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Theory of Mind in the wild

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Theory of Mind (ToM) — the ability to infer others' mental states — is a fundamental part of human social cognition. For decades, researchers have studied whether nonhuman primates have similar representational capacities. While the majority of studies investigating nonhuman primate ToM have been conducted with captive populations, this review focuses on the insights gained from work with two naturally living populations: rhesus macaques (*Macaca mulatta*) at the Cayo Santiago research station and chimpanzees (*Pan troglodytes*) in Budongo Forest. Not only have these two populations provided further evidence that nonhuman primates track the mental states of other agents, but also they have improved our understanding of the representational differences between human and nonhuman ToM, specifically in cases that involve tracking the perspective of others. Future work with these and other non-captive populations should take advantage of the breadth of nonhuman primate social behaviors to delve into the nuances of their ToM.

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Introduction

When a rhesus macaque sees a conspecific looking at a coconut, does he represent the conspecific's knowledge of that desirable food? When a chimpanzee covertly mates with a subordinate male behind a rock, can she represent the ignorance (or even the false belief) of a nearby dominant male? For more than 40 years, researchers have debated whether nonhuman primates (hereafter primates) understand and predict others' behaviors by attributing mental states to those other agents — a capacity known as Theory of Mind (hereafter ToM; [1]).

While many reviews to date have explored the nature of ToM in primates (e.g. [2,3]), the goal of this review is to specifically discuss the contributions of ToM studies conducted with wild primate populations. Work with naturally living populations offers several advantages relative to studies conducted with captive populations. First, testing primates in naturalistic conditions allows researchers to study primates' cognitive abilities under more ecologically valid conditions. In addition, more naturalistic contexts may increase subjects' motivation on tasks, revealing cognitive competencies that may be masked in captive settings. Some field sites also boast large populations of primates enabling researchers to collect larger sample sizes and to have the opportunity to run one-shot single-trial experiments. In this way, studies with naturally living primates provide a valuable compliment to studies with smaller captive populations.

As we review in detail here, naturally living populations have revealed important nuances in the representations underpinning primate ToM as well as limitations in our understanding of when and how primates might use ToM in more naturalistic contexts. We argue that studies with wild and free-ranging populations can allow researchers to test ToM competence across a broader range of mental states and naturalistic social interactions.

Bringing the lab to the field: exploring knowledge representation on Cayo Santiago

Imagine that you watch as a friend places a new plant on her windowsill. You now represent that friend as having *knowledge* of the plant's location. Moreover, she will still know the plant's location even if she leaves her house, even if the plant's leaves change color, even if the plant wilts, and even if you move the plant to water it and then place it back in the same spot on the windowsill.

Knowledge representations like these are a fundamental component of the larger set of ToM abilities that our own species possesses, and over the last decade, primate researchers have explored this capacity in greater detail . However, despite a wealth of research showing that primates can predict the behavior of knowledgeable agents [4–10], there is still much debate about whether primates make such predictions using the same representations as humans. Many scholars have historically treated knowledge representation as a binary capacity (e.g. a given primate species either can or cannot represent other agents as knowledgeable or ignorant, see Refs. [8–10]), while newer work has argued that some primates may have a partial understanding of others' knowledge states, which may be more fragile [11–15]. For this reason, it has become even more important to carefully examine exactly how primates — especially those in naturally living populations — represent what other agents do and do not know.

Researchers have recently started to investigate the nuances of knowledge representation in the free-ranging rhesus macaques (*Macaca mulatta*) living on Cayo Santiago ([16]; Figure 1). Researchers testing monkeys in this population take inspiration from developmental psychology methods to test these free-ranging primate subjects. In one common method — the looking time task — researchers measure monkeys' duration of looking as they watch a human demonstrator witness a desirable reward — in this case, a lemon — hidden inside one of two boxes (Figure 2a). Subjects then see the demonstrator reach either into the box where the lemon is hidden (expected event) or into the empty box (unexpected event; Figure 2b). Several studies have found that subjects look longer when the demonstrator reaches into the empty box, suggesting that macaques expect a knowledgeable demonstrator to search where the lemon is located [4,10].

Horschler and colleagues [11,12] have built upon this simple paradigm to examine the limitations of primate knowledge representations: under what circumstances will rhesus macaques continue to expect an agent to act consistently with their prior knowledge, despite changes happening outside of that agent's visual access? In one study, a human demonstrator watched as a lemon moved into a box. The demonstrator's view was then blocked and only the subject saw the lemon move out of and then back into the same box (Figure 2c). A human participant witnessing this display would naturally predict that the demonstrator still knew where the lemon was, but macaque subjects showed a different effect. Even though this change did not affect the lemon's final location, the monkeys no longer expected the demonstrator to reach correctly to the lemon's actual location [12]. Critically, however, when the demonstrator watched the lemon's movement directly, macaques maintained their expectation, suggesting that they expect the demonstrator to dynamically update their representation of the reward's location in this case [4,6]. These results provided the first evidence that rhesus macaques' representations of other agents' knowledge are more fragile than those of humans.

In a follow-up study, Horschler et al. [12] explored the specific kinds of changes that cause macaques to stop representing the demonstrator as knowledgeable — would *any* change in the scene occurring outside of the demonstrator's awareness be sufficient to interrupt the macaques' attribution of knowledge to the demonstrator? In this experiment, macaques watched a similar sequence of events as described above, but instead of the lemon moving, the box containing the lemon flipped open and closed (Figure 2d), creating a brief change in the scene that did not affect the location of the reward. Even though the box flip occurred outside of the demonstrator's awareness and lasted for the same duration as the lemon movement in the previous study, subjects continued to treat the demonstrator as knowledgeable and expected the demonstrator to reach to the box where the lemon was located. Therefore, even though primates' attributions of knowledge may be more fragile than humans', not all changes are sufficient to interrupt their knowledge attribution.

Figure 1

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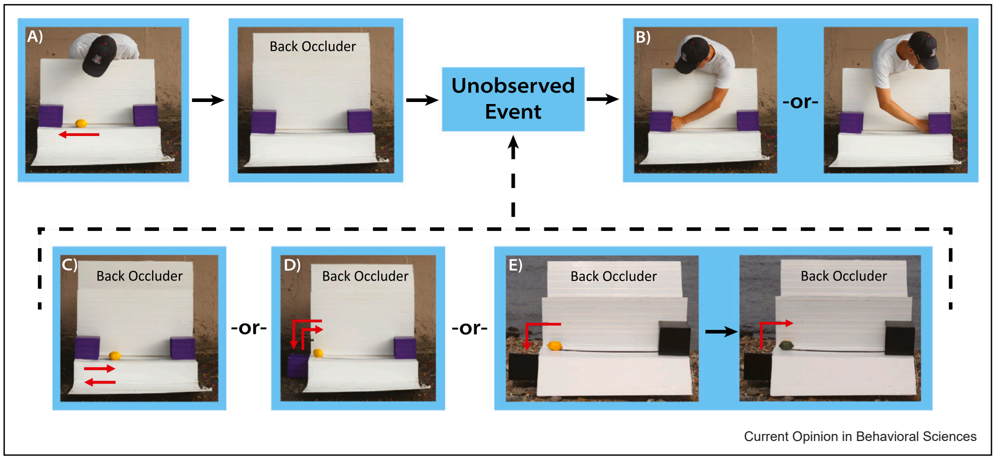
During ToM studies on Cayo Santiago, free-ranging rhesus macaques have their gaze recorded as they watch a demonstrator interact with objects on a small stage. The question of interest is whether macaques represent the knowledge state of the demonstrator.

Figure 2



A depiction of the studies conducted by Horschler et al. [11,12]. In conventional tests of knowledge-tracking (e.g. [4]), **(a)** first, a demonstrator watches as a lemon moves into a box, **(b)** then the agent either reaches towards the correct or incorrect box. In order to test what types of events interrupt primates' representation of the demonstrator's knowledge, different changes occurred in between the agent seeing the lemon being hidden **(a)** and the final reach **(b)**. In each manipulation, a back occluder was raised so that the demonstrator could not see what was happening on the stage. In one study, either **(c)** the lemon moved out of the box and then back into the same box, or **(d)** the box itself flipped open and closed while the lemon remained stationary. Similarly, in another study, **(e)** the lemon changed color when the demonstrator was not looking.

These two changes, however, only temporarily manipulated the physical location of objects in the scene outside of the demonstrator's awareness. Humans, on the other hand, can track what others know about an object's location even when features of the object itself change (e.g. when a plant wilts, as discussed above). Do primates also expect an agent to know something about an object's location even after the object's features change outside of the agent's perceptual access? Surprisingly, the answer seems to depend on which features change. Horschler and colleagues [11] found that when an object changes color outside of the demonstrator's visual access (e.g. a lemon changing from yellow to green, Figure 2e), rhesus macaques continue to expect the demonstrator to maintain their prior knowledge of the lemon's location and to reach to the correct box. However, when an object changes shape outside the demonstrator's visual access (e.g. a flower blooms and consequently increases in size), then the macaques do not expect the demonstrator to reach towards the correct box [11]. These findings again suggest that primates' representations of others' knowledge are more easily interrupted than humans', but not all changes in a scene cause them to treat an agent as ignorant.

Taken together, these findings suggest that primates' knowledge representations may be importantly different from those of humans. When an object changes its size or temporarily shifts location outside of an agent's awareness, rhesus macaques no longer expect a previously knowledgeable agent to search for the object in its correct location. These and related findings [9,10,13] have prompted some researchers to argue that rather than representing *knowledge* per se, primates may instead have a more basic, fragile representation of others' 'awareness' [14,15]. Crucially, these awareness representations seem to have an on/off quality: any change to what an agent was previously aware of seems to disrupt primates' representation of that agent's awareness. To see this on/off quality of awareness representations in action, consider how you might track your friend's knowledge of the location of her plant as described in the example above. Under an awareness representation account, you would begin by attributing an awareness representation to your friend — she started off as *aware* of the plant's location — but if the plant wilted while she was away, this change to the scene would cause you to drop your representation of your friend's awareness. As such, when your friend returns, you would have no prediction about whether she would still know where the plant was (and importantly you would not be surprised by any of her plant-directed behaviors because you have no expectations to be violated). Researchers have argued that this awareness representation account of primate ToM abilities also explains primates' lack of egocentric errors on past false belief tasks (e.g. [9,10] but see Ref. [17]).

The findings of Horschler and colleagues [11,12] thus provide insight into what specific scene changes might break primates' awareness representations, and hints about how primates' capacities may critically differ from humans' more robust knowledge representations. These findings also help clarify some long-standing debates about the richness of primates' mental state representations. Historically, discussions of primates' performance on ToM tasks have centered around two types of competing hypotheses: rich mentalistic accounts that propose that primates possess human-like ToM capacities and more deflationary non-mentalistic accounts that argue that primates succeed on ToM tasks using simple behavioral rules (e.g. if a competitor orients towards a piece of food, they will then approach it; [18]) or domain-general mechanisms (e.g. automatic attention and encoding of certain event configurations, which apply to even non-social situations; [19]). The findings from the Cayo Santiago rhesus macaques provide a further possible account that can be viewed as an intermediary between these alternatives. If primates are indeed representing agents' awareness, then this capacity is more limited than human-like knowledge representation, but it is still rich enough to track the behavior of other agents by representing an unobservable mental state (i.e. awareness).

When do nonhuman primates track the mental states of others?

The work on Cayo Santiago adapts human developmental methods for use in the field. As such, these studies focus on tightly controlled variations of a simple reaching event. Although this approach has proved beneficial in understanding the limitations of primate ToM, it leaves open significant questions about when primates might use their ToM in more naturalistic contexts with conspecifics. Humans use their ToM to predict and understand others' behavior across a wide range of social situations: we use it to outsmart competitors [20], to understand others' ambiguous communicative utterances [21,22], to evaluate others' actions [23,24], and to decide what to teach others [25,26]. Until recently, most tasks examining primate ToM have used just a small subset of these situations: usually competing against a conspecific for a food reward [7–9,13,27] or predicting how an agent will search for a food reward [4,10]. Indeed, ToM tasks using non-competitive situations with captive populations have produced mixed findings [28–32]. Therefore, it is unclear whether primates can robustly track others' mental states outside of contexts involving food competition. Recently, however, work with chimpanzees (*Pan troglodytes schweinfurthii*) in Budongo Forest has improved our understanding of how chimpanzees employ their ToM representations in other types of social interactions [33,34].

Crockford and colleagues [33] tested whether chimpanzees track what their group members have seen and whether they try to inform ignorant group members of a nearby threat. Researchers placed a plastic snake in the path of a group of chimpanzees. When one chimpanzee saw the snake, that individual was significantly more likely to produce an alarm call if their group members were unaware of the snake compared to when the group members had already seen the snake or heard an alarm call. This field study provided the first evidence that chimpanzees track others' awareness of potential threats in the environment and use that representation to selectively inform group members that are unaware of the danger.

However, since the chimpanzees could see their group members prior to producing an alarm call, it is possible that subjects were engaging in a sophisticated form of behavior-reading. That is, they could have been responding to their group member's behavior, rather than representing and responding to their group member's knowledge. To rule out this alternative, Crockford et al. [34] conducted a follow-up that simulated the presence of a knowledgeable or ignorant group member. Before a subject could see the snake, a prerecorded call from a group member was played on a nearby speaker. Subjects either heard a rest hoo (a control call that is irrelevant to the snake) or an alert hoo (indicating that the group member was reacting to and aware of the snake). Although the chimpanzees could not see the behavior of their nearby 'group member,' they produced significantly more alarm calls when they heard a rest hoo relative to when they heard an alert hoo.

Although researchers have studied the flexibility of primate vocalizations for decades [35–39], Crockford and colleagues' elegant field studies are the first to suggest that ToM may play a critical role in the production of some vocalizations. However, some have argued that this pattern of vocalizations could be the result of the signaler's own arousal rather than their capacity to represent a group member's awareness. Under this deflationary account, subjects who heard the pre-recorded alert hoo may have vocalized less because they were unsurprised when they actually encountered the snake since the call had already alerted them to the threat. Although further work is needed to clarify why chimpanzees increased their vocalizations after hearing a rest hoo (see Refs. [33,35] for additional evidence against this account), it is worth noting that chimpanzees also exhibit other behaviors in this context which suggest that they are tracking the awareness of their group members. Specifically, both when an actual group member and an implied group member were unaware of the snake, subjects were more likely to shift their attention towards their recipient and 'mark' the location of the snake by pausing near the threat and alternating their gaze between the snake and their group member. Additionally, when subjects were in the presence of a real ignorant group member, they most often stopped marking the threat once the group member also emitted an alert hoo. This further suggests that chimpanzees not only track whether conspecifics are aware of a nearby threat, but they also use that representation to shape their signaling behavior to inform ignorant group members.

Future directions

While studies with wild and free-ranging populations can be challenging to design and execute [40], they offer a valuable compliment to the methods employed with captive primate populations. In this short review, we only touched on work from two such sites, but there are a number of other research programs that have contributed to our understanding of social cognition in a broader range of species and contexts (e.g. Inakwu Vervet Project [41], the Okavango Delta baboons [42], and Barbary macaques in the Trentham Monkey Forest [43]). Further investigations with wild populations of primates should continue to delve into the nuances of ToM representations and their use across different social contexts. For example, future work would benefit from exploring primate goal inference, which — like knowledge representation — is a rich capacity [44–48], but has been under-studied in nonhuman subjects. Past studies hint that primates attribute goals to other agents [49–51] and expect other agents to pursue those goals using the most direct path [52,53], but little work to date has explored whether primates' expectations share the same structure as human goal inferences, such as the assumption that agents will behave in ways that are utility-maximizing [45,54]. Similarly, work with wild primate populations offers the exciting opportunity to study ToM in new social contexts. For example, anecdotal reports of deictic manual gestures (which may be used informatively; [55]) and deceptive vocalizations during infant-handling interactions [42] represent only two of the diverse behaviors that may also be supported by attributing mental states to conspecifics.

Over 40 years ago, researchers asked "Does the chimpanzee have a theory of mind?" Now, thanks in part to studies conducted with wild and free-ranging primate populations, researchers are learning new answers to even more nuanced questions about primate ToM. Scholars have begun exploring not just whether primates represent others' knowledge, but whether those knowledge representations are robust in the same way as humans' knowledge representations. Researchers are also using wild populations to explore whether primates use their knowledge representations outside of food competition contexts. The initial answers to these questions to date have given researchers new insight into primate ToM and have set the groundwork for future studies and new theoretical frameworks.

Conflict of interest statement

Nothing declared.

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• of special interest
•• of outstanding interest.

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