

REVIEW ARTICLE

A Decade of Theory of Mind Research on Cayo Santiago: Insights Into Rhesus Macaque Social Cognition

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Over the past several decades, researchers have become increasingly interested in understanding how primates understand the behavior of others. One open question concerns whether nonhuman primates think about others' behavior in psychological terms, that is, whether they have a theory of mind. Over the last ten years, experiments conducted on the free-ranging rhesus monkeys (*Macaca mulatta*) living on Cayo Santiago have provided important insights into this question. In this review, we highlight what we think are some of the most exciting results of this body of work. Specifically we describe experiments suggesting that rhesus monkeys may understand some psychological states, such as what others see, hear, and know, but that they fail to demonstrate an understanding of others' beliefs. Thus, while some aspects of theory of mind may be shared between humans and other primates, others capacities are likely to be uniquely human. We also discuss some of the broader debates surrounding comparative theory of mind research, as well as what we think may be productive lines for future research with the rhesus macaques of Cayo Santiago. *Am. J. Primatol.* © 2014 Wiley Periodicals, Inc.

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INTRODUCTION

Few people can observe nonhuman primates for any length of time without being struck by the richness of their social lives. While the earliest observations of primates in the wild often focused on providing detailed descriptions of social interactions, researchers in the last few decades have focused on the question of how primates think about others' social behaviors. As human primates, we think about the causes of others' behaviors in terms of mental states such as desires, intentions, perceptions, knowledge, beliefs, and so forth. Thinking of behavior in such mental state terms provides humans with a powerful means with which to predict, interpret, and manipulate others' behavior. But do other primates share our human-like "theory of mind", the ability to attribute these sorts of mental states to others?

Over the past decade, experiments conducted on the population of free-ranging rhesus monkeys (*Macaca mulatta*) living on the island of Cayo Santiago have provided important insights into this question. The primary goal of this review is to highlight what we think are some of the most exciting results of this body of work. Prior to doing so however, we first provide a brief historical account of theory of mind research in nonhuman primates (hereafter, primates) in order to set the stage for the experiments conducted on Cayo Santiago. In addition,

following a discussion of some of our own work, we examine some of the broader debates that surround this area of study and suggest what we believe will be productive directions for future research.

HISTORICAL BACKGROUND

Present day research exploring other primates' mentalizing abilities can be traced back to Premack and Woodruff's [1978] seminal paper questioning whether one of our closest living relatives, the chimpanzee (*Pan troglodytes*), has a theory of mind. In this paper, the authors presented a single chimpanzee subject with staged videos of a human actor struggling to solve a variety of problems. When faced with this task, the chimpanzee was able to correctly select which of a set of photos showed the

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correct solution to the problem. Premack and Woodruff interpreted the chimpanzee's success as demonstrating an understanding of the actor's goal. Despite the fact that many scholars raised both theoretical and practical issues regarding this interpretation [e.g., Dennett, 1978; Pylyshyn, 1978; Savage-Rumbaugh et al., 1978], Premack and Woodruff's paper was influential enough to launch a heated debate that continues to the present day over the kinds of evidence required to show that another species attributes mental states to others.

Premack and Woodruff's paper initiated a productive line of empirical work in developmental psychology testing theory of mind development in children [see review in Wellman et al., 2001], but the initial response from comparative psychologists was notably quieter. The next major step forward came a decade later when Whiten and Byrne [1988] [see also Byrne & Whiten, 1990] collected anecdotal reports of ostensible tactical deception across different primate species. These candidate instances of tactical deception were organized into different classes according to their social function and hypothesized representational complexity—that is, the cognitive capacities implied by the behavior. Whiten and Byrne noted a wide range of behaviors in the complete catalogue, including instances of individuals actively concealing visual or auditory information from others and cases in which primates appeared to manipulate others' attention. For example, one report described how a female baboon (*Papio hamadryas*) who was watched by a dominant male gradually shifted her position towards a subadult male hidden behind a rock. Once the female was positioned so that the dominant male could only see her back and the top of her head, she began to groom the hidden male. Whiten and Byrne noted that the use of such a tactic seemed to depend upon the female baboon's ability to represent the dominant male's perspective.

Notably, Whiten and Byrne [1988] motivated the development of this catalogue in part by emphasizing the need to integrate hypotheses concerning the evolution and function of primate intelligence with work explicitly exploring the kinds of representations underlying the apparently sophisticated social skills of primates. Proposals that primates had evolved superior cognitive skills and large brains in response to the challenges posed by complex social environments [Humphrey, 1976; Jolly, 1966] were the focus of much attention at the time, and interest in primates' social knowledge had rarely been greater. Furthermore, by framing the question of primate theory of mind in both representational and functional terms, Whiten and Byrne [1988] effectively brought together the related fields of comparative cognition and ethology [see review in Call, 2007].

Of course, Whiten and Byrne's approach was limited in that their catalogue was essentially a

collection of anecdotes. In this way, Whiten and Byrne [1988]'s work made salient the need for more controlled experiments on primate theory of mind understanding. The decade that followed the Whiten and Byrne [1988] paper saw a flurry of such experiments, many of which revealed striking limitations in primates' understanding of psychological states [e.g., Anderson et al., 1996; Call & Tomasello, 1994, 1999; Cheney & Seyfarth, 1990; Kummer et al., 1996; Povinelli et al., 1991, 1994; Povinelli & Eddy, 1996]. In one example, Povinelli and Eddy [1996] found that chimpanzees who were given the opportunity to beg for food did so equally often from an experimenter who had an opaque bucket over her head and one who had a bucket next to her head; this result and others like it initially suggested that primates had a very limited understanding of the nature of seeing. Indeed, this overall pattern of data was strong enough to force Tomasello and Call [1997] to end their comprehensive review of the primate theory of mind literature by concluding that there was no convincing evidence that nonhuman primates understood the psychological states of other agents [for a similar conclusion, see Heyes, 1998].

Despite this early skepticism about primates' mindreading abilities, several researchers noted some discrepancies between the kinds of competencies observed in the field and those observed within the lab environment [e.g. Hare et al., 2001]. In addition, there was also evidence that at least some primates followed the direction of others' gaze in a flexible, non-reflexive manner. For example, Tomasello et al. [1999] reported that chimpanzees followed a human demonstrator's gaze geometrically, looking past distractor objects that were not within the demonstrator's line of sight as well as behind barriers. Furthermore, when chimpanzees followed others' gaze to a distal location and failed to find anything of interest, they would sometimes look back at the demonstrator, as if to verify that they were looking in the appropriate direction [Call et al., 1998]. This pattern of performance in gaze following tasks was at least consistent with the idea that primates possessed the ability to model others' visual perspective and thus possessed somewhat richer theory of mind capacities.

In an important paper, Hare et al. [2000] argued that previous theory of mind studies in primates failed to simulate the kinds of social problems that primates typically encountered in nature. To explore whether previously untapped competencies might be revealed in a more ecologically inspired social situation, Hare and colleagues conducted a series of experiments in which a subordinate chimpanzee competed with a more dominant chimpanzee for food. Hare and colleagues were primarily interested in whether the subordinate chimpanzee would use information about which foods the dominant chimpanzee could and could not see to strategically gain

access to food. Across a number of different experiments, Hare and colleagues found that subordinate chimpanzee subjects preferentially targeted food that was not visible to the dominant chimpanzee, suggesting that this species was sensitive to other individuals' perspectives. Hare et al. [2000]'s paper marked a sort of turning point in comparative theory of mind research [Whiten, 2013], ushering in a new wave of studies that used more ecologically valid testing paradigms, not just in chimpanzees but in other species as well [for reviews, see Call, 2007; Call & Tomasello, 2008; Rosati et al., 2010; Whiten, 2013]. We now turn to how this revolution shaped work on theory of mind in macaque monkeys, focusing particularly on work using the Cayo Santiago colony.

COGNITIVE WORK WITH A SEMI-FREE RANGING POPULATION: CHALLENGES AND BENEFITS

In some ways, the Cayo Santiago field station is not an obvious setting for the cognitive research required to study primate theory of mind. Typical cognition studies take place in lab environments, where it is possible to completely physically isolate a single individual from other group members, greatly minimizing the risk of interference. This allows laboratory-based test sessions to be quite long, since distractions are minimized and subjects' movements are restricted. Captive primate subjects can also be trained for months on various features of a task and can be presented with numerous control trials to gauge task understanding. The free-ranging Cayo Santiago colony presents quite a different testing environment. Monkeys in this population roam freely around an island, making it impossible to fully isolate any one individual. In addition, when testing a subject monkey in this population, researchers face a constant risk that a more dominant monkey will displace the subject or that a fight might break out between neighboring groups, causing the subject monkey to lose interest in the experiment. As a consequence, experimental sessions must be quite short, typically involving a single trial that takes no longer than a few minutes. This time limitation severely restricts the amount of within-experiment training that subjects can receive, meaning testing designs used on Cayo Santiago must often rely on behaviors exhibited spontaneously by the monkeys.

Nevertheless, recent work in the Cayo Santiago population clearly demonstrates that the challenges to cognitive work in this population are far outweighed by the benefits. Indeed, Cayo Santiago has some special features that make it an important resource for those interested in the cognitive abilities of primates. Perhaps most obviously, the Cayo Santiago Field Station provides the opportunity to

test primates living in an environment that is more similar to their natural habitat than is typically the case in psychological research [although for a discussion of some potential differences between the Cayo Santiago population and other rhesus macaque populations, see Maestriperi & Hoffman, 2012]. Whereas primates living in captive settings are often housed either alone or in small groups, the Cayo Santiago monkeys live in naturalistic and constantly fluctuating social networks [Brent et al., 2013]. Females are able to remain in their natal groups surrounded by kin, and males can transfer between groups throughout their lives, just as they would in wild populations [Drickamer & Vessey, 1973; Lindburg, 1971; Sade, 1972]. Although work specifically exploring how theory of mind skills vary between primate populations living in more or less species-typical environments is lacking, primates living in captivity do sometimes exhibit non-normative patterns of behavior. Note that this does not necessarily mean that we should expect free-ranging monkeys to outperform their captive counterparts on all cognitive tasks. Indeed, there is evidence that captive animals may actually perform better on some kinds of tasks, such as those that require them to solve novel problems or engage in exploratory behaviors [Reader & Laland, 2003]. Still, it is reasonable to hypothesize that the emergence of specific sociocognitive abilities may be in part dependent on the richness of an individual's social environment. As a consequence, primates living in captive environments with non-naturally sized social group structures may not exhibit the same competencies as their wild counterparts. Cayo Santiago also provides the opportunity to test a very large and diverse sample. Most cognitive experiments with primates lack sufficient sample sizes to be able to look at how different demographic variables affect performance. Cayo Santiago is home to hundreds of monkeys, all of which can be identified relatively easily using ear notches and tattoos. This means that researchers have access to a sufficient number of subjects to be able to detect sex-related variation in performance, as well as assess how cognitive skills differ across development [e.g., Hughes & Santos, 2012; see Rosati et al., 2014 for a discussion of the importance of these comparisons].

Further adding to the appeal of testing free-ranging primates like those on Cayo Santiago is the fact that researchers have been able to overcome many of the challenges of testing by flexibly adapting the techniques commonly used in comparative psychology. Just as in traditional lab settings, researchers on Cayo Santiago have figured out ways to use the monkeys' natural interest in desirable food items to tap into their cognitive capacities across a number of different domains [e.g., Santos et al., 2001; Santos et al., 2002]. Still, methods

that involve actively feeding free-ranging primates have some limitations. Whereas captive subjects are fed a significant proportion of their daily diet during test sessions in order to help motivate animals to participate in the task, food on Cayo Santiago must be provisioned very sparingly. As a consequence, researchers working on Cayo Santiago often used a methodology that doesn't require food provisioning: a technique known as the looking time method. The looking time method was originally developed for use with human infants. The logic of looking time is that individuals will look longer at events that they see as violations of the physical or social world. To date, hundreds of published studies have used the looking time method to test physical and social knowledge in both human infant [e.g., Hamlin et al., 2007; Kovács et al., 2010 ; Onishi & Baillargeon, 2005; Saxe et al., 2005; Wynn, 1992] and animal participants [e.g., Rochat et al., 2008; Santos et al., 2005, 2006a; Santos & Hauser, 1999; Uller, 2004; Uller et al., 2001; West & Young, 2002]. Using the looking time method on Cayo Santiago has proven particularly useful because it provides a minimally disruptive way to test the cognitive capacities of free-ranging monkeys [Cherries et al., 2006; Marticorena et al., 2011; Martin & Santos, 2014; Munakata et al., 2001; Santos & Hauser, 2002]. Furthermore, by modeling macaque studies on those conducted with human infants, researchers can more directly compare performance across these two populations.

THEORY OF MIND RESEARCH ON CAYO SANTIAGO

Rhesus macaques' understanding of others' perceptions

In one of the first studies to explore theory of mind abilities in the Cayo Santiago population, Flombaum and Santos [2005] developed a competitive foraging task modeled after that used by Hare et al. [2000] to test chimpanzees. Informal observations of the monkeys living on Cayo Santiago suggested that the monkeys were often hesitant to approach food items close to humans, suggesting that they viewed people as potential competitors. Flombaum and Santos [2005] reasoned the monkeys might think of humans as dominant individuals and thus might be more likely to take food that a human competitor was unable to see. To test this, Flombaum and Santos presented monkeys with two similar looking experimenters each holding a grape. Next, the experimenters simultaneously placed the grapes on small platforms and placed these platforms on the ground. Each then adopted a different position in relation to the food item. Critically, one of the experimenters was positioned such that he could see his grape while the other was unable to see his grape. The experimenters then held these positions

for one minute, or until the subject approached and took one of the grapes.

In the first experiment, one of the experimenters remained facing forward towards his grape whereas the other turned so that his back was to his grape. If monkeys understood that only the experimenter facing forward would be able to see them approach and take the contested food item, then they should prefer to steal from the experimenter whose back was turned. Overwhelmingly, this is exactly what the monkeys did. Although this pattern of performance was consistent with the possibility that the monkeys represented the competitors' visual perspective, subjects may have simply avoided the experimenter facing forward because they had learned that an agent oriented towards them was more likely to react to an approach. To address this, Flombaum and Santos [2005] conducted follow-up experiments in which the monkeys' understanding of visual perception was tested under a number of different conditions. In a second experiment, Flombaum and Santos tested whether monkeys would continue to steal from the competitor who could not see the contested food item even when both competitors adopted a similar orientation relative to the monkey. After showing the subject monkey a grape, each experimenter placed the platform holding the grape to his side rather than directly in front of him, and then oriented ninety degrees away from the monkey. One experimenter oriented towards the grape (so the grape was directly in front of him) and one oriented away from the grape (so the grape was directly behind him). Even though from the subject's perspective both competitors were in profile, monkeys still preferred to approach the one who had his back to the grape, suggesting that the macaques were taking into account the relationship between each competitor and the food item, rather than just responding egocentrically to the orientation of the competitor alone. Additional experiments revealed that monkeys were not just sensitive to the competitors' overall body orientation relative to the food, but to the role of the head and eyes specifically. In one experiment subjects even discriminated between an experimenter holding a small occluder over the eye region of his face versus one holding an occluder over his mouth, suggesting that they understood the role that objects play in visual occlusion. This overall pattern of performance in Flombaum and Santos [2005]'s studies is consistent with the interpretation that rhesus macaques understand that agents perceive objects in the environment that are within their line of sight and fail to perceive objects when visual access is blocked in a variety of ways. Thus, these data provide evidence that the monkeys are sensitive to not only gaze direction but also to visual perception—in other words, that rhesus macaques understand what others can see.

Of course, individuals can learn about the world using information acquired through many different

perceptual modalities, not just vision. Primates in particular often acquire information through auditory feedback. For example, specific calls or sequences of calls can aid in avoiding predators, locating food resources, maintaining group cohesion, and acquiring information about dominance relationships [for a review, see Zuberbühler, 2012]. Nevertheless, to date few experimental studies have tested whether primates are sensitive to what others can and cannot hear [although see Brauer et al., 2008; Melis et al., 2006]. This is somewhat surprising because many purported instances of primate deception in the wild involve the strategic suppression of auditory cues [Byrne & Whiten, 1990; Whiten & Byrne, 1988]. For instance, male chimpanzees may avoid making noise when patrolling their borders or hunting for monkeys [Boesch & Boesch-Achermann, 2000; Watts & Mitani, 2001], and females primates sometimes do not produce copulation calls when mating with a subordinate male in the vicinity of a more dominant one [de Waal, 1986; Hauser, 1990].

To explore whether rhesus monkeys would take into account what a human experimenter could hear in a competitive foraging task, Santos et al. [2006b] presented the Cayo Santiago monkey subjects with the option of taking a piece of food from inside a container that made a noise when it was contacted or from a container that made no noise. Subject monkeys first watched a human competitor baiting two containers with grapes. One of these containers had bells attached to it so the baiting process was quite noisy. The other container also had bells, but the balls inside the bells were removed so that the baiting of this second box was relatively quiet. After the experimenter had demonstrated the auditory properties of the two boxes, he knelt behind the boxes with his head and eyes down, rendering him unable to see the subject monkey or the containers. Santos and colleagues reasoned that if the monkeys understood that taking food from the noisy container would attract the attention of the experimenter but that taking food from the silent box would not, then subjects should prefer to approach the silent box. Monkeys showed exactly this pattern of performance, reliably avoiding the noisy container. Furthermore, on trials in which the competitor knelt with his head oriented upwards facing the boxes and the approaching monkey, subjects no longer showed a preference for the silent box. This control condition is important because it rules out a number of relatively simple explanations for monkeys' original preference. First, it shows that monkeys were not afraid of the noisy container and avoiding this container regardless of the orientation of the competitor. Second, it suggests that monkeys did not adopt a simple rule whereby they always avoided making noise when approaching a food item in the presence of the competitor. Instead, monkeys selectively avoided making noise only when auditory cues

were in the unique position of attracting the attention of an otherwise ignorant experimenter. This suggests that not only did the rhesus macaques take into account what the competitor could hear, but also that they were able to integrate this information with what the competitor could see in meaningful ways. In other words, rhesus monkeys seem to be able to flexibly combine representations of others' perceptual states from two separate sensory domains.

Rhesus macaques' understanding of others' knowledge and beliefs

Taken together, the results of Flombaum and Santos [2005] and Santos et al. [2006b] suggest that rhesus monkeys are sensitive to the visual and auditory perceptions of others. But do macaques also track what other agents have seen previously? In a now seminal study, Hare et al. [2001] tested whether subordinate chimpanzees would take into account what a more dominant chimpanzee had recently seen when competing for food, reasoning that if the subordinate represented the dominant's previous visual access, they would be more likely to try to retrieve a food item when the dominant lacked information about its location. Results showed that subordinates were indeed more likely to obtain food hidden in the absence of a dominant chimpanzee, treating the dominant partner as if he knew about the location of the food that he saw hidden previously and as though he was ignorant of food hidden in his absence.

To explore a similar capacity in the Cayo Santiago macaques, Marticorena et al. [2011] used a looking time method modeled after a previous study not with 15-month-old human infants [Onishi & Baillargeon, 2005]. Marticorena and colleagues presented monkeys with a small stage that had two opaque boxes on either side. The sides of the boxes facing the center of the stage were open to allow an object to enter them but the openings were covered with leaves making it impossible for either the subject or an experimenter to see the object once it was inside the box. In an initial study, monkeys saw the experimenter watch as a lemon traveled on a track into one of the two boxes. Once the lemon was inside the box, the experimenter reached either into the box where she had just seen the lemon hidden or into the opposite box. If monkeys expected the experimenter to act on the basis of what she had recently seen—that is, her knowledge—then they should be surprised when she searched in the wrong box. Consistent with this, monkeys looked longer at the display stage when the experimenter searched in the box that did not contain the lemon.

The results of Marticorena et al. [2011] suggest that like chimpanzees, rhesus monkeys understand that others' behavior will be guided by previous

perceptions. However, other studies have revealed a striking limitation on chimpanzees' mental state attributions: they systematically fail to take the beliefs of others into account [Call & Tomasello, 1999; Kaminski et al., 2008; O'Connell et al., 2003; although see Krachun et al., 2009 for limited evidence suggesting that chimpanzees may possess some implicit understanding of others' beliefs]. Primates' inability to represent others' beliefs is significant because an important feature of beliefs is they can be incongruent with the actual state of the world—that is, they can be false [e.g. Dennett, 1978; Pylyshyn, 1978]. Indeed, merely tracking what others have and have not seen (i.e. what researchers have referred to as understanding others' knowledge and ignorance) does not necessitate the ability to actively represent false content. Because of this, demonstrating sensitivity to the false beliefs of others is often considered to be the most powerful way to demonstrate mindreading capacities [e.g., Wellman et al., 2001]. For this reason, it is noteworthy that chimpanzees fail to track others' false beliefs. In one study, Kaminski et al. [2008] allowed a chimpanzee subject and a conspecific partner to watch food placed in one location. The food was then secretly moved to another location that the subject but not the partner watched. Kaminski and colleagues found that the subject chimpanzee failed to behave as if he expected his partner to search for the food in its original location. In this way, chimpanzees don't seem to realize that other conspecifics will act on the basis of their beliefs.

Unfortunately, most studies exploring belief understanding in primates to date have used active behavioral measures as the dependent variable of interest [e.g., Kaminski et al., 2008]. We know from work in human infants that such active behavioral measures sometimes mask cognitive capacities that can be observed using more sensitive looking time measures [e.g. Onishi & Baillargeon, 2005]. To test whether primates might demonstrate false belief understanding using a more sensitive looking time task, Marticorena et al. [2011] conducted a second experiment in which the experimenter had a false belief about the lemon's location: she thought the lemon was in one box when in fact it was in the alternative box. In this new experiment, monkeys saw the experimenter watch a lemon go into one of the boxes. Then, while the experimenter was hidden behind an occluder and unable to see the stage, the monkeys saw the lemon move into the other box. If the monkeys attribute a false belief to the experimenter then they should expect her to search in the original box for the lemon and should therefore look longer at the case in which the experimenter fails to act in a manner consistent with this belief. In fact, the monkeys looked equally long at the display when the experimenter reached into either of the two boxes [for similar results in chimpanzees, see Hare et al.,

2001; Kaminski et al., 2008]— they seemed to not make any prediction about where she should look for the lemon. This pattern of results is intriguing for several reasons. First, the monkeys did not simply expect the experimenter to search for the object where it was actually located; in this way, monkeys did not merely expect the experimenter to search where they themselves thought the lemon was. Second, monkeys on this task performed differently from 15-month-old-human infants; in contrast to human infants, monkeys showed no evidence of attributing a false belief to the experimenter.

Taken together with previous findings, these results suggest that monkeys understand that others have visual access but not beliefs. But why did monkeys fail to represent the experimenter's false beliefs in the Marticorena et al. [2011] task? One possibility is that monkeys failed to perform well on this experiment because the task was more complex than it needed to be. It is possible then that monkey might be able to track the experimenter's belief in a simpler task. Fortunately, human infant researchers have developed just such a task, one that has revealed evidence of belief understanding even in very young infants. Specifically, Kovács et al. [2010] developed a visual object detection task in which even 7-month-old infants seemed to automatically represent the belief of another agent. Infants were shown a video of a ball rolling around on a table. The ball sometimes went behind an occluder on the table, blocking it from view, and sometimes it rolled off the video screen entirely. The critical manipulation involved varying whether the infant and another cartoon agent depicted on the screen had a true or a false belief regarding the location of the ball. In the test portion of the trial the occluder was dropped to reveal that no ball was present. The surprising finding was that even when the infants themselves did not expect the ball to be behind the occluder, they looked longer when the agent falsely thought that the ball was behind the occluder compared to when the agent also knew that the ball was not there. Thus, infants' looking times were modulated both by their own belief as well as the belief of another agent, even when that agent's belief was completely irrelevant to the task.

Martin and Santos [2014] recently explored whether rhesus macaques in the Cayo Santiago population would successfully represent false beliefs when tested on this more streamlined Kovács et al. [2010] design. Using an apparatus similar to the one used in Marticorena et al. [2011], Martin and Santos presented subject monkeys with a series of events in which an experimenter observed an apple move across a stage between two boxes. Just as in the Kovács et al. [2010] study, the session ended when one of the boxes was revealed to be empty. Events were manipulated so that the empty box violated the belief of the subject monkey, the experimenter, or

both. Independently manipulating whether the monkey and the experimenter had a true or a false belief about the contents of the box allowed Martin and Santos to assess whether subjects' looking times were affected by only their own belief or also by the belief of the other agent. In contrast to the performance of human infants [Kovács et al., 2010], Martin and Santos found that the other agent's belief did not impact monkeys' looking behavior at all. These results suggest that monkeys do not track others' beliefs even when tested on a simpler belief representation test than that of Marticorena et al. [2011].

In sum, looking time studies on Cayo Santiago provide strong support for the hypothesis that primates' failures on false belief tasks are not the product of extraneous task demands but rather reflect a genuine limitation on their representational abilities. Although null results must always be interpreted with caution, these results provide some of the best evidence to date that primates may not be able to track the beliefs of others.

ISSUES OF INTERPRETATION

Up until this point, we have been discussing the results of experimental work on Cayo Santiago in relatively rich mentalistic terms. That is, we have suggested that the studies described above provide evidence that rhesus monkeys attribute (some) psychological states to other agents. It may come as no surprise to readers that this rich mentalistic interpretation is somewhat controversial. While most researchers agree that the Cayo Santiago macaques and other nonhuman primates show sophisticated performance on theory of mind tasks, there is much debate as to why these species show such successful performance. Some researchers have argued that primates' performance provides evidence for rather sophisticated cognitive capacities. Tomasello and his colleagues, for example, have argued that primates' behavior on theory of mind tasks shows that they represent basic psychological states such as intentions, perceptions, and knowledge [e.g. Buttelmann et al., 2007; Call, 2007; Call & Tomasello, 2008; Kaminski et al., 2008; Melis et al., 2006; Tomasello et al., 2003]. Along with our colleagues, we have endorsed a similar position in recent years [e.g. Rosati et al., 2010; Santos et al., 2006c]. Those who defend a mentalizing account of the data typically argue that although primates' behavior on any single study could in principle be explained via nonmentalistic processes, the most parsimonious explanation for the overall pattern of data would grant at least some primates an understanding of basic psychological states. Furthermore, it has been argued that the mindreading account of the data can uniquely predict not only primates' successes but also their failures in a way

that other nonmentalistic accounts cannot [Fletcher & Carruthers, 2013].

Other researchers, however, have argued against this sort of rich interpretation of primates' performance. This is because primates' performance on theory of mind tasks can often be explained by an appeal to "behavior reading" rather than mental state understanding [see Heyes, 2014a; Perner & Ruffman, 2005 for similar arguments]. Consider, for example, the performance of macaques tested in the Flombaum and Santos [2005] study. Some have argued that macaques in this study could have discriminated between the two experimenters without actually representing the two experimenters' mental states; instead, monkeys may have merely reasoned that agents do not respond in cases where they are not facing the food. Similarly, in Marticorena et al. [2011], monkeys could have succeeded merely by knowing that agents tend to search for objects in their true location in all cases in which they were oriented towards those objects when the objects were first hidden. Note that in neither of these examples do we need to make reference to any mental state information; in both cases monkeys merely use another agent's behavior to make the predictions needed for successful performance. These sorts of nonmentalistic interpretations pose a potential challenge for comparative psychologists interested in the evolutionary origins of theory of mind. In fact some primate researchers [e.g. Penn & Povinelli 2007, 2013; Povinelli & Vonk, 2003, 2004] are skeptical that the studies implemented to date could even in principle answer whether primates have a theory of mind, since all leave open the possibility that subjects are simply reasoning about a partner's observable behavior.

The ongoing debate concerning the exact representations underlying primates' performance on theory of mind tasks should not overshadow the fact that comparative researchers on both sides of the debate often agree on some important points. First, most researchers agree that many primates—including monkeys in the Cayo Santiago population—display a variety of impressive skills in social situations that researchers several decades ago would likely have found surprising [see Tomasello & Call, 1997]. Second, most researchers agree that whatever cognitive strategies primates employ to solve these social challenges likely rely on the use of abstract representations. In other words, explanations based on purely associated processes and unstructured monitoring of statistical relationships between various behaviors are unlikely to provide a satisfactory account of the data. Third, most scholars agree that there is currently no evidence that primates represent the beliefs of other agents. In this sense, primates' performance on theory of mind tasks is quite different from that of human infants even in their first year of life. Finally, despite the oft

used term “theory of mind”, primates’ understandings of other minds need not actually be fully human-like, theory-like, or involve the ability to reason about false representations to qualify, at least in a minimal sense, as mentalistic. Though there will certainly be scholars who disagree with one or more of these points, we do not think that these issues systematically separate those comparative psychologists who endorse a mindreading account from those that do not.

It is additionally important to keep in mind that the human theory of mind literature is subject to some of the same critiques that have been levied against the primate theory of mind work. Although experiments conducted over the past decade have demonstrated that infants are capable of sophisticated socio-cognitive reasoning on an impressive variety of tasks [for a comprehensive review of the literature, see Apperly, 2011], and many developmental psychologists interpret these studies as evidence that infants can reason about the contents of other minds, there are certainly those who disagree [Heyes, 2014a; Perner & Ruffman, 2005]. Indeed, even studies of theory of mind in adult humans may be open to multiple interpretations [Heyes, 2014b]. In this way, the issue of whether primates have a theory of mind is at least partially orthogonal to the issue of cognitive continuity. There may be cases in which there is good evidence that both humans and other primates are using the same kind of strategy to solve a particular social problem, but that opinions will differ regarding whether this strategy is properly mentalistic.

CONCLUSIONS AND FUTURE DIRECTIONS

Understanding the origin of the human mind presents an enormous challenge. We simultaneously marvel at the uniqueness of the human intellect and are astonished at how like us in their understanding of the world other species seem to be. As comparative psychologists, much of our work involves parsing out precisely which cognitive capacities are unique to humans and which are shared more widely across species. In doing so, the goal is not simply to delineate those abilities that set us apart from other animals, but also to shed light on the evolutionary history of our own cognitive architecture and to enable scientists to develop more informed hypotheses regarding the contexts under which different sets of cognitive skills are likely to have evolved.

As we hope to have demonstrated, over the past decade the Cayo Santiago Field Station has produced a number of exciting discoveries regarding primates’ theory of mind capacities that are relevant to these challenging questions. Specifically, rhesus macaques seem to understand something about the nature of others’ visual perceptions, even demonstrating sensitivity to the position of a human competitor’s eyes

alone when competing for food [Flombaum & Santos, 2005]. This population of macaques is also able to integrate representations of others’ perceptions across two separate sensory modalities and to use these representations in strategic ways [Santos et al., 2006b]. Finally, rhesus monkeys attribute knowledge to other individuals based on what they have seen in the recent past, but they fail to understand that other can have beliefs that differ from their own [Marticorena et al., 2011; Martin & Santos, 2014]. Thus, while clearly not possessing a fully human-like theory of mind, rhesus macaques do behave in ways that suggest they may attend to the unseen psychological causes of behavior.

Despite these intriguing results, it is worth noting that to date most of the cognitive studies conducted on Cayo Santiago have not taken advantage of one of the most unique features of the site—specifically, the fact that it affords the opportunity to test an unusually large and diverse sample. One exciting future direction could therefore involve documenting in detail species-typical patterns of socio-cognitive development in rhesus macaques. This is important because investigating interspecies variation in development can provide important insights into the mechanisms underlying theory of mind capacities in nonhuman primates and the extent to which these mechanisms may be conserved across phylogeny [Gomez, 2005; Rosati et al., 2014; Wobber et al., 2014]. For example, one striking finding from the human literature is that different skills related to theory of mind emerge in a relatively fixed order across ontogeny. Testing whether primates show the same kind of consistency in development will undoubtedly be critical to evaluating various hypotheses concerning human uniqueness [Rosati et al., 2014; Wobber et al., 2014]. Fortunately, the large population of macaques living on Cayo Santiago provides researchers with the opportunity to address just this kind of question. Another area where developmental work in primates will be critical concerns the development of gaze following skills, a critical prerequisite to developing theory of mind capacities [Baron-Cohen, 1995]. Although current work suggests that macaques begin to follow gaze around six months of age and do so with increasing sophistication throughout the life course [Ferrari et al., 2000, 2008; Teufel et al., 2010; Tomasello et al., 2001], we do not yet know how this developmental timeline relates to rhesus macaques’ performance on a variety of other mindreading tasks, such as those that require subjects to use information about others’ perceptions strategically. Furthermore, little work has addressed how macaques develop the ability to integrate representations of others’ knowledge states into their gaze following behaviors. Exploring these and similar questions can help researchers assess the interdependence of different skills.

Future work on Cayo Santiago can also shed light on the extent to which primates exhibit individual differences in their propensities to attribute psychological states to others. Humans, for example, are known to exhibit sex differences in mentalizing [e.g., Baron-Cohen, 2002], but it is unclear whether similar variance characterizes the performance of other primates [although see Hermann et al., 2007]. In addition, little work has explored how other biologically relevant traits—factors such as dominance rank, social network position, and reproductive success—are related to cognitive abilities like theory of mind. Exploring relationships between specific cognitive abilities (or suites of abilities) and these types of factors is of interest since an organism's cognitive architecture is generally assumed to have evolved in response to the challenges it has faced throughout its evolutionary history. Linking performance on cognitive tasks to real world outcomes can provide researchers with insights into the precise nature of these relationships and the contexts under which they are likely to obtain. In the case of primates, exploring the connection between social cognition and other biologically relevant factors is of particular theoretical interest. Indeed, if primates evolved superior cognitive skills and large brains in response to the challenges posed by complex social environments [e.g. Jolly, 1966; Humphrey, 1976], then we might expect to find some evidence that superior socio-cognitive skills are linked to greater reproductive success. The Cayo Santiago population's large colony, which varies along a variety of individual difference dimensions [e.g., Brent et al., 2013], affords a unique opportunity to test these predictions and explore the connection between reproductive dimensions and theory of mind capacities.

In sum, although much debate remains concerning how primates make sense of their social world, we have seen major strides in understanding how primates think about the actions of others. As reviewed above, the unique population of free-ranging monkeys living on Cayo Santiago has provided important insights in this domain, offering new experimental evidence as to how monkey social cognition is both similar to and different from that of humans. The next decade of work on theory of mind in the Cayo Santiago monkeys promises to be equally valuable in helping us gain further insights into the factors that allow primates to make sense of the minds of others.

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