Animal Behaviour 134 (2017) 193–199

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Do rhesus macaques, *Macaca mulatta*, understand what others know when gaze following?

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ARTICLE INFO

Article history:
Received 17 April 2017
Initial acceptance 6 June 2017
Final acceptance 28 August 2017
Available online 21 November 2017
MS. number: A17-00337R

Keywords:
gaze following
rhesus macaque
theory of mind

A basic tendency to look where others are looking provides animals with the opportunity to learn about important objects in the environment, such as the location of conspecifics, food and predators. Although research has shown that many social species are able to follow others' gaze, the extent to which different species rely on sophisticated cognitive capacities when gaze following is debated. Whereas some species follow gaze via a relatively inflexible orienting response, gaze following in other species may reflect a deeper understanding of the visual perspective and attentional states of agents. Identifying the mechanisms underlying gaze following in different species is the critical first step to addressing the challenging ultimate question of why different species vary in their gaze-following skills. Therefore, we explored whether rhesus macaques have a mentalistic understanding of gaze. Specifically, we tested whether rhesus macaques are able to incorporate representations of a partner's knowledge state into their gaze-following response. In our study, macaques saw a human actor look to a distant location in a surprised manner. We manipulated whether or not the actor had previously seen the very first object in his line of sight. We found that monkeys looked for an alternative target of the actor's gaze more quickly when the actor had previously seen the object compared to when he had not. This suggests that rhesus macaques may have a mentalistic understanding of gaze cues.

Gaze following, the ability to follow the direction in which others are looking, is an important cognitive skill that allows animals to detect significant objects and events in the environment through the observation of conspecifics. As such, gaze following has been widely studied in nonhuman animals, and a basic tendency to co-orient with others has been demonstrated in numerous species (e.g. Barbary macaques, *Macaca sylvanus*: Rosati & Santos, 2017; bonobos, *Pan paniscus*: MacLean & Hare, 2012; capuchins, *Cebus apella*: Amici, Aureli, Visalberghi, & Call, 2009; chimpanzees, *Pan troglodytes*: Bräuer, Call, & Tomasello, 2005; MacLean & Hare, 2012; Okamoto-Barth, Call, & Tomasello, 2007; dogs, *Canis familiaris*: Miklósi, Polgardi, Topal, & Csanyi, 1998; dolphins, *Tursiops truncatus*: Pack & Herman, 2004; gibbons, *Hylobates pileatus*: Horton & Caldwell, 2006; goats, *Capra hircus*: Kaminski, Riedel, Call, & Tomasello, 2005; lemurs, *Lemur catta*: Shepherd & Platt, 2008; marmosets, *Callithrix jacchus*: Burkhart & Heschl, 2006; orangutans, *Pongo pygmaeus*: Bräuer et al., 2005; ravens, *Corvus corax*: Bugnyar, Stöwe, & Heinrich, 2004; tortoises, *Geochelone carbonaria*: Wilkinson, Mandl, Bugnyar, & Huber, 2010; rhesus macaques: Emery, Lorincz, Perrett, Oram, & Baker, 1997; wolves, *Canis lupus*: Werhahn, Virányi, Barrera, Sommese, & Range, 2016).

Although the ability to follow gaze is fairly widespread, the cognitive mechanisms that support gaze following vary widely across species (for a review, see Davidson, Butler, Fernández-Juricic, Thornton, & Clayton, 2014). Whereas some species follow gaze via a relatively inflexible orienting response (e.g. marmosets: Burkhart & Heschl, 2006), gaze following in other species may reflect a deeper understanding of the visual perspective and attentional states of agents (e.g. chimpanzees: Bräuer et al., 2005; Okamoto-Barth et al., 2007; ravens: Bugnyar et al., 2004). In other words, gaze following in some species may reflect a cognitive capacity known as a 'theory of mind', an understanding that other agents have mental states and that these mental states play a causal role in their behaviour.

Chimpanzees, for example, are able to use representations of what others have and have not previously seen as input when gaze following. In a study by MacLean and Hare (2012), chimpanzees were presented with a human actor who looked to a distant location in a surprised manner. In one condition, the very first object in the actor's line of sight was one that the actor had previously seen, but in the other condition the object was one that he had not

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https://doi.org/10.1016/j.anbehav.2017.10.016
0003-3472/

previously seen. In other words, sometimes the actor knew about the object and sometimes he did not know about it. When the actor knew about the very first object, chimpanzee subjects tended to search for an alternative target of the actor's attention. In contrast, when the actor did not know about the object, chimpanzees were less likely to search for an alternative object. This study indicates that chimpanzee gaze-following processes operate on representations of what others have and have not seen; in other words, chimpanzee gaze-following processes operate on mentalistic representations.

Understanding the cognitive mechanisms underlying gaze-following behaviours across different species is an important goal for comparative psychologists, as doing so can help inform our understanding of how different gaze-following skills have emerged across phylogenies. It is possible that although many species follow gaze, very few have a mentalistic understanding of gaze cues. In addition, identifying the mechanisms underlying gaze following in different species is the first step to addressing the challenging ultimate question of why different species vary in their gaze-following skills (Davidson et al., 2014; Rosati & Hare, 2009). Therefore, in our study we explored the extent to which a species of Old World monkey, the rhesus macaque, has a mentalistic understanding of gaze. Specifically, we tested whether rhesus macaques are able to incorporate representations of a human experimenter's knowledge state into their gaze-following response. This pattern of performance would provide compelling evidence that macaque gaze-following processes operate on mentalistic representations of what others see and know.

Importantly, previous work has demonstrated that rhesus macaques spontaneously follow the gaze of both conspecifics (Deaner & Platt, 2003; Emery et al., 1997; Shepherd, Deaner, & Platt, 2006; Tomasello, Call, & Hare, 1998) and humans (Itakura, 1996; Rosati, Arre, Platt, & Santos, 2016; Tomasello, Hare, & Fogleman, 2001). Past studies also suggest that there is some degree of flexibility in macaque gaze-following responses. For example, the social status of a conspecific model modulates the extent to which rhesus macaques follow the model's gaze (Shepherd et al., 2006). In addition, several studies have demonstrated that macaques can represent what other individuals see and know outside the context of gaze following (see review in Drayton & Santos, 2016). For example, work has shown that macaques preferentially steal food from a competitor who cannot see them over one who can (Flombaum & Santos, 2005), and can represent what others know when making predictions about an actor's future actions (Marticorena, Ruiz, Mukerji, Goddu, & Santos, 2011). Nevertheless, it remains an open question as to whether knowledge representations are available as input to macaque gaze-following systems. It is possible that despite possessing many of the constituent skills necessary to engage in sophisticated gaze following, rhesus macaques are not able to integrate these skills in a way that gives rise to an ape-like gaze-following response.

To address this question, we modified the method developed by MacLean and Hare (2012) for use with free-ranging rhesus monkeys. In our experiment, rhesus macaques saw a human actor look to a distant location in a surprised manner. We manipulated whether or not the actor had previously seen the very first object in his line of sight. We did this by varying whether the object had been placed on a platform close to the actor by the actor himself (knowledge condition), or by a second experimenter while the actor was not watching (ignorance condition). We reasoned that if the monkeys were able to use information about what the actor had previously seen to infer the current target of his attention, they should expect the actor's gaze to be directed towards the object on the platform only when the actor had not previously seen it. In contrast, when the actor had previously seen the object on the platform, subjects should be more likely to infer that the actor's surprise response was directed at an alternative more distal target. However, if the monkeys were insensitive to mentalistic information when gaze following, they should not have different expectations about the target of the actor's attention in the two conditions.

Note that although we have described the actor as looking ‘surprised’, our primary question was not whether monkeys understand a human's surprised reaction per se. Rather, our core question was whether monkeys were sensitive to the knowledge state of another agent in a gaze-following context. However, to ensure that the actor's gaze-eliciting behaviour was generally meaningful to the monkey, we also included a third baseline condition in which the object was present but not located in the actor's line of sight when he performed the gaze-eliciting behaviour. This condition was included to confirm that the actor's surprised response induced measurable gaze following to a distal location when no obvious proximal target object was present.

METHODS

Subjects

We tested 175 free-ranging rhesus macaques living on the island of Cayo Santiago in Puerto Rico. Monkeys living on Cayo Santiago have been studied for over half a century, and are therefore well habituated to the presence of human experimenters (Rawlins & Kessler, 1986). Individual monkeys in this population are easily identified by the presence of unique chest tattoos and ear notches. All work was approved by the Institutional Animal Care and Use Committees of Yale University (no. 2014-11624) and Cayo Santiago (no. 8310106) and conformed to ASAB/ABS Guidelines for the use of animals in research.

We used a between-subjects design in which each monkey participated in a single session that consisted of a single trial of just one of the three conditions (knowledge condition: $N = 56$; ignorance condition: $N = 60$; baseline condition: $N = 59$). Although we could have attempted to test the same monkeys three times (one time in each condition), it is often extremely difficult to locate a particular monkey in the Cayo Santiago population, due both to the size of the population and the size and terrain of the island. Thus, we adopted a between-subjects design. The average age of the monkeys was 5.7 years and 71% were male. Only monkeys that were at least 1 year of age were tested. The target sample size for the study was determined prior to the onset of data collection and pre-registered with the Open Science Framework (https://osf.io/jmuym/).

An additional 179 sessions were conducted but were not included in the analyses. Of these, 103 sessions were aborted before the experimenter engaged in the looking behaviour designed to elicit gaze following (described below). The majority of these were aborted because the subject monkey was inattentive or moved, or another monkey interfered during the presentation ($N = 101$). Two additional sessions were aborted due to procedural errors. In the remaining 76 sessions not included in the analyses, the experimenter engaged in looking behaviour, but the data from these videos were not extracted because (1) the subject began to walk away during the critical 10 s observation period immediately following the actor's surprised response ($N = 22$), (2) the subject was not looking at the experimenter at the onset of the looking behaviour ($N = 3$), (3) there was a procedural error after the onset of the looking behaviour ($N = 3$), (4) the subject monkey's head was forcibly moved by another monkey during the 10 s testing interval ($N = 1$), (5) the subject was a monkey who had already been tested ($N = 45$; note that we always analysed data from the monkeys' first session), (6) the video was not able to be recovered due to a camera error ($N = 1$), or (7) the inclusion of the subject would have resulted in exceeding the predetermined maximum number of subjects per condition ($N = 1$). The rate of excluded sessions is similar to that of other published studies using this population.

Procedure

Subjects were randomly assigned to one of three conditions: an ignorance condition, a knowledge condition, or a baseline condition. At the start of ignorance and knowledge condition trials, an experimenter (E1, the actor) knelt on the ground approximately 3 m in front of the subject monkey. Note that for practical reasons we used a human rather than a conspecific partner. This is a fairly common practice in primate gaze-following studies since primates follow the gaze of humans and conspecifics at similar rates (Rosati & Hare, 2009). In addition, previous work has shown that that rhesus macaques follow the gaze of humans (Itakura, 1996; Rosati et al., 2016; Tomasello et al., 2001) and represent what humans have previously seen in non-gaze-following contexts (Marticorena et al., 2011); thus, we had reasonable a priori reasons for thinking that the use of a human demonstrator would not significantly negatively impact monkeys' behaviour.

After E1 knelt down, he placed a stand with a small square platform to his left side at arm's length. The second experimenter (E2, the cameraperson) stood approximately 1 m behind the stand. What happened next differed depending upon the condition. In the ignorance condition (see Fig. 1a), E1 oriented his head and torso to the right so that he was unable to see the stand or E2. E2 then quietly stepped towards the stand and removed a novel object (a small stuffed animal) from a paper bag. She briefly played with the object by tossing it gently back and forth between her hands five times and up in the air three times. She then placed the object on the platform and returned to her original position 1 m behind the stand. When she placed the object on the platform, she gave a quiet verbal cue that the object was in place. During this time, E1 remained oriented away from the stand. Thus, he did not see E2 place the object on the stand and thus did not know about the object.

The knowledge condition was similar to the ignorance condition except that in this condition E1 removed the object from the bag, played with it, placed it on the platform and gave a quiet verbal cue that the object was in place (see Fig. 1b). Thus, the actor knew about the object. The actor then turned so that he was oriented away from the stand, just as he was during the ignorance condition. E1 maintained this position for 4 s. This 4 s delay was included to ensure that the time between placement of the object on the stand and E1's gaze-eliciting behaviour was the same in the different conditions. In addition, it ensured that E1 was always oriented away from the object just prior to the onset of his gaze-eliciting behaviour (described below).

We also included a third baseline condition in which the object was present but was not in E1's line of sight when he performed the gaze-eliciting behaviour. This baseline condition was identical to the knowledge condition except that during the initial set-up E1 placed the stand on his right side rather than on his left side (see Fig. 1c). He then took the object out of the bag, played with it, placed it on the stand, turned to the right and waited for 4 s. The primary purpose of this condition was simply to ensure that monkeys would respond to the experimenter's surprised gaze differently in this condition (in which the object was not a plausible target of the actor's surprised gaze since it was not in his line of sight) compared to the ignorance condition (in which the object was a plausible target of the actors' surprised gaze because it was both in his line of sight and because he had not previously seen that object).

In all conditions, E1 next oriented forward towards the subject monkey to be sure he had the subject's attention. If the monkey was not paying attention, E1 attempted to obtain the subject's attention. Once the subject was looking at E1, he then turned to the left (i.e. the same direction as the object in the knowledge and ignorance conditions) in a surprised manner (Fig. 1d–f). Specifically, E1 turned quickly while giving a soft vocalization, bobbed up and down, looked at the monkey, turned again towards the object, bobbed up and down again, and then remained still. The subject's behaviour was filmed for 10 s following the onset of E1's surprised vocalization. Note that this gaze-eliciting behaviour is more complex than behaviours used in many studies. We chose to use this more complex behaviour because informal piloting of various looking gaze behaviours revealed that this behaviour was particularly effective at eliciting gaze following.

Video Coding and Data Analysis

To allow us to examine the effect of object exposure on gaze following, a single coder reviewed the videos to determine the amount of time between the placement of the object on the platform and the onset of E1's gaze-eliciting behaviour. We were not able to code this variable for two videos because the verbal cue indicating that the object was being placed on stand could not be heard on the videos due to background noise. To examine subjects' latency to search for an alternative target of the actor's attention, two coders who were blind to condition independently examined each frame of the 10-second interval (30 frames = 1 s) following E1's vocalization using MPEG Streamclip. Search latency was operationally defined as the time (from the onset of E1's vocalization) that it took for the subject to look in the direction of E1's gaze past the object on the platform (ignorance and knowledge conditions) or the equivalent location in space (baseline condition). Any subject that did not engage in the defined search behaviour was assigned a latency of 10 s. Examples of subjects' looking behaviours are depicted in Fig. 2. Coders also rated the amount of time that subjects spent searching for an alternative target of the actor's attention in each condition. Search duration was operationally defined as the total time that the subject spent looking in the direction of E1's gaze past the object on the platform (ignorance and knowledge conditions) or the equivalent location in space (baseline condition) during the 10 s interval. Any subject that did not engage in the defined search behaviour was assigned a search time of 0 s.

After completing the experiment, we also decided to code how long subjects spent looking at the object on the platform and at E1. We predicted that if the monkeys in the knowledge condition thought that the actor's gaze was directed at the object on the platform, then his behaviour towards that object should be somewhat surprising. In contrast, if the monkeys in the ignorance condition thought that the actor's gaze was directed at the object on the platform, then his behaviour towards that object should be relatively unsurprising. Therefore, we predicted that in addition to looking for an alternative target of the actor's attention more quickly in the knowledge condition than in the ignorance condition, monkeys might actually also look at the object and actor longer in the knowledge condition than in the ignorance condition. Much work to date has shown that rhesus monkeys and other species look longer at events that they find unexpected (e.g. Cheries, Newman, Santos, & Scholl, 2006; Onishi & Baillargeon, 2005; Rochat, Serra, Fadiga, & Gallese, 2008; Woodward, 1998; Wynn, 1992). Note that we chose to combine looks towards E1 and towards the object into a single measure because it was difficult to distinguish looks between E1 and the object given that looks between them involved relatively subtle saccades on the part of the subject monkey. Inter-rater reliability for all three variables was

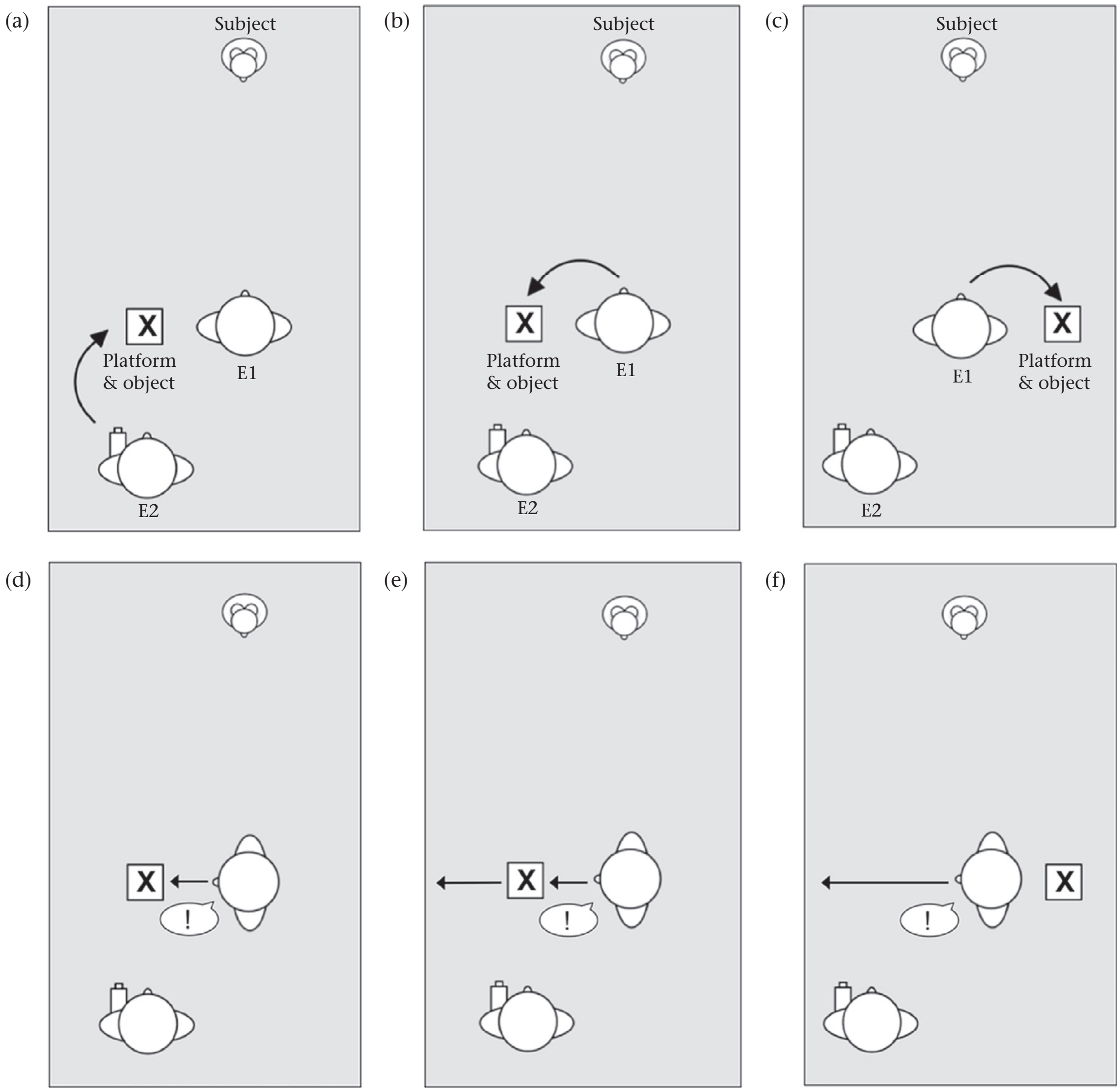

Figure 1. Schematic of the testing set-up in the (a) ignorance condition, (b) knowledge condition and (c) baseline condition. Arrows in panels (a), (b) and (c) indicate which experimenter placed the object on the platform in the three conditions. Arrows in panels (d), (e) and (f) indicate the direction of E1's gaze in relation to the object on the platform in the three conditions.

good (Pearson correlation: search latency: $r = 0.98$; search duration: $r = 0.91$; looking time at object/E1: $r = 0.86$).

RESULTS

We found significant differences in monkeys' search latency across conditions (linear regression: $F_{2,172} = 11.81$, $P < 0.001$, $\eta^2 = 0.121$; Fig. 3). Monkeys in the baseline condition searched for an alternate target more quickly than monkeys in either the ignorance condition ($F_{1,117} = 23.43$, $P < 0.001$, $\eta^2 = 0.167$) or the knowledge condition ($F_{1,113} = 5.67$, $P = 0.019$, $\eta^2 = 0.048$). This was expected, as in the baseline condition there was no plausible proximal target of the actor's attention since the object was present but not directly in the actor's line of sight. More interestingly, there was also a significant difference in monkeys' search behaviour between the knowledge and ignorance conditions ($F_{1,114} = 5.83$, $P = 0.017$, $\eta^2 = 0.049$). As predicted, when the actor had previously seen the object on the platform, subjects searched for an alternative target more quickly than when the actor had not previously seen the object. Presumably, this is because monkeys assigned to the knowledge condition were more likely to think that the actor's surprised gaze was directed at a more distal object in the environment than were monkeys assigned to the ignorance condition.

We then examined search duration and again observed condition differences in how long subjects spent searching for an alternative target (linear regression: $F_{2,172} = 3.39$, $P = 0.036$, $\eta^2 = 0.038$). In the baseline condition, monkeys spent more time engaged in search behaviour than they did in either the ignorance condition ($F_{1,117} = 5.17$, $P = 0.025$, $\eta^2 = 0.042$) or the knowledge condition ($F_{1,113} = 4.46$, $P = 0.037$, $\eta^2 = 0.038$). In other words, when there was no plausible proximal target of the actor's attention, the monkeys spent more time searching for a distal target of the actor's attention. However, we did not find any differences in search duration between the knowledge and ignorance conditions ($F_{1,114} = 0.20$, $P < 0.657$). Monkeys spent equal amounts of time searching for an alternative target when the actor had previously seen the very first object in his line of sight compared to when he had not seen it.

Next, we compared how long subjects spent looking at the object/actor in the 10 s interval immediately following the actor's

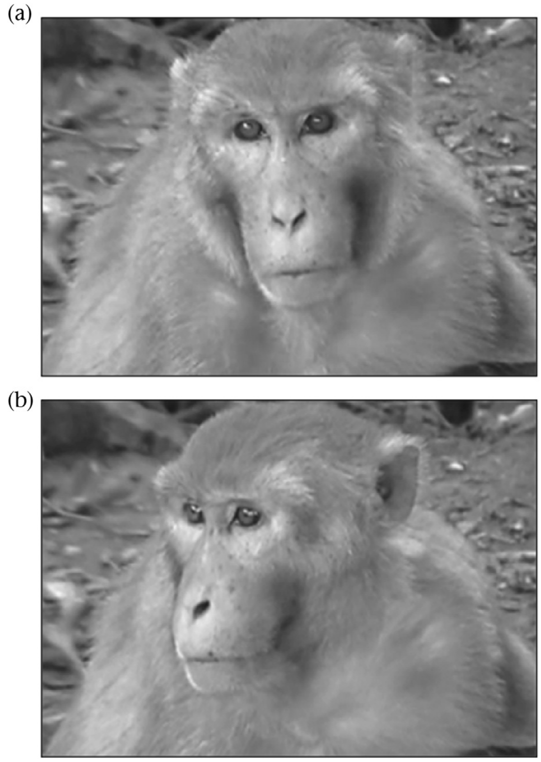

Figure 2. Example video frame of a subject monkey (a) looking at the object on the platform and (b) looking past the object on the platform.

surprise response. Again, we found significant condition differences ($F_{2,172} = 3.189$, $P = 0.044$, $\eta^2 = 0.036$; Fig. 4). As predicted, subjects looked at the object/actor longer in the knowledge condition than in the ignorance condition ($F_{1,114} = 4.20$, $P = 0.043$, $\eta^2 = 0.036$). This may be because monkeys found the actor's surprised response towards the object unexpected in the knowledge condition, but not in the ignorance condition. Monkeys' looking time also differed significantly between the knowledge condition

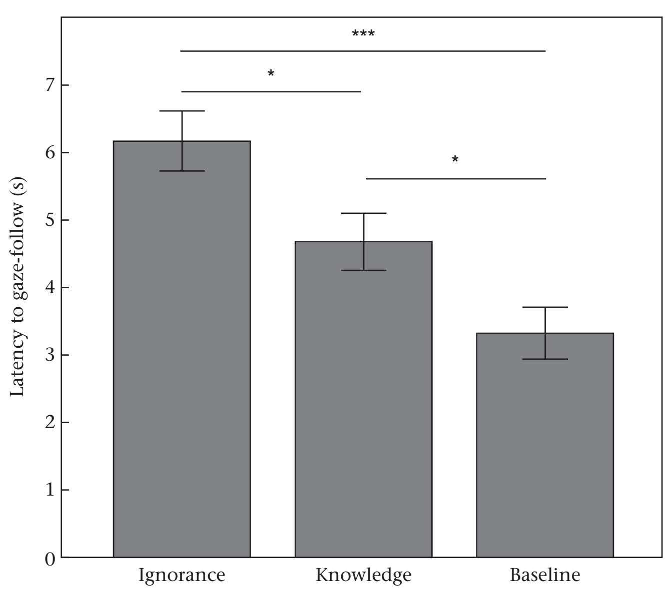

Figure 3. Monkeys' latency (±SEM) to search for an alternative target of the actor's attention across the three conditions. *$P < 0.05$; ***$P < 0.001$.

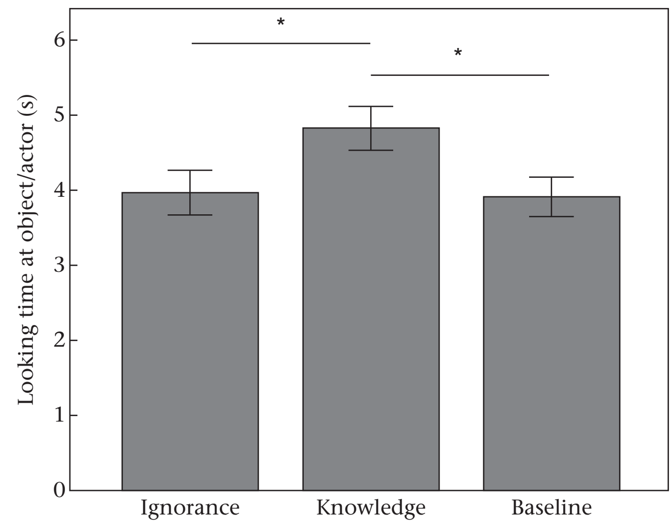

Figure 4. Time monkeys spent looking (±SEM) at the object on the platform and at the actor across the three conditions.*$P < 0.05$.

and the baseline condition ($F_{1,113} = 5.51$, $P = 0.021$, $\eta^2 = 0.046$). This is again likely because monkeys did not find the actor's behaviour unexpected in the baseline condition.

Finally, we confirmed that subjects assigned to the different conditions did not differ in the amount of time they were exposed to the object prior to the actor's gaze-eliciting behaviour (linear regression: $F_{2,170} = 0.11$, $P = 0.896$).

DISCUSSION

Rhesus macaques' gaze-following behaviour in the baseline condition suggests that our gaze-eliciting manipulation prompted reliable and measurable gaze following from monkey subjects. Monkeys looked for a distal target of the actor's attention more quickly in the baseline condition (in which there was no proximal target of the actor's attention) compared to either the knowledge or ignorance condition (in which a plausible proximal target was present). In addition, comparisons of subjects' behaviour in the knowledge and ignorance conditions suggest that rhesus macaques may be sensitive to what other do and do not know when gaze following. Monkeys searched for an alternative target of the actor's attention more quickly when the actor had previously seen the very first object in his line of sight compared to when he had not.

Furthermore, subjects' looking times towards the object and actor were longest in the knowledge condition. One interpretation of this pattern of looking is that subjects looked longer at the object and the actor in the knowledge condition because the actor's behaviour towards the object was unexpected. Indeed, increased duration of looking often occurs in response to events that are unexpectedness in both human (e.g. Onishi & Baillargeon, 2005; Woodward, 1998; Wynn, 1992) and nonhuman primate participants (e.g. Cheries et al., 2006; Rochat et al., 2008). Under this view, macaques did not expect the actor to emote towards an object that he had already seen. This pattern is again consistent with the hypothesis that the monkeys had an understanding of the actor's knowledge state.

In contrast, we found that although monkeys searched for an alternative target of the actor's attention for longer durations in the baseline condition than in either the knowledge or ignorance condition, monkeys did not search for longer in the knowledge condition compared to the ignorance condition. This was somewhat unexpected, as we had predicted that in addition to searching for an alternative target of the actor's attention more quickly in the knowledge condition, monkeys would also search for longer amounts of time. One possibility is that monkeys did not think that the object on the platform was a particularly implausible target of the actor's surprised gaze response, even when the actor had in fact previously seen the object. This may have been because the object was fairly interesting. It is possible that using a different novel object would have elicited different patterns of looking.

One limitation of our study concerns how the actor obtained his knowledge of the object. In the knowledge condition, the actor not only saw the object, but also played with it and placed it on the platform. We chose to have the actor play with the object to make sure that it was clear to the monkey that the actor knew about the object. However, our design made it possible that the differences we observed in the monkeys' behaviour in the knowledge and ignorance conditions may not have been based solely on whether the actor had previously seen the object on the platform. Monkeys might have been responding to differences in the actor's interactions with the object more broadly. Future work should examine in more detail which features of the actor's interaction with the object were most important in shaping monkeys' inferences about the target of the actor's gaze. This will inform whether our results are best interpreted as evidence that monkeys represent what others have previously seen (versus touched, etc.) in a gaze-following context. We also note that because our gaze-eliciting response was directed to the side, rather than up, some of the 'search behaviours' that the monkeys engaged in were likely not in response to the actor. However, even if our estimates of rhesus monkeys' tendency to gaze-follow are somewhat inflated, this does not explain the differences detected between the three conditions.

In addition to demonstrating that rhesus macaques may have a mentalistic understanding of gaze, our results are the first to conceptually replicate previous work by Marticorena et al. (2011) demonstrating that rhesus macaques attribute knowledge to other agents. Furthermore, our study found that rhesus monkeys represented another agent's knowledge in a very different context from that of the previous study. In this previous study, researchers found that monkeys expected a human experimenter to manually search for a piece of food in the location in which she had previously seen it hidden. In other words, they expected the experimenter to search for the food where she 'knew' it to be. In contrast to previous studies, our experiment did not involve food. In the past, some researchers (e.g. Hare & Tomasello, 2004; Lyons & Santos, 2006) have suggested that primates' theory of mind can only be used in a domain specific manner, namely, in competitive situations. Although the task that Marticorena et al. (2011) used did not involve any overt food competition, it could nevertheless be argued that this study presented monkeys with a situation in which they would be motivated to try to steal the food, and thus track the knowledge state of the actor. The fact that monkeys tracked the knowledge state of an actor when no food was present provides evidence that rhesus macaques' mentalizing capacities are not necessarily domain specific. Our finding thus adds to the growing body of work showing that primates in general can use their theory of mind skills across a variety of contexts (e.g. Crockford, Wittig, & Zuberbühler, 2012; Drayton & Santos, 2014; MacLean & Hare, 2012; Warneken & Tomasello, 2006; Yamamoto, Humle, & Tanaka, 2012).

Our study provides evidence that rhesus macaques possess many of the same mentalizing capacities as chimpanzees (although see Krupenye, Kano, Hirata, Call, and Tomasello (2016) for evidence that chimpanzees, unlike rhesus macaques (Marticorena et al., 2011), may represent others' false beliefs). Like chimpanzees (Hare, Call, Agnetta, & Tomasello, 2000; Hostetter, Russell, Freeman, & Hopkins, 2007), rhesus macaques understand what others see, including the particular role that eyes play in perception (Flombaum & Santos, 2005). Also like chimpanzees (Melis, Call, & Tomasello, 2006), rhesus macaques are able to strategically integrate information pertaining to others visual and auditory perceptions (Santos, Nissen, & Ferrugia, 2006). Indeed, the results of a recent cognitive battery consisting of 16 different tasks revealed that there were few systemic differences in the performance of apes and Old World monkeys (Schmitt, Pankau, & Fischer, 2012). Nevertheless, chimpanzees have demonstrated greater flexibility in their use of mental state representations, as well as an understanding of certain mental states that to our knowledge have not been tested or observed in monkeys. For example, chimpanzees reportedly understand something about the kinds of inferences others make (Schmelz, Call, & Tomasello, 2011), as well as others' preferences (Schmelz, Call, & Tomasello, 2013). Whether more distantly related primate species are able to make these kinds of mental state attributions remains an important direction for future research to explore.

To summarize, our results demonstrate that rhesus macaques have a fairly sophisticated understanding of gaze. Specifically, rhesus macaque gaze-following processes seem to operate on representations of what others have and have not seen. This finding suggests that rhesus macaques, like apes, have a mentalistic understanding gaze. Macaque monkeys do not simply reflexively orient in the direction that others are looking, but rather represent their partner as 'seeing' some object or event in the environment.

Acknowledgments

This research was supported by the National Institute of Mental Health (R01MH096875) and a National Center for Research Resources grant CM-5-P40RR003640-13 award to the Caribbean Primate Research Center, the University of Puerto Rico-Medical Sciences Campus. L.R.S. was supported by a James S. McDonnell Foundation Award (no. 220020242) and Yale University. L.A.D. was supported by a National Science Foundation Graduate Research Fellowship. Any opinions, findings and conclusions or recommendations expressed in this material are those of the authors and do not necessarily reflect the views of the National Science Foundation. We thank Alysa Arre for data coding, Andrew Beguin for his help running the study and Angelina Ruiz Lambides, Nahiri Rivera Barreto and Giselle Caraballo Cruz for research support at Cayo Santiago.

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