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Do non-human primates really represent others' ignorance? A test of the awareness relations hypothesis

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ABSTRACT

Non-human primates can often predict how another agent will behave based on that agent's knowledge about the world. But how do non-human primates represent others' knowledge states? Researchers have recently proposed that non-human primates form "awareness relations" to attribute objectively true information to other minds, as opposed to human-like representations that track others' ignorance or false belief states. We present the first explicit test of the awareness relations hypothesis by examining when rhesus macaques' understanding of other agents' knowledge falters. In Experiment 1, monkeys watched an agent observe a piece of fruit (the target object) being hidden in one of two boxes. While the agent's view was occluded, either the fruit moved out of its box and directly back into it, or the box containing the fruit opened and immediately closed. We found that monkeys looked significantly longer when the agent reached incorrectly rather than correctly after the box's movement, but not after the fruit's movement. This result suggests that monkeys did not expect the agent to know the fruit's location when it briefly and arbitrarily moved while the agent could not see it, but did expect the agent to know the fruit's location when only the box moved while the agent could not see it. In Experiment 2, we replicated and extended both findings with a larger sample, a different target object, and opposite directions of motion in the test trials. These findings suggest that monkeys reason about others' knowledge of objects by forming awareness relations which are disrupted by arbitrary spatial manipulation of the target object while an agent has no perceptual access to it.

1. Introduction

As adult humans, we recognize that other agents act in ways that are consistent with the facts they have about the world. We understand that other individuals *know* things and we use these representations of others' knowledge to make predictions about how individuals will behave. But adult humans also recognize what it means for others to be *ignorant*. We predict that people who lack information about the world will get things wrong, will sometimes search for missing information, and so on.

Much recent work in primate cognition has explored whether humans are alone in this understanding of others' knowledge and ignorance states, or whether non-human primates understand these states as well. A number of studies have shown that non-human primates (hereafter primates) are generally quite skilled at predicting how a knowledgeable agent will behave (Bray, Krupenye, & Hare, 2014; Flombaum & Santos, 2005; Hare, Call, & Tomasello, 2000, 2001; Kaminski, Call, & Tomasello, 2008; MacLean & Hare, 2012; Sandel, MacLean, & Hare, 2011; Santos, Nissen, & Ferrugia, 2006). For example, primates correctly predict that an agent who knows where a desired object is will reach for that object in its correct location (Marticorena, Ruiz, Mukerji, Goddu, & Santos, 2011). Interestingly, primates succeed in making predictions about how knowledgeable agents will behave even though they typically fail to correctly predict how an agent will behave when he or she has a false belief (Call & Tomasello, 1999; Kaminski et al., 2008; Krachun, Carpenter, Call, & Tomasello, 2009, 2010; Marticorena et al., 2011; Martin & Santos, 2014; but see Krupenye, Kano, Hirata, Call, & Tomasello, 2016; Buttelmann, Buttelmann, Carpenter, Call, & Tomasello, 2017 for evidence that great apes sometimes succeed in implicit false belief tasks).

These findings are often explained through appeal to a knowledge-ignorance account of primate theory of mind. Under this view, primates

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are able to represent what others do and do not know, even though they fail to represent what others believe (Call & Santos, 2012; Call & Tomasello, 2008; Kaminski et al., 2008; Rosati, Santos, & Hare, 2010; Whiten, 2013). Nevertheless, some researchers have begun to point out an important problem with the knowledge-ignorance account of primates' performance in these tasks—although there is abundant evidence that primates make positive predictions about how knowledgeable agents will behave (e.g., Marticorena et al., 2011), there is no evidence that primates make positive predictions about how agents will behave when they are ignorant (see Martin & Santos, 2016 for a review of these findings). For example, studies of primate deception suggest that primates do not actively induce states of ignorance in others by hiding information, even though they do avoid making others knowledgeable (Byrne & Whiten, 1991; Karg, Schmelz, Call, & Tomasello, 2015; Whiten & Byrne, 1988; but see Hare, Call, & Tomasello, 2006).

These and other findings led Martin and Santos (2016) to propose a new framework to explain why primates succeed at representing others' knowledge, but fail to make positive predictions when others are ignorant or have a false belief. As an alternative to the knowledge-ignorance account, they argue that primates form "awareness relations," which link other agents to information about the world that the subject represents as true. Awareness relations are mentalistic representations but are fundamentally different than knowledge- or belief-based representations; awareness relations are hypothesized to have an "on/off" quality such that primates either represent an awareness relation linking a (true) piece of information to the agent or fail to represent any relation between the agent and the information whatsoever. The awareness relations hypothesis predicts that if the information linked to an agent changes while outside that agent's awareness, the awareness relation is 'turned off', regardless of whether this event results in a mismatch between reality and the agent's belief. In this way, primates tend to make no predictions about how an agent will behave when he or she is ignorant or holds a false belief.

The awareness relations hypothesis is able to explain a host of confusing results concerning when primates do and do not succeed in representing what others know, including a strange pattern of results observed by Kaminski et al. (2008). In this study, a subject and a competitor chimpanzee watched as a high-quality food item was hidden in one of three buckets. While the competitor's view was blocked, an experimenter either moved the food to a different bucket ("unknown shift" condition), or simply lifted the food and placed it back into its original location ("unknown lift" condition). The competitor was then allowed to choose a bucket while the subject's view was blocked. After the competitor's choice, the subject could either choose a bucket (take a chance at obtaining the high-quality food) or opt for a guaranteed low-quality food reward. Even though the competitor did not know the high-quality food's location in the unknown shift condition but did in the unknown lift condition, subjects behaved as if the competitor did not know the food's location in both cases, opting to forgo the low-quality food for a chance at the high-quality food more often than in two control conditions. These findings are difficult to explain from a knowledge-ignorance perspective, because the competitor maintained an accurate representation of the food's location in the unknown lift condition, yet subjects failed to expect the competitor to search accurately. However, the results can be explained by an awareness relations account if the connection the subject represents between the competitor and true information is disrupted in the unknown lift condition when the food briefly moves while the competitor has no perceptual access to the movement. Similarly, Marticorena et al. (2011) found that rhesus macaques seemed to make no prediction about where an agent with a false belief would reach for a hidden piece of food. In this and other studies, rather than failing change-of-location false belief tasks egocentrically as human children often do before 4 years of age (Tomasello, 2018b; Wellman, Cross, & Watson, 2001), primates seem to have no expectations about an agent's knowledge after the object moves (Drayton & Santos, 2018; Hare, Call, & Tomasello, 2001; Kaminski et al., 2008; Marticorena et al., 2011; Martin & Santos, 2014; but see Buttelmann et al., 2017; Krupenye et al., 2016), consistent with the proposed on/off quality of awareness relations. In each of these studies, regardless of whether the dependent measure was looking behavior (Drayton & Santos, 2018; Marticorena et al., 2011; Martin & Santos, 2014) or object-choice/reaching behavior (Hare et al., 2001; Kaminski et al., 2008), when an object was spatially manipulated while an agent could not see it, primates seemed to no longer have any expectations about the agent's knowledge. While it is challenging to entirely rule out low-level explanations for this pattern based on behavior-reading (Lurz, Kanet, & Krachun, 2014; Povinelli & Vonk, 2003), our perspective is that primates do form inferences about the mental states of agents in these studies, as supported by recent experimental work on chimpanzees' understanding of what others can see in the absence of a direct line of gaze (Lurz, Krachun, Mahovetz, Wilson, & Hopkins, 2018).

Although previous studies have produced findings which are consistent with the awareness relations account, there have been no formal tests of this hypothesis. Here, we present the first explicit test of the awareness relations hypothesis by examining monkeys' expectations about an agent's knowledge of a target object when this object, or other environmental features are manipulated outside the agent's perceptual access. We used a violation of expectation looking time paradigm in which rhesus macaques watched as an agent saw a piece of fruit (the target object) move into one of two boxes. While the agent's view was blocked, the fruit briefly moved out of and back into the box. The agent then reached into either the correct or incorrect box to search for the fruit. If monkeys represent these events in terms of the agent's knowledge and ignorance, we would expect monkeys to look significantly longer when the agent reached to the incorrect location rather than the correct location (i.e. the monkey's expectation of the agent's behavior should be violated by an incorrect reach). However, if monkeys represent these events using awareness relations, then we would predict a more counterintuitive pattern of results. According to Martin and Santos (2016), awareness relations are disrupted by *any manipulation* of the object's location when it is outside the agent's awareness. The awareness relations hypothesis therefore predicts that monkeys' awareness relations between the agent and the target object should be broken when that object briefly moves while the agent cannot see it. Thus, monkeys should make no predictions about where the agent will search and should look for equal durations in the two test conditions.

To provide the most controlled test of the awareness relations account possible, we also added a control condition in which a different feature of the scene changed while the agent was not watching, one that was irrelevant to the awareness relations monkeys formed between the agent and the position of the fruit. In this control condition, monkeys saw the same event in which an agent watched a piece of fruit move into one of two boxes. This time, however, when the agent's view was blocked, the box containing the fruit flipped open and closed, briefly revealing the fruit in the same location. Note that although this box movement (like the fruit movement) occurred outside the agent's awareness, the event should not break monkeys' awareness relations because it did not physically affect the object the agent cared about while the agent was unaware. In other words, because the box is not a key element in the awareness relation (which links the fruit to the agent), manipulation of the box should not disrupt the monkeys' predictions about the agent's subsequent behavior, whereas manipulation of the fruit should. In this way, the awareness relations hypothesis predicts that monkeys should correctly predict where the agent will reach in this "box moves" condition, and thus should look longer when the agent reaches to the incorrect rather than the correct location.

Table 1
Descriptive statistics of the sample in each condition of both experiments, including sample size (n), age in years (mean ± standard deviation), number of males, and number of females.

Experiment	Test Event	Reach	n	Age	Male	Female
1	Fruit Moves	Correct	37	4.35 ± 4.40	22	15
		Incorrect	35	4.54 ± 3.66	21	14
	Box Moves	Correct	36	4.17 ± 3.56	21	15
		Incorrect	36	4.22 ± 3.40	22	14
2	Fruit Moves	Correct	50	4.46 ± 3.29	32	18
		Incorrect	49	4.33 ± 2.99	31	18
	Box Moves	Correct	50	4.48 ± 4.26	32	18
		Incorrect	50	4.22 ± 2.84	32	18

2. Experiment 1

2.1. Methods

2.1.1. Subjects

We tested 144 free-ranging rhesus macaques at the Cayo Santiago Field Station (Rawlins & Kessler, 1986). This population is well habituated to participation in cognitive and behavioral experiments, including those using violation of expectation paradigms (Drayton & Santos, 2018; Marticorena et al., 2011; Martin & Santos, 2014). Individual monkeys can be identified via a unique three-digit alphanumeric tattoo. Our sample included 86 males and 58 females (mean age 4.32 ± 3.74 years, see also Table 1). Other monkeys were approached for testing but did not contribute to our final subject group because they failed to watch critical components of the presentation (n = 61), left the presentation area (n = 64), became distracted due to interference from other monkeys (n = 19), had been tested previously in the same experiment (n = 15), or due to experimental error (n = 6). Decisions to abort were made by the cameraperson, who was blind to all conditions to ensure that condition played no role in decisions to abort. The rate of aborts and exclusions was similar to previously published studies in this population (Drayton & Santos, 2018; Marticorena et al., 2011; Martin & Santos, 2014).

2.1.2. Method and apparatus

To assess monkeys' expectations about an agent's awareness of a target object's location, we used a violation of expectation looking time method. All trials were conducted with one experimenter and one cameraperson. Subjects were approached opportunistically when relatively isolated from other group members to minimize potential distractions or interference from other monkeys. In each trial, the experimenter knelt behind the apparatus approximately 2 m in front of the subject, with the cameraperson filming the subject's face while standing approximately 1 m behind the experimenter. Consistent with previous expectancy violation studies, we used a foamcore stage for our presentation (Drayton & Santos, 2018; Marticorena et al., 2011; Martin & Santos, 2014). The stage for Experiment 1 was 76 cm long × 26 cm wide, sitting 14 cm off the ground with a 56 cm tall back panel (Fig. 1). Two boxes, situated on opposite ends of the stage, measured 15 cm × 15 cm × 15 cm. A front occluder (50 cm tall) could be raised to block the subject's view of the stage, and a back occluder (20 cm tall) could be raised to block the experimenter's view. A 71 cm long track was cut into the stage between the boxes along which a plastic lemon could travel. The side of each box facing the center of the stage was cut out so that the lemon could enter and exit both boxes. Both boxes were fixed to the outside of the stage, allowing them to flip open over the side of either end of the stage. Neither the experimenter nor the subject had visual access to the contents of either box while the boxes were sitting on the stage. As in previous studies, the experimenter controlled the movement of the lemon and the boxes behind the stage surreptitiously via wooden dowels attached to each object such that the subject could not see the experimenter's actions (Marticorena et al., 2011; Martin & Santos, 2014).

2.1.3. Procedure

Subjects were divided in a 2 × 2 design with *type of movement* (fruit moves or box moves) and *reach direction* (correct reach or incorrect reach) as factors.

All testing sessions consisted of two familiarization trials and one test trial (Fig. 1). Familiarization trials were the same in all conditions and served to familiarize the subject to the apparatus and the potential for the experimenter to reach into a box. In the first familiarization trial, the experimenter dropped the front occluder to reveal a lemon situated on the stage between the two boxes. When the occluder dropped, the experimenter stared downward at the lemon and said "now" to begin the 10 s trial, throughout which both the experimenter and the lemon remained motionless. After the first familiarization trial, the cameraperson announced the condition using a numeric code. Subjects were assigned to conditions pseudo-randomly to balance mean ages and sex ratios across conditions. The condition was announced after the first familiarization trial because a subject's condition determined which box the experimenter reached into in the second familiarization trial.

In the second familiarization trial, the experimenter dropped the front occluder and reached into one of the two boxes while the lemon was no longer visible. Which box the experimenter reached into (left vs. right) was balanced between subjects within each condition (correct vs. incorrect reach; described below) but was always consistent with which box the experimenter ultimately reached into in the test trial. The experimenter held the reaching motion and said "now" to begin the 10 s trial, remaining motionless throughout.

After the second familiarization trial, the test trial began. In the test trial, the experimenter dropped the front occluder to reveal the lemon situated on the stage between the two boxes, and subsequently watched the lemon as it moved into one of the boxes. The experimenter then raised the back occluder to block his view of the stage. What occurred next depended on the experimental condition.

Fruit moves condition. While the experimenter's view was occluded, the lemon traveled out of the box toward the center of the stage and then back into the same box, such that it was visible to the subject for approximately 2 s. After the lemon was back in the box, the experimenter dropped the back occluder such that he could again see the stage, and then reached into either the correct or incorrect box. The experimenter held the reaching motion and said "now" to begin the 10 s trial, remaining motionless throughout.

Box moves condition. The "box moves" condition was identical to the "fruit moves" condition with the exception that while the experimenter's view was occluded, instead of the lemon traveling out of the box and then back into it, the box that contained the lemon flipped open and then closed, such that the lemon was visible to the subject for approximately 2 s but never moved. After the box was closed, the experimenter dropped the back occluder such that he could again see the stage, and then reached into either the correct or incorrect box.

2.1.4. Video coding

All test trials were coded independently by two coders using the programs MPEG Streamclip or BORIS (Friard & Gamba, 2016). Each video was clipped such that coders were blind to the condition. Coders assessed each 10 s trial at 30 frames/second beginning immediately after the experimenter said "now" by recording each frame where the subject was looking at the apparatus. Interrater reliability between coders was excellent (Pearson's $R = 0.87$).

2.2. Results

Analyses were conducted in the R environment (v3.3.1; R Core & Team, 2016), and looking times were log-transformed in all analyses to improve model fit. To assess differences in looking time between

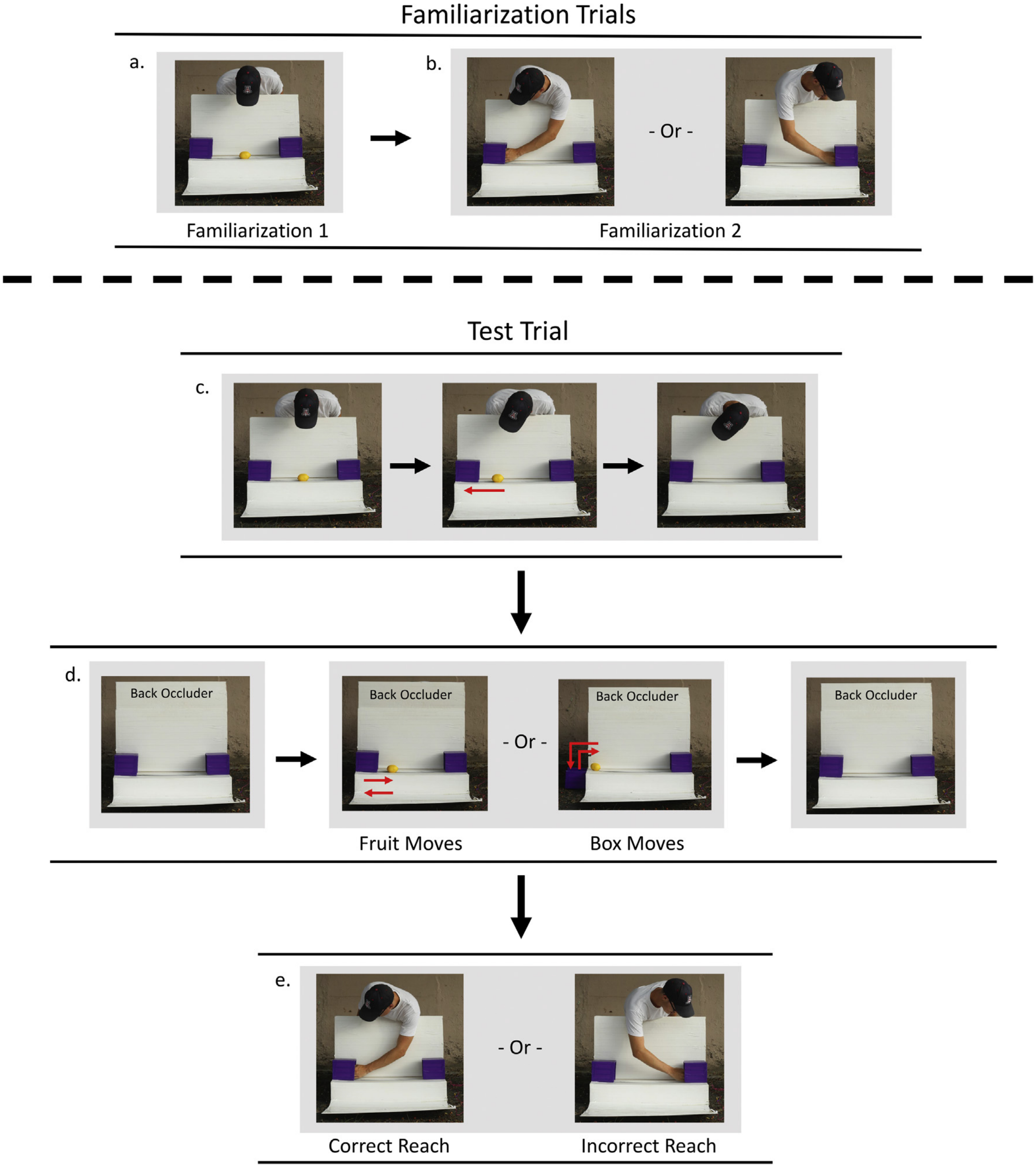

Fig. 1. A depiction of the procedure for Experiment 1. (a) Familiarization #1: The agent stared at the fruit positioned in the middle of the stage for 10 s. (b) Familiarization #2: The agent reached into one of the two boxes (consistent with the final reach direction in the test trial) for 10 s. (c) Test trials: All monkeys watched as the agent observed the fruit moving into one of the two boxes. (d) While the agent's view of the stage was occluded, the fruit either moved out its box towards the center of the stage and then directly back into the same box, or the box hiding the fruit opened over the end of the stage and then closed, without the fruit moving. (e) Finally, the agent reached into either the correct or incorrect box while the monkey's looking behavior was recorded for 10 s.

monkeys who saw the agent reach incorrectly (n = 35; $M = 3.54$ s) versus correctly (n = 37; $M = 3.64$ s) in the "fruit moves" condition, we used an independent samples *t*-test. There was no significant difference in looking time between the monkeys in the "fruit moves" condition who saw an incorrect reach and those who saw a correct reach ($t(66.74) = 0.41$, $p = .68$; Table 2; Fig. 2a). This suggests that monkeys had no expectation about the agent's behavior based on his knowledge of the fruit's location. Even though the agent saw where the fruit was hidden, and it never changed hiding places (i.e. the agent maintained a true belief), monkeys were no more surprised when the agent reached to the incorrect versus the correct location. We also performed independent samples *t*-tests on looking time between groups on both familiarization trials to confirm that there were no general differences in how interested each group of monkeys was in viewing events on the stage. There were no significant differences in looking time between monkeys who ultimately saw an incorrect reach versus monkeys who ultimately saw a correct reach in either the first ($t(65.10) = -0.04$, $p = .97$) or second ($t(69.84) = 1.09$, $p = .28$) familiarization trial in the "fruit moves" condition (Table 2).

In the "box moves" condition, an independent samples *t*-test revealed that monkeys who saw an incorrect reach (n = 36; $M = 3.19$ s) looked significantly longer than those who saw a correct reach (n = 36; $M = 2.32$ s; $t(69.86) = 2.05$, $p = .04$), with a medium effect size ($d = 0.48$; Table 2; Fig. 2b). This suggests that monkeys did have an expectation that the agent had knowledge of the fruit's location and would reach correctly, even after the box hiding the fruit moved while

Table 2
Mean looking time ± standard error for each trial in both experiments broken down by group (i.e. monkeys who ultimately saw an incorrect reach versus a correct reach in the test trial), along with test statistics for all comparisons, including mean difference in log-transformed looking times [95% CI], *t* statistics, degrees of freedom, and *p*-values. Asterisks indicate significant differences at an alpha level of 0.05.

Experiment	Test Event	Trial	Looking Time: Incorrect Reach Group	Looking Time: Correct Reach Group	Log (Mean Difference)	*t*	*df*	*p*
1	Fruit Moves	Familiarization 1	5.57 ± 0.43	5.91 ± 0.41	−0.006 [−0.34, 0.32]	−0.04	65.10	0.97
		Familiarization 2	4.80 ± 0.45	4.18 ± 0.40	0.17 [−0.14, 0.49]	1.09	69.84	0.28
		Test	3.54 ± 0.35	3.64 ± 0.39	0.08 [−0.28, 0.43]	0.41	66.74	0.68
	Box Moves	Familiarization 1	4.84 ± 0.41	4.42 ± 0.35	0.08 [−0.21, 0.37]	0.56	69.98	0.58
		Familiarization 2	4.00 ± 0.31	4.06 ± 0.30	−0.005 [−0.27, 0.26]	−0.04	68.90	0.97
		Test	3.19 ± 0.34	2.32 ± 0.25	0.31 [0.008, 0.61]	2.05	69.86	0.04*
2	Fruit Moves	Familiarization 1	5.66 ± 0.36	6.65 ± 0.35	−0.20 [−0.44, 0.04]	−1.66	93.83	0.10
		Familiarization 2	4.69 ± 0.33	4.97 ± 0.35	−0.08 [−0.34, 0.17]	−0.63	94.02	0.53
		Test	3.63 ± 0.31	3.62 ± 0.35	0.08 [−0.22, 0.38]	0.52	94.61	0.60
	Box Moves	Familiarization 1	6.31 ± 0.36	6.15 ± 0.33	0.01 [−0.19, 0.22]	0.16	97.68	0.87
		Familiarization 2	5.02 ± 0.34	4.98 ± 0.32	−0.01 [−0.23, 0.22]	−0.08	97.26	0.94
		Test	3.65 ± 0.29	2.36 ± 0.24	0.49 [0.25, 0.74]	3.95	96.89	< 0.001*

the agent had no perceptual access to it. Therefore, manipulation of the awareness relation's target object while the agent could not see it in the "fruit moves" condition was likely responsible for breaking the monkeys' awareness relations, rather than more general cognitive demands stemming from attending to or tracking any object motion during the period before the experimenter reached. As in the "fruit moves" condition, independent samples *t*-tests on looking time between the incorrect and correct reach groups on both familiarization trials revealed no significant differences (Familiarization 1: $t(69.98) = 0.56$, $p = .58$; Familiarization 2: $t(68.90) = -0.04$, $p = .97$; Table 2).

To assess differences in looking time across test trials in all conditions, we also fit a multiple regression model including *type of movement* (fruit moves or box moves), *reach direction* (correct reach or incorrect reach), and a *type of movement* × *reach direction* interaction term as predictors of log-transformed looking time. Results from a Type-III ANOVA showed a significant main effect of *type of movement* ($F(1, 140) = 4.68$, $p = .03$) such that monkeys looked significantly longer in the "fruit moves" condition ($M = 3.59$ s) as compared to the "box moves" condition ($M = 2.75$ s). There was no significant main effect of *reach direction* ($F(1, 140) = 3.48$, $p = .06$), nor was there a significant *type of movement* × *reach direction* interaction ($F(1, 140) = 1.01$, $p = .32$). Thus, while pairwise comparisons revealed an effect of reach direction when the box moved, but not when the fruit moved, we did not detect a significant interaction in a regression model across all conditions, perhaps due to limited statistical power.

2.3. Discussion

Consistent with previous work (Drayton & Santos, 2018; Marticorena et al., 2011), we found that monkeys who saw an agent watch a lemon enter one of two boxes expected that agent to search correctly for the lemon, even if the box holding the lemon briefly moved while it was outside the agent's view. In contrast, monkeys failed to maintain a similar expectation if the lemon itself briefly moved while it was outside of the agent's view. This pattern of performance in the "fruit moves" condition is consistent with other counterintuitive findings in the primate theory of mind literature (e.g. Kaminski et al., 2008′s unknown lift condition). Importantly, the pattern we observed across the two movement conditions cannot be explained by the knowledge-ignorance account of primate theory of mind. Instead, this pattern of results is better explained by an awareness relations account. Specifically, these results support the hypothesis that monkeys' awareness relations are disrupted when a target object is manipulated outside of the agent's view, but not when an object irrelevant to the awareness relation is manipulated.

Although we did detect a statistically significant difference in looking time at correct and incorrect reaches within the "box moves" condition but not the "fruit moves" condition, we did not find a significant interaction between type of movement and reach location, perhaps due to limited statistical power. Therefore, in Experiment 2, we attempted to replicate the main findings from Experiment 1 with a larger sample, and to extend these findings by controlling for other possible confounding factors. Specifically, in the "fruit moves" condition of Experiment 1, the fruit moved out of its hiding location towards the center of the stage, while in the "box moves" condition the box flipped away from the center of the stage. Consequently, it is possible that the "fruit moves" condition drew subjects' attention toward the center of the stage, making it more likely for subjects to attend to the fact that the (centrally positioned) agent no longer had perceptual access to the stage. Conversely, when the boxes flipped open toward the periphery of the stage, it is possible that subjects' attention was drawn away from the experimenter's perspective during this manipulation. Thus, in Experiment 2, we reversed the direction of motion of both the fruit and box to control for this possible alternative explanation.

3. Experiment 2

3.1. Method

3.1.1. Subjects

We tested 199 rhesus macaques, including 127 males and 72 females with a mean age of 4.37 ± 3.37 years (Table 1). Other monkeys were approached for testing but did not contribute to our final subject group because they failed to watch critical components of the presentation (n = 84), left the presentation area (n = 15), became distracted due to interference from other monkeys (n = 34), had been

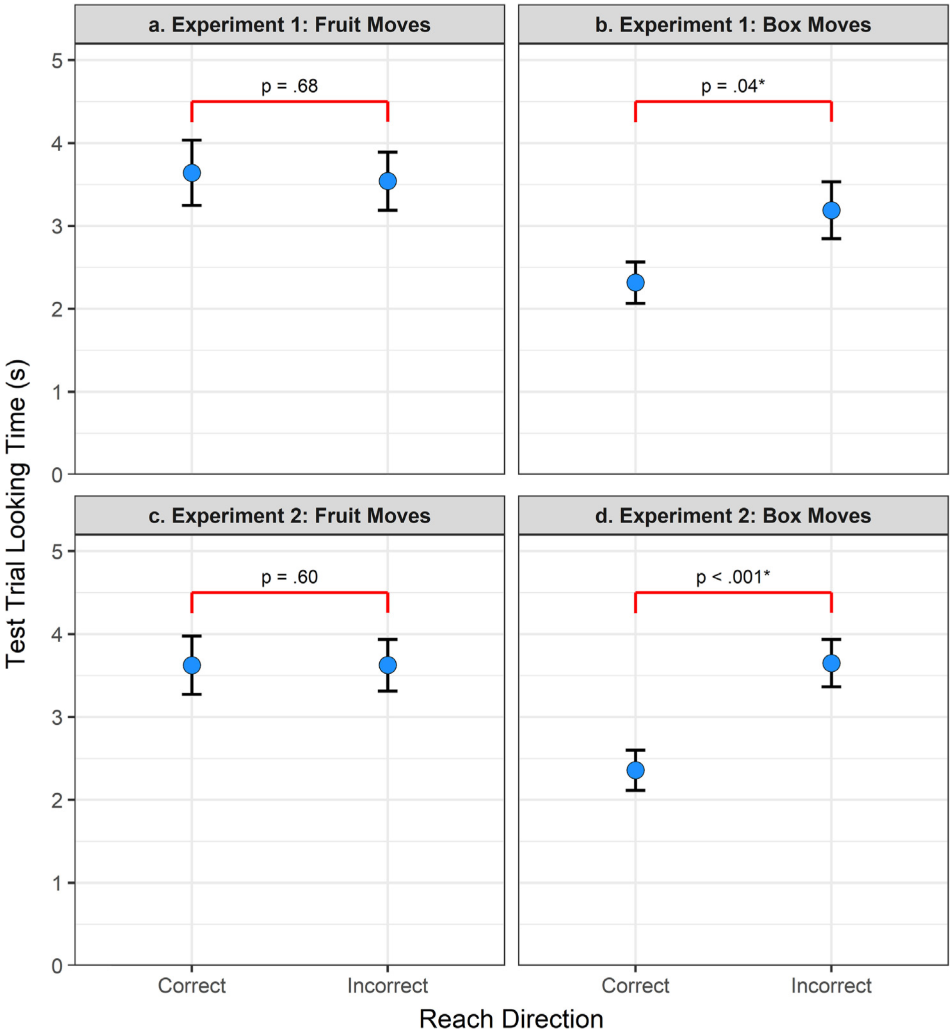

Fig. 2. Mean looking time in seconds ± standard error after correct and incorrect reaches in the test trials of (a) the "fruit moves" condition and (b) the "box moves" condition of Experiment 1, along with (c) the "fruit moves" condition and (d) the "box moves" condition of Experiment 2. Asterisks indicate significant differences at an alpha level of 0.05.

tested previously in the same experiment (n = 40), or due to experimental error (n = 5).

3.1.2. Apparatus

We again used a similar foamcore stage for our presentation. The stage was 91 cm long by 23 cm wide, sitting 12 cm off the ground with a 56 cm tall back. Two boxes, situated 11 cm from each end of the stage, measured 10 cm × 10 cm × 10 cm. Both occluders were the same size as in Experiment 1. A 70 cm long track was cut into the stage between the boxes, along which a plastic apple could travel. There was an additional 9 cm of track between each box and each end of the stage. The sides of each box facing the center and outside of the stage were cut out so that the apple could enter and exit both boxes from either side. Both boxes were fixed to the stage with a hinge that allowed them to flip open towards the center of the stage. Thus, the primary differences from the apparatus used in Experiment 1 was that in Experiment 2, the boxes could flip open toward the center of the stage rather than off the sides of the stage, and the fruit could move out of the boxes away from the center of the stage rather than towards it.

3.1.3. Procedure

The familiarization procedure and process for assigning subjects to conditions was identical to Experiment 1. Test trials were also identical to Experiment 1 with the exceptions that in the "fruit moves" condition, an apple (rather than a lemon) traveled out of the box towards the periphery of the stage (rather than the center) and in the "box moves" condition the box containing the apple flipped open toward the center of the stage (rather than toward the periphery).

3.1.4. Video coding

All video processing and coding procedures were the same as in Experiment 1. Because interrater reliability between coders on Experiment 2 was initially only moderate (Pearson's $R = 0.79$), we examined differences in looking times between the two coders across trials, which revealed nine outliers in which the times coded differed by more than three standard deviations (3.39 s) of the mean difference between coders on all test trials. For these nine trials, a third blind coder assessed looking times, and we used the third coder's assessment in all analyses (sensitivity analyses revealed no difference in the overall result regardless of which coder's scores were used for these trials, or if these trials were dropped entirely). Interrater reliability between coders on the other 191 test trials was excellent (Pearson's $R = 0.90$).

3.2. Results and discussion

There was again no significant difference in looking time between monkeys in the "fruit moves" condition who saw an incorrect reach (n = 49; $M = 3.63$ s) versus a correct reach (n = 50; $M = 3.62$ s; t

$t(94.61) = 0.52$, $p = .60$; Table 2; Fig. 2c) using an independent-samples *t*-test. There were also no significant differences in looking time between groups on the first or second familiarization trials (Familiarization 1: $t(93.83) = -1.66$, $p = .10$; Familiarization 2: $t(94.02) = -0.63$, $p = .53$; Table 2).

In the "box moves" condition, an independent-samples *t*-test revealed that monkeys who saw an incorrect reach (n = 50; $M = 3.65$ s) again looked significantly longer at the stage than those who saw a correct reach (n = 50; $M = 2.36$ s; $t(96.89) = 3.95$, $p < .001$), but with a large effect size ($d = 0.79$; Table 2; Fig. 2d). There were again no significant differences in looking time between groups on the first or second familiarization trials (Familiarization 1: $t(97.68) = 0.16$, $p = .87$; Familiarization 2: $t(97.26) = -0.08$, $p = .94$; Table 2).

To assess differences in looking time across test trials in all conditions, we again fit a multiple regression model including *type of movement* (fruit moves or box moves), *reach direction* (correct reach or incorrect reach), and a *type of movement* × *reach direction* interaction term as predictors of log-transformed looking time. Results from a Type-III ANOVA showed a significant *type of movement* × *reach direction* interaction ($F(1, 195) = 4.38$, $p = .04$). Tukey's HSD tests correcting for family-wise error at a 95% confidence level showed that monkeys did not look significantly longer at an incorrect as compared to a correct reach in the "fruit moves" condition ($p = .94$), but did look significantly longer at an incorrect as compared to a correct reach in the "box moves" condition ($p = .003$). Therefore, with a larger sample size, a different target object, and reversed directions of motion in the tests trials, Experiment 2 successfully replicated the main results from Experiment 1.

4. General discussion

Our findings support the hypothesis that monkeys reason about others' mental states using awareness relations which are easily disrupted by (inconsequential) spatial manipulations of a target object while it is outside an agent's perceptual awareness. The "fruit moves" condition of Experiment 1 showed that even after monkeys see an agent observe where a target object is hidden, they have no expectations about the agent's knowledge of the object's location after it moves and returns to its original location while the agent cannot see it. In contrast, the "box moves" condition of Experiment 1 showed that monkeys do expect an agent to have knowledge of the object's location when it remains stationary, and instead, the box hiding it is spatially manipulated. The latter finding controls for the potential alternative explanation that monkeys had no expectation about the agent's behavior in the "fruit moves" condition due to task demands relating to attention or working memory. Both the "fruit moves" and "box moves" conditions involved spatial manipulations of items on the stage and temporal delays before the agent reached, yet monkeys had different expectations about the agent's behavior between conditions. Experiment 2 replicated both findings using a different target object and showed that the directions of motion in the test trial did not significantly influence results, ruling out an alternative explanation for the findings from Experiment 1. Taken together, these results suggest that monkeys do not represent others' knowledge with reference to an agent's knowledge and ignorance. A subject who represented these events in terms of the agent's knowledge/ignorance should have expected the agent to reach correctly regardless of whether the fruit or the box moved when the agent could not see, as in both cases the agent maintained knowledge of the object's ultimate location. Instead, monkeys' conceptions of the agent's knowledge of the fruit's location appear to be disrupted, or rendered null, when the target object moves while out of the agent's view.

Additionally, our results offer a new explanation for why primates often fail false belief tasks using change-of-location paradigms. In these tasks (Call & Tomasello, 1999; Hare et al., 2001; Kaminski et al., 2008; Krachun, Carpenter, Call, & Tomasello, 2009; Marticorena et al., 2011; Martin & Santos, 2014), a false belief is induced when a target object changes hiding locations while the agent is not able to see it. Classically, failure to predict the agent's behavior has been attributed to an inability to conceptualize the mismatch between what is objectively true about the world and what an agent believes. Our results suggest that performance in such tasks could be due to a much simpler mechanism. Namely, *any* movement of the target object while the agent cannot see it may disrupt the subject's initial attribution of awareness of the object's location to the agent. Interestingly, in two cases where great apes performed significantly worse than chance in change-of-location tasks (Call & Tomasello, 1999; Krachun et al., 2009) – potentially indicating a positive (but incorrect) prediction about an agent's mental state as opposed to the lack of any prediction whatsoever – apes' performance may be explained by social cue-following (of a cooperator's communicative marker placement and a competitor's effortful reaching respectively) in the more cognitively demanding false belief conditions. Krachun et al. (2010) found chance-level performance in chimpanzees using a change-of-contents rather than a change-of-location false belief paradigm, but a small sample size (n = 5) may have be primarily responsible for the null result given that three of the individuals were correct on less than 25% of false belief trials. However, even if apes did perform significantly worse than chance at a group level given a larger sample size in this task, it is possible that non-social cue-following (of differently colored containers) may explain their performance. In contrast, a cue-following explanation is not viable in change-of-location tasks where primates perform at chance (Kaminski et al., 2008; Marticorena et al., 2011; Martin & Santos, 2014), or make no discrimination between an uninformed and misinformed competitor (Hare et al., 2001), further supporting the idea that primates make no explicit predictions about others' mental states when others are ignorant or have false beliefs.

However, two recent studies have claimed that great apes may show some understanding of false beliefs in an anticipatory looking task (Krupenye et al., 2016) and an interactive helping task (Buttelmann et al., 2017). Krupenye et al. (2016) found that chimpanzees, bonobos, and orangutans looked preferentially at a hiding location where an agent falsely believed an object to be, presumably anticipating the agent to search for the object in that location. Testing the same group of species, Buttelmann et al. (2017) found that apes helped an agent to open a box at different rates after witnessing the agent mistakenly attempt to open an empty box when that agent falsely believed the object to be in the empty box versus when the agent had a true belief or was ignorant about the object's location. However, it is important to note that in this study apes acted to help the agent open the correct and incorrect boxes at the same rate (i.e. at chance) both when the agent had a true belief and when the agent was ignorant, raising concerns about the apes' understanding of the true belief condition. Even the authors of these studies have argued that more research is needed to better elucidate what apes understand about false beliefs in these tasks and how (if at all) they can use false belief representation to guide their behavior (see Tomasello, 2018a). It is still noteworthy that, in contrast to these great ape findings, monkeys have failed all false belief tasks to date, including those using implicit looking measures (Marticorena et al., 2011; Martin & Santos, 2014), suggesting possible differences in implicit theory of mind between monkeys and great apes. Thus, future work will profit from directly testing the awareness relations hypothesis in great apes using a similar expectancy violation task.

The awareness relations account supported by our findings is also congruent with a recent proposal that primates fail to conceptualize false beliefs primarily because they appear not to exhibit shared intentionality (Tomasello, 2018b). In this account, humans, but not other primates come to understand false beliefs through extensive experience forming joint attention with others, which often forces one to assess differences between reality, one's own perspective, and another's perspective from a "bird's eye view". Given that there is no strong evidence for joint attention in primates (but see MacLean & Hare, 2013; Hopkins et al., 2014; Hopkins et al., 2014), Tomasello (2018b) argues that primates likely do not have the same opportunities as humans to learn that others can have perspectives that are not objectively true. This inability to parse differences between objective truth and subjective perspective is critical to the awareness relations account, as awareness relations only allow subjects to link true information to other agents. Tomasello (2018b) also argues that great apes' recent success in some implicit false belief tasks (Buttelmann et al., 2017; Krupenye et al., 2016) does not require a robust understanding of belief via tracking and comparing objective reality with one's own view and an agent's view per se, but rather only requires tracking what an agent has seen to predict behavior.

It is also important to situate our findings within the context of theory of mind research on the development of belief representation in human children. Traditionally, researchers have argued that false belief understanding emerges in human children around 4–5 years of age (Tomasello, 2018b; Wellman et al., 2001; Wellman, 2018). Some studies have found evidence of implicit false belief understanding before 2 years of age using expectancy violation paradigms (Baillargeon, Scott, & He, 2010; Kovacs, Teglas, & Endress, 2010; Onishi & Baillargeon, 2005), but recent analyses have questioned their replicability (Kulke & Rakoczy, 2018). Regarding true belief understanding, Oktay-Gür and Rakoczy (2017) note an interesting U-shaped curve apparent when describing children's performance in true belief tasks. Unsurprisingly, 3-year-old children consistently pass true belief tasks and fail false belief tasks whereas 6-year-old children pass both. However, 4- to 6-year-old children pass false belief tasks even though they fail the true belief tasks that 3- and 6-year-olds pass (Fabricius, Boyer, Weimer, & Carroll, 2010). Some researchers have argued for a performance limitation account positing that this failure of true belief tasks in 4- to 6-year-olds may be due more to the pragmatics of the situation than a representational competence limitation; children at this age may see a question about an agent's true belief as a "trick question" to which the answer is obvious, leading the child to believe they are misunderstanding the situation (Oktay-Gür & Rakoczy, 2017). Support for this explanation has emerged from the finding that children of this age group pass two true belief tasks that better control for the salience of this question (i.e. by adding another agent to the scene who has a false belief while the agent being asked about has a true belief; Oktay-Gür & Rakoczy, 2017).

While monkeys fail implicit false belief tasks and pass true belief tasks in which the agent sees all information about the scene (Marticorena et al., 2011; Martin & Santos, 2014), our results show that monkeys fail a condition similar to the true belief tasks 4- to 6-year-old children also fail (Fabricius et al., 2010). In these tasks, after an agent hides an object in one of two boxes and then leaves, a different experimenter removes the object from its box, contemplates putting it in a different box, and then ultimately decides to place it back into its original box before the agent returns to retrieve it (Fabricius et al., 2010). Thus, just as in the "fruit moves" condition in our study (as well as the unknown lift condition in Kaminski et al., 2008), the target object is spatially manipulated while the agent does not have perceptual access to it, but ultimately ends up in the location where the agent believes it to be. As noted by Oktay-Gür and Rakoczy (2017), this sort of manipulation models the classic epistemological "Gettier problem" (Gettier, 1963) which argues that an agent can have a justified true belief about a situation without having "knowledge" about it if the agent does not witness all of the events relevant to the situation (i.e. if the agent's reasoning for the justified true belief is not entirely complete or true).

To our knowledge, no experiments modeled after the true belief tasks passed by 4- to 6-year-olds in Oktay-Gür and Rakoczy (2017) have been conducted with primates. However, performance limitations seem unlikely to explain monkeys' failure to predict the agent's reach direction in the "fruit moves" condition of our study; to explain our results through an appeal to performance limitations, one must argue that monkeys viewed the "fruit moves" condition as an obvious, artificially trivial, or trick question about the agent's true belief which led monkeys to look for equal durations regardless of where the agent reached, whereas there was no such interpretation or misunderstanding of the "box moves" condition. However, the situations presented in the "fruit moves" and "box moves" conditions should have a roughly equal probability of being interpreted as trivial or trick questions about the agent's mental state if this interpretation hinges on the idea that the agent's true belief and subsequent reaching behavior is overly obvious. Therefore, while more research is needed to better relate the results of human developmental theory of mind studies to those in primates, we believe that monkeys' pattern of performance is better explained by the awareness relations hypothesis than by performance limitations rooted in pragmatics.

Lastly, there are several important and currently unresolved questions regarding how and why awareness relations may be disrupted under various conditions. While we hypothesize that spatial manipulation of the target object outside of the agent's view may 'turn off' an awareness relation, it is alternatively possible that monkeys maintain this initial representation but fail to integrate it with a second, more recent representation of the target object moving out of and back into the hiding location while the agent could *not* see it. In this scenario, the original representation linking information to the agent remains unchanged but is superseded by a more recent representation in which the agent is unaware about the same information. This type of failure to *integrate* two different representations to guide expectations about an agent's behavior may explain why monkeys did not expect the agent to reach correctly in the "fruit moves" condition of our study. Presumably this sort of integration issue would not have affected monkeys' expectations in the "box moves" condition because there was no spatial manipulation of the target object after the initial awareness relation was formed, and thus there was no relevant second representation to integrate with the first. More research is needed to explore whether awareness relations are completely dissolved in these and similar circumstances, or whether monkeys do maintain these initial representations but fail to maintain their expectations about others' behavior by not appropriately integrating the initial representation with a newly-formed conflicting representation (i.e. integrating a representation in which the agent does view the object moving into a hiding location with a second representation in which the agent does not).

Future work should also explore how different manipulations of target and non-target objects influence monkeys' expectations about others' behavior. Given that the awareness relations hypothesis predicts that *any* spatial manipulation of the target object outside of the agent's view should disrupt awareness relations, it would be informative to explore whether awareness relations are similarly disrupted when the target object moves out of and back into a hiding location without moving closer to or farther from a different hiding location. Additionally, awareness relations should be disrupted in conditions where both the target object and a non-target object (e.g. the box) are spatially manipulated outside of the agent's view at the same time, but not when neither object moves while the agent cannot see them (as in Marticorena et al., 2011). These types of situations could lead to more robust tests of the awareness relations hypothesis and would likely provide us with a more precise understanding of the mechanisms by which awareness relations are disrupted.

To summarize, our findings support the idea that rhesus macaques mentalize using awareness relations, a heuristic for linking others to true information in the environment. Our findings suggest that these awareness relations are disrupted by physical movement of objects being tracked by an agent when this movement occurs outside the agent's awareness, but not by other superficially similar manipulations not involving the object of interest. However, we still know little about the psychological properties of awareness relations and the range of factors that can influence them. For example, do non-spatial object manipulations (e.g. changes in object color) disrupt subjects' expectations about an agent's awareness? Similarly, when awareness relations break down, do subjects expect that the agent is no longer aware of the *location* of the object, or alternatively that the agent is no longer aware of the object's *existence* more generally? Answers to these types of questions will be critical in developing clearer formulations of what awareness relations may entail, testing the explanatory power of this hypothesis, and delineating how and why behavior guided by awareness versus human-like representational relations may differ.

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Conflict of interest

The authors declare no conflict of interest.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.cognition.2019.04.012.

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