesus monkeys with a version of the looking time method developed by Kovács et al. (2010). Specifically, we examined whether macaques, like human adults and infants, are automatically influenced by another agent's beliefs when tracking an object's location.

2. Method

2.1. Subjects

All subjects were rhesus macaques living on the island of Cayo Santiago in Puerto Rico (Rawlins & Kessler, 1987). The monkeys in the population free-range on the island, are familiar with human experimenters, and have previously shown reliable results in looking-time studies (e.g., Cheries, Newman, Santos, & Scholl, 2006; Marticorena et al., 2011; Shutts, Condry, Santos, & Spelke, 2009). Monkeys in this population (n = over 1000 monkeys) are identifiable by unique tattoos and ear notch combinations, which allowed the experimenters to identify specific individuals. We successfully tested 121 monkeys. Additional monkeys were approached by the experimenters for testing but did not complete the experiment or contribute to the analysis because of too much disinterest to complete testing ($n = 30$), walking away from the apparatus and out of the camera frame ($n = 78$), approach toward the apparatus ($n = 21$), interference by other monkeys ($n = 40$), experimenter or equipment error ($n = 20$), poor video quality that made coding impossible ($n = 8$), disagreement of more than 3 s between the two independent blind coders ($n = 7$) or because the cameraperson or coder determined that the monkey did not watch the relevant events in the session (i.e., the monkey was looking away when the presenter called "now", $n = 10$). This rate of aborted sessions is similar to that of previously published studies using similar procedures (e.g., Marticorena et al., 2011), and all aborted trials could not be coded (e.g., since monkeys did not watch the relevant events in across all three trials). Importantly, all decisions to abort a trial during testing were made by the cameraperson who was blind to condition during testing. Monkeys were allowed to participate in the study only once, and thus we had to exclude from our analysis an additional 19 monkeys who completed testing a second time.

2.2. Apparatus

We presented monkeys with events on a white foam-core stage with a base (measuring approximately 58 cm across, 15 cm high from the ground, and 21 cm deep), a back wall that measured 58 cm across and 41 cm high (see Fig. 1), and a front screen (58 cm × 74 cm). The front screen was used to occlude the stage from the monkey's view before and after each trial. The size of our stage was similar to the one used in Marticorena et al. (2011). Two black boxes (13 cm × 13 cm × 13 cm) with three sides each were affixed on either end of the stage floor (33 cm apart). A track was cut into the stage floor so that the presenter could surreptitiously slide a plastic apple between the two boxes. The apple was moved using a handle surreptitiously attached to the fruit from the back of the stage. The box on the presenter's left (from here on referred to as Box-1) was constructed so that it could be flipped down and opened such that its contents would be revealed; this box served as the "occluder" as in the Kovács et al. (2010) method. We added a hidden trap door on the back wall of the stage behind Box-1 (8 cm × 8 cm) that allowed the presenter to surreptitiously remove the apple on some conditions. We also affixed a hinged flap to the back wall of the stage (58 cm × 29 cm). This flap covered the presenter's face when it was raised making it such that the presenter could not see the movements of the apple on the stage.

2.3. Procedure

Two experimenters ran each session: the presenter and the cameraperson. The presenter served as the agent and acted out all the events on the stage. The cameraperson videotaped the subject using a portable Panasonic digital videocamera. Each monkey was tested on one of four conditions, which was chosen randomly by the cameraperson and announced using a numerical code immediately before the last trial; only the presenter knew which number corresponded to which conditions, which allowed the cameraperson to remain blind to condition throughout the study. After testing, the experimenters noted each subject's identity to ensure that each subject was tested only once.

All monkeys saw the same two *familiarization trials* followed by one of four different *test trials*. We used the two familiarization trials to show monkeys that the apple could move along the stage, that the presenter could sometimes watch this movement, and that Box-1 had the capacity to flip open. In the first familiarization trial, the presenter lowered the front screen, and then watched as the apple emerged from Box-2, crossed the stage floor, and slid into Box-1. Box-1 then flipped open to reveal the apple. The presenter then called "now" and remained stationary looking at the apple for 10 s while the monkey's duration of looking was recorded. After 10 s, the cameraperson called "stop" to end the trial; the presenter then raised the front screen to cover the stage. In the second familiarization trial, the presenter lowered the screen and watched as the apple emerged from Box-1, crossed the stage, and moved into Box-2. Box-1 then flipped open to reveal nothing. The presenter then called "now" and remained stationary while looking at the empty space for 10 s. After 10 s, the cameraperson called "stop" to end the trial; the presenter then raised the front screen to cover the stage. Note that in both familiarization trials, Box-1 flipped open to reveal an outcome consistent with both the presenter's and the monkeys' beliefs about the location of the apple.

After the two familiarizations, each monkey saw one of four possible test trials depending on condition. We use the term "Agent" in our condition names to refer to the presenter, in order to maintain consistent condition names between our experiment and the experiment of Kovács et al. (2010). Our four conditions corresponded to those used in Kovács et al. (2010) but were adapted for our apparatus. Importantly, just as in the Kovács et al. (2010) method, all test events ended with Box-1 flipping open to reveal nothing inside. Once Box-1 flipped open, the presenter called "now" and remained stationary looking at the empty space for 10 s during which looking was recorded. After 10 s, the cameraperson called "stop" to end the trial. Monkeys in the *Agent and Monkey True Belief* condition (ATB-MTB, $n = 28$) saw the presenter watch the apple emerge from Box-2, cross the stage, move inside Box-1, emerge

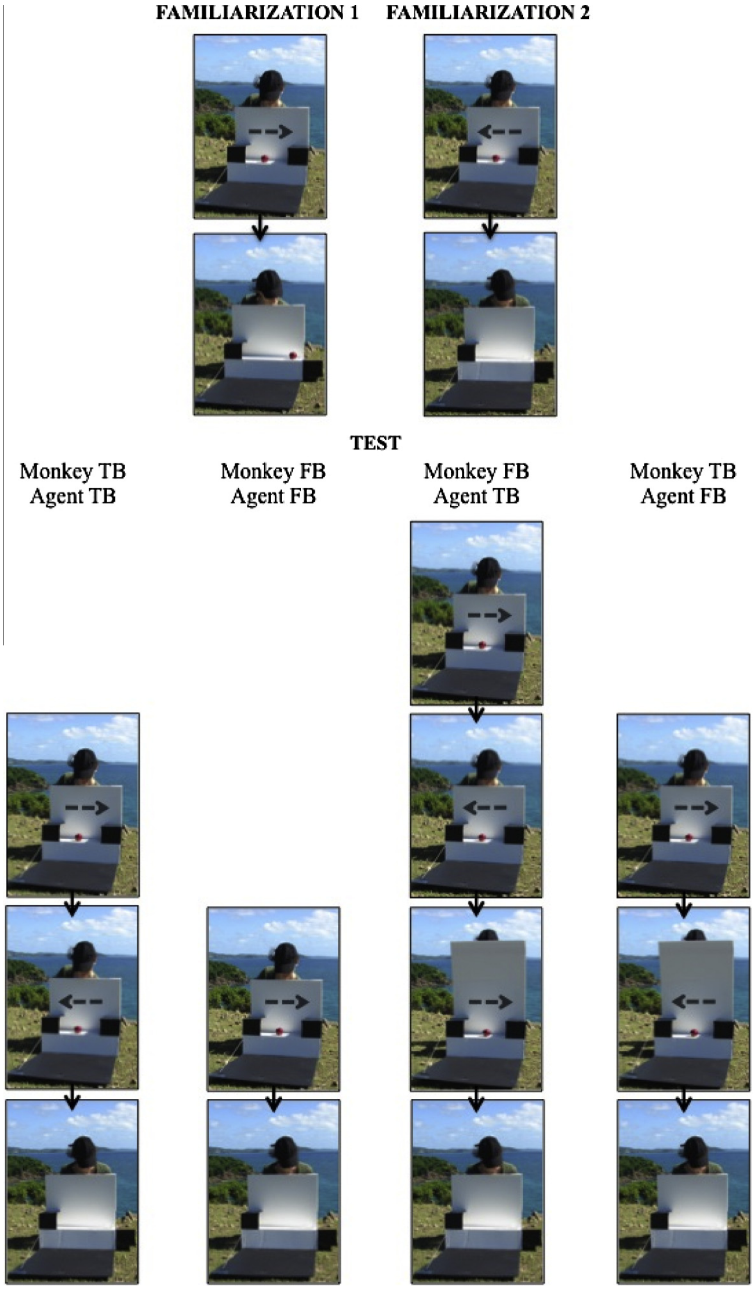

Fig. 1. A depiction of the procedure across different conditions, with black arrows representing the movement of the apple from one box to another. All monkeys first saw the two familiarization trials. The movements of the apple and the visual access of the presenter in the test trials varied by condition. The test outcome was consistent across conditions (Box-1, on the presenter's left, flips open and is revealed to be empty).

from Box-1, cross back across the stage, and then re-enter Box-2. In this case, the final test outcome (no apple inside Box-1) was consistent with both the monkeys' and agent's beliefs. Monkeys in the *Agent and Monkey False Belief* condition (AFB-MFB, $n = 33$), in contrast, saw the presenter watch the apple emerge from Box-2, cross the stage, and move inside Box-1. In this condition, the final test outcome was inconsistent with both the monkeys' and agent's beliefs. (The presenter was able to achieve this seemingly magical event by surreptitiously removing the apple using the trap door). In a third condition, *the Agent True Belief Monkey False Belief* condition (ATB-MFB, $n = 29$), monkeys saw the presenter watch the apple emerge from Box-2, cross the stage, move inside Box-1, emerge from Box-1, cross back across the stage, and then re-enter Box-2. Then the presenter lifted the flap on the back wall of the stage that blocked her view. After her view of the stage was occluded, the monkey alone saw the apple emerge from

Box-2, cross the stage, and move inside Box-1. In this condition, the final test outcome was inconsistent with the monkeys' beliefs, but consistent with the agent's belief. In the final and critical *Agent False Belief Monkey True Belief* condition (AFB-MTB, $n = 31$), monkeys saw the presenter watch the apple emerge from Box-2, cross the stage, move inside Box-1. Then the presenter lifted the flap on the back wall of the stage that blocked her view. After her view of the stage was occluded, the monkey alone saw the apple emerge from Box-1, cross the stage, move inside Box-2. In this condition, the final test outcome was inconsistent with the presenter's belief, even though monkeys should find it expected.

2.4. Video coding

As in previous studies (e.g., Marticorena et al., 2011), the cameraperson filmed only the monkey's face, which allowed the cameraperson to remain blind to the events taking place on the stage. This footage was uploaded to a Macintosh laptop. We used the video editing program Final Cut Pro to place markers in each video to denote the 10 s looking window (starting when the presenter called "now"). Coders blind to condition then coded these trials without listening to the audio track. A single coder examined frame by frame looking (30 frames = 1 s) during the 10 s looking time portion of each trial, using the programs MPEG Streamclip and Supercoder (Hollich, 2005). A second blind coder coded the test trials of all completed sessions ($n = 128$) and trials with over 3 s of disagreement between the two coders were excluded ($n = 7$). The excluded monkeys were distributed evenly across conditions (AFB-MFB: $n = 2$; ATB-MTB: $n = 1$; AFB-MTB: $n = 2$; ATB-MFB: $n = 2$). Reliability for the remaining trials was high (Pearson's $R = .89$).

3. Results

A two-factor Monkey Belief (True or False) by Agent Belief (True or False) ANOVA performed on the test trial data revealed only a main effect of monkey belief ($F(1,117) = 5.151$, $p = 0.025$, $\eta^2 = .042$) (see Fig. 2). Monkeys looked longer at test events that violated their own beliefs (AFB-MFB and ATB-MFB conditions; $M = 2.663$ s, $SD = 1.745$ s) than at those that were consistent with their own beliefs (ATB-MTB and AFB-MTB conditions; $M = 1.954$ s, $SD = 1.737$ s). We observed no main effect of Agent Belief ($F(1,117) = 0.075$, $p = 0.784$, $\eta^2 = .001$). Importantly, we also observed no interaction between monkey and agent belief ($F(1,117) = 0.635$, $p = 0.427$, $\eta^2 = .005$), suggesting that an agent's belief did not affect the monkeys' duration of looking either when the monkey had a true or false belief. The same Monkey Belief by Agent Belief ANOVA performed on the sum of the data from the two familiarization trials revealed no significant main effects for either monkey belief ($F(1,117) = 0.002$, $p = 0.966$, $\eta^2 < .001$) or agent belief ($F(1,117) = 0.000$, $p = 0.986$, $\eta^2 = .001$) and no interaction ($F(1,117) = 1.519$, $p = .220$, $\eta^2 = .013$).

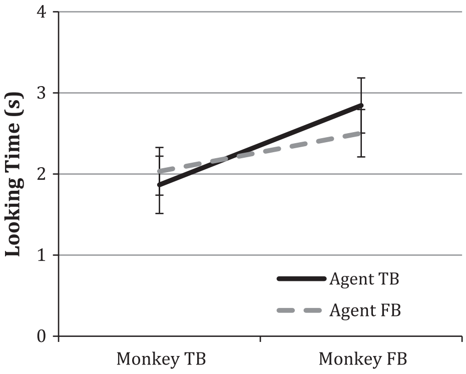

Fig. 2. Results. Mean looking time (in s) ±SEM across monkeys in each condition: Monkey Belief (True or False) and Agent Belief (True or False).

4. Discussion

Rhesus macaques looked longer at events that violated their own beliefs than at events that were consistent with their beliefs. In contrast to human infants and adults, however, macaques do not seem to differentiate between events in which another agent's belief is violated or confirmed. This pattern of performance suggests that monkeys were attending to the events they witnessed—they tracked where the object was and reacted with longer looking when their own expectations were violated—but unlike human infants and adults, monkeys' expectations were not automatically influenced by the beliefs of another agent in the scene (Kovács et al., 2010).

This pattern of performance is consistent with previous research suggesting that macaques (Marticorena et al., 2011) and other non-human primates (Call & Tomasello, 1999; Kaminski et al., 2008; Krachun et al., 2009) reason about other agents' knowledge states, but not their beliefs. However, the current findings go beyond previous work to demonstrate that non-human primates fail to represent others' beliefs even in a task that requires only an automatic representation of others' beliefs. All previous tests of non-human primates' belief reasoning to date have required subjects to predict or interpret an agent's behavior on the basis of her false beliefs (Call & Tomasello, 1999; Kaminski et al., 2008; Krachun et al., 2009; Marticorena et al., 2011). Tasks that require such inferences about the agent's behavior are often thought to involve processing demands that require more than a mere understanding of another agent's beliefs. Consider, for example, the competitive false belief task developed by Kaminski et al. (2008) to test chimpanzees' belief understanding. Even three-year-old human children—who successfully represent others' beliefs in looking time measures of false belief understanding (e.g., Clements & Perner, 1994)—perform poorly on Kaminski et al.'s (2008) competitive false belief task, suggesting that producing the appropriate response in this task may require a set of abilities unrelated to belief understanding. Similarly, although Marticorena et al. (2011) found that rhesus macaque perform poorly on a looking time false belief understanding measure similar to that of Onishi and Baillargeon (2005), recent work with human infants suggests that even this task may be correlated with executive function abilities that are not specific to belief representation (Yott & Poulin-Dubois, 2011). As such, it is possible that previous studies of belief representation in non-human primates failed to observe evidence for this capacity mostly due to performance demands. Our results, however, suggest that macaques still fail to represent another agent's beliefs when tested using an automatic belief representation task, perhaps the simplest task developed to date. Since the task we used in our study taps into belief representation without the need to predict or interpret an agent's behavior, it is arguably the most liberal test of an organism's belief attribution. Specifically, since our belief measure does not require prediction or interpretation of another agent's *behavior* on the basis of a false belief, it should not require additional executive function capacities in the same way as other false belief tasks (e.g., Onishi & Baillargeon, 2005). Indeed, 7-month-old infants who lack rich executive function capacities, and adults tested under cognitive load, successfully demonstrate false belief understanding on this automatic task (Kovács et al., 2010). Although executive function—or domain-general cognitive mechanisms more generally—may be an essential component of using belief representations to understand and predict others' behavior (Leslie, Friedman, & German, 2004; Leslie, German, & Polizzi, 2005), these processes are likely not required for performance on Kovács et al. (2010)'s automatic belief task. Thus our finding that rhesus monkeys fail to track beliefs in this liberal task of belief representation provides important evidence that monkeys may truly lack a system for representing others' beliefs.

Although we interpret monkeys' performance on our task as evidence that they lack the capacity to automatically represent others' beliefs, there is another possible interpretation of monkeys' failures. Perhaps monkeys, unlike human infants and adults, are unable to represent *any mental states* automatically. Monkeys may use mental state attribution only when it could contribute to their own social decision-making (e.g., when there is a potential opportunity to steal food from another agent). The ability to automatically represent others' mental states when such representations are irrelevant to one's own behavior might then be human-unique. However, the current results cannot speak to the question of whether monkeys lack an ability to attribute mental states more broadly because success in the Kovács et al. (2010) task requires that the subject specifically represent others' beliefs—that is representing the contents of another agents mind. Infants tested in Kovács et al. (2010)'s infant-true-belief/agent-false-belief condition had to represent the specific content of the agent's belief—namely that an apple was present behind the occluder—in order to show longer looking when the apple was revealed to be absent. Since the Kovács et al. (2010) task taps into representations of beliefs specifically, this task cannot be used to determine whether a subject has the ability to represent mental states other than beliefs (e.g., an understanding of another agent's visual perspective or knowledge). However, future research could examine more directly the possibility that monkeys are unable to automatically represent other kinds of mental states by adapting tasks used in humans to measure automatic attribution of others' visual perspectives (e.g., Samson et al., 2010). Another important direction for future work would be to investigate automatic belief attribution in non-human primates who are more closely related to humans. By testing chimpanzees and other ape species, we could determine whether macaques' failures reflect broader limitations on primate belief representation or whether such limitations are present only in more distantly related primates.

Monkeys' failures to represent others' beliefs in this liberal test of false belief understanding suggests that researchers may need to be more critical of the view that belief representation is a core knowledge domain, at least in terms of how views of core knowledge domains have typically been conceptualized to date. Recent work suggests that belief representation clearly fulfills two of the main empirical features typical of core knowledge domains: it emerges early in the first year of life in human development (Kovács et al., 2010; Luo, 2011; Onishi & Baillargeon, 2005; Surian et al., 2007) and the limits of this early system can still be observed into adulthood (Apperly, 2011; Kovács et al., 2010; Low & Watts, 2013; van der Wel, Sebanz, & Knoblich, 2014). However, our findings suggest that non-human primates do not share humans' ability to automatically represent others' beliefs. How are we to reconcile evidence from human infants and adults that is consistent with a core knowledge view of belief representation with this new evidence from non-human primates demonstrating consistent failures on false belief tasks? One possibility is that our human system for automatically representing others' belief is not a core knowledge system like, for instance, our ability to reason about objects or number (Feigenson, Dehaene, & Spelke, 2004; Kinzler & Spelke, 2007), and that further empirical investigation will reveal other important differences between the structure of our belief reasoning system and these other core systems. However, given the many parallel features already discovered between belief understanding and other core knowledge systems, a more likely possibility might be that belief understanding is in fact a core knowledge system, but one that evolved specifically in the human lineage and not in other close phylogenetic relatives. Although most core systems proposed to date are have been found to be shared across closely related primates (e.g., object cognition: Kinzler & Spelke, 2007; number: Feigenson et al., 2004; spatial cognition: Spelke, 2003), the current work raises the possibility that there may be systems of representation in human cognition that work like core systems— they emerge early in development, operate automatically in adults, and exhibit signature processing limits— but are not shared with non-human primates. Such systems may have evolved specifically to deal with phylogenetic problems faced uniquely in the human evolutionary environment; in this way, such systems may be phylogenetically old (i.e., they evolved early in the *Homo* lineage) but also unique to humans, in contrast to other core domains of knowledge. Whether or not humans possess other unique core knowledge systems in addition to belief understanding and whether these systems might have features that differ reliably from core knowledge systems that are shared with non-human primates are important questions for future research. Additionally, more work will be needed to investigate the difficult question of *why* a core system for belief attribution might be human-unique; some have theorized that our belief representation system may have evolved in the human lineage to more flexibly exploit the sorts of social strategies we shared with non-human primates (e.g., deception, responding to gaze: Povinelli & Giambrone, 2001), to facilitate cooperative and communicative interactions (Tomasello, 2009), or as a prerequisite to or consequence of the evolution of language (de Villiers, 2007; de Villiers & de Villiers, 2000; Malle, 2002). Although there is clearly still some controversy regarding how to rethink the nature of the human belief reasoning system in light of primates' belief reasoning failures (see discussions in Apperly, 2011; Marticorena et al., 2011; Rosati et al., 2010), we contend that the present results hint that researchers may need to think more flexibly about the nature of core knowledge systems generally, and think more carefully about what kind of systems are used by different species to attribute mental states more specifically.

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