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What do monkeys know about others' knowledge?

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ABSTRACT

Recently, comparative psychologists have suggested that primates represent others' knowledge states. Evidence for this claim comes from studies demonstrating that primates expect others to maintain representations of objects when those objects are not currently visible. However, little work has explored whether nonhuman primates expect others to share the more sophisticated kinds of object knowledge that they themselves possess. We therefore investigated whether primates attribute to others knowledge that is acquired through the mental transformation of a static object representation. Specifically, we tested whether rhesus macaques (*Macaca mulatta*) expected a human demonstrator to solve a difficult rotational displacement task. In Experiment 1, monkeys watched a demonstrator hide a piece of fruit in one of two boxes. The monkey and the demonstrator then watched the boxes rotate 180°. We found that monkeys looked longer when the demonstrator reached into the box that did not contain the fruit, indicating that they expected her to be able to track the fruit to its current location. In Experiment 2, we ruled out the possibility that monkeys simply expected the demonstrator to search for the food in its true location. When the demonstrator did not witness the rotation event, monkeys looked equally long at the two reaching outcomes. These results are consistent with the interpretation that rhesus macaques expect others to dynamically update their representations of unseen objects.

1. Introduction

A central feature of human cognition is that people not only know things about the world, but they also attribute this same knowledge to others. Take a simple case of physical understanding like watching a golfer hit a golf ball into a hole. As adult humans, we would not only maintain a static representation of the (now unseen) ball inside the hole, but we would expect others to represent the ball's continued existence as well. We would predict that the golfer would search for his ball in the hole, and would be surprised if he didn't do so. In addition, we know that like ourselves, other people dynamically update their static object representations by imaging potential or actual changes in object attributes. For example, if we saw the golfer hit the ball down the fairway and out of sight, we could imagine the trajectory of the ball and would have some idea of where to search for it. We would expect the golfer to make similar inferences about the trajectory of the ball, and would be surprised if he came to radically different conclusions about where the ball was likely to be. This capacity to attribute to others both the static and dynamic object information that we ourselves represent is an important part of our so-called *theory of mind* capacity. Indeed, attributing a simple knowledge of objects to others is essential for normal social functioning as it facilitates complex forms of cooperation, communication through language, and many other uniquely human

behaviors (Apperly, 2010).

In order to understand the specific role that a theory of mind played over the course of human evolution, psychologists have examined the possibility that nonhuman primates (hereafter, primates) also represent the knowledge that others have about objects and their motions. Comparative psychologists have generated a considerable amount of evidence that primates expect others to maintain static representations of objects when those objects are not currently visible (e.g., Hare, Call, & Tomasello, 2001; Kaminski, Call, & Tomasello, 2008; MacLean & Hare, 2012; Martcorena, Ruiz, Mukerji, Goddu, & Santos, 2011). However, little work has explored whether primates expect others to share the more dynamic object knowledge that they themselves possess. This is an important question, because to date primates have only demonstrated the ability to represent what others do and do not know in a very limited range of contexts. If primates only attribute static object representations to others, then this would constitute an important representational limitation on primate theory of mind capacities. In addition, showing that primates are able to track what others have seen across a range of scenarios would provide important confirmatory evidence that primates' performance in theory of mind tasks actually involves representations of what others have seen rather than simpler mechanisms that might explain performance (e.g., Heyes, 2015; Penn & Povinelli, 2007). We therefore investigated whether

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primates attribute to others knowledge that is acquired through the mental transformation of static object representations.

Before turning to what primates understand about others' object knowledge though, it's important to first better understand what primates *themselves* know about objects and their trajectories. After all, primates will likely attribute to others only those representations that they themselves have about the world. Conveniently, comparative psychologists have learned much about how primates represent objects and their motions. One of the most relevant aspects of physical objects is the fact that they typically exist as *static* permanent entities. Primates seem to recognize this as well; they know that objects do not randomly enter into and out of existence (Beran, 2004; Call, 2001; de Blois & Novak, 1994; de Blois, Novak, & Bond, 1998; Deppe, Wright, & Szelistowski, 2009; Flombaum, Junge, & Hauser, 2005; Jolly, 1964; Mathieu, Bouchard, Granger, & Herscovitch, 1976; Mendes & Huber, 2004; Menzel, 1973; Neiworth et al., 2003; Rosati & Hare, 2012; Santos, Barnes, & Mahajan, 2005; Santos, Sulkowski, Spaepen, & Hauser, 2002; Schino, Spinozzi, & Berlinger, 1990; Schneider, 1992; Uller, Hauser, & Carey, 2001; Vaughter, Smotherman, & Ordy, 1972; Wise, Wise, & Zimmerman, 1974; Wood, Moriarty, Gardner, & Gardner, 1980). For example, experiments based on Piagetian search paradigms have demonstrated that primates will search for food that they have seen hidden under or behind an occluder (e.g. Call, 2001; de Blois & Novak, 1994; Mendes & Huber, 2004; Neiworth et al., 2003). Looking time tasks assessing primate numerical competencies have also shown that primates are able to detect a mismatch between the number of objects that are placed behind an occluder and the number of objects that are subsequently revealed behind that occluder (e.g. Beran, 2004; Flombaum et al., 2005; Santos et al., 2005; Uller et al., 2001). Finally, naturalistic foraging tasks have confirmed that primates are able to recall the location of hidden food items, sometimes even after substantial delays (e.g. Menzel, 1973; Rosati & Hare, 2012; Santos et al., 2002).

In sum, there is a large body of work showing that primates themselves maintain static object representations. But do primates attribute these same static object representations to others? Much theory of mind work to date has focused on this question. Previous work using at least three kinds of tasks has shown that primates expect others to recall where specific objects are located in space. In a study involving food competition, Hare et al. (2001) showed that chimpanzees (*Pan troglodytes*) were able to use information about what a more dominant chimpanzee knew to strategically acquire food items that had recently been hidden in a central testing room. Subject chimpanzees targeted the food that the dominant had not seen hidden and avoided the food that the dominant had seen hidden (see also Kaminski et al., 2008). Likewise, looking time studies have observed that primates successfully track what others know about the location of hidden food items. In Marticorena et al. (2011), rhesus monkeys watched a human experimenter observe a lemon move into one of two differently colored opaque boxes. The experimenter either reached into the box where she had just seen the lemon go or into the alternative box. Rhesus monkeys looked longer when the experimenter reached into the box that did not contain the lemon, indicating that they were surprised that she did not act on the basis on her knowledge. Finally, gaze following tasks have explored whether primates follow gaze flexibly based on what a particular individual has recently seen. MacLean and Hare (2012) allowed chimpanzees to watch as an experimenter vocalized emotively while looking at an object several meters away. When the experimenter had previously seen the object in that location, chimpanzees looked in the direction of the experimenter's gaze past the object, as if searching for an alternative object. Taken together, the results of these studies provide converging evidence that primates expect others to maintain representations of where objects are and expect those representations to influence agents' subsequent behaviors (Call & Tomasello, 2008; Rosati, Hare, & Santos, 2009; Whiten, 2013; but see Heyes, 2015; Penn & Povinelli, 2007).

Interestingly, although primates attribute static object representations to others across different experimental contexts, it is unclear whether primates can successfully predict how another agent will behave when the agent's representation of the static object is based on outdated or inaccurate information (see review in Martin & Santos, 2016). Specifically, there is evidence that primates often fail to make positive predictions about the behavior of an agent who lacks an accurate static object representation. Marticorena et al. (2011) tested where monkeys expected an experimenter to search for a hidden food item when she had a false belief about the food's location. In this experiment, rhesus monkeys again watched a human experimenter observe a lemon move into one of two different colored opaque boxes. Next, an occluder was raised preventing the experimenter from seeing the stage. With the occluder raised, the lemon moved into the alternative box. The experimenter then reached either into the box where she believed the lemon to be, or in the box where the lemon was actually located. In this case, monkeys looked *equally* long at the two reaching outcomes. This suggests that monkeys neither expected the experimenter to search for the lemon in its true location, nor did they expect the experimenter to search for the lemon on the basis of her false belief about its location. Instead, monkeys appeared to have no expectation regarding where the experimenter would search for the lemon.

Kaminski et al. (2008) observed a similar pattern of performance in great apes (but see Krupenye, Kano, Hirata, Call, & Tomasello, 2016). In their study, subject chimpanzees played a competitive food retrieval game with a competitor chimpanzee who either did or did not see a high-quality reward hidden in one of several possible locations. Subjects could then choose between this high-quality reward and a safer low-quality reward after the competitor made his own choice. Critically however, the subject could not see which food item the competitor chose. Thus, the subject had to infer what the competitor was likely to have done by tracking what the competitor did and did not know about the location of the rewards. Overall, chimpanzee subjects tended to choose the high-quality reward both when the competitor had not seen that reward being hidden—that is, when the competitor was *ignorant* of the reward. However, subject chimpanzees also chose the high-quality reward when, after hiding the high-quality reward in presence of the competitor, the experimenter simply revealed the high-quality reward and *placed it back into the same container* when the competitor was not looking. That is, even when the competitor had a true belief about the location of the food, chimpanzees failed to make a positive prediction that the partner would search for the food on the basis of this belief. Thus, primate's representations of others knowledge seem to be disrupted as soon as the competitor's representation of the static object no longer obtains.

But primates themselves do more than merely reasoning about static representations of objects. In addition to thinking about static objects, primates are also able to dynamically *transform* static object representations (Call, 2000). Whereas maintaining static representations allows an organism to recall the location of an object, transforming static representations allows an organism to imagine potential or actual changes in an object's location. Continually updating an object's location when it is not currently visible is likely to be more cognitively demanding than simply recalling the location of a stationary object. Nonetheless, primates are able to dynamically update their representations of an object's location in some contexts (e.g. Barborica & Ferrera, 2004; Barth & Call, 2006; Beran & Minahan, 2000; Call, 2003; Collier-Baker & Suddendorf, 2006; Hughes & Santos, 2012; Iversen & Matsuzawa, 2003; Natale, Antinucci, Spinozzi, & Poti, 1986). For example, primates are able to visually anticipate the reappearance of a target that momentarily disappears behind an occluder, taking into account the direction and speed of the hidden target (e.g. Barborica & Ferrera, 2004; Iversen & Matsuzawa, 2003). Primates are also able to infer the location of objects following invisible displacements (e.g. Collier-Baker & Suddendorf, 2006; de Blois et al., 1998;

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