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

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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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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