Mentalizing in Nonhuman Primates

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Humans effortlessly infer the mental states of other agents, spontaneously making swift and accurate predictions about how others will act based on these inferences. These theory of mind capacities are early emerging, with human infants beginning to make accurate predictions about how other agents should act based on the other agent's mental states within the first 2 years of life (Buttelmann, Carpenter, & Tomasello, 2009; Helming, Strickland, & Jacob, 2014; Luo, 2011; Onishi & Baillargeon, 2005; Scott & Baillargeon, 2017; Sodian, 2011). The end result is a sophisticated set of social cognitive abilities that make the human species an outlier in most domains, especially in terms of our hyper-collaboration and unique cultural evolution (Seed & Tomasello, 2010; Tomasello, 2000; Tomasello, Carpenter, Call, Behne, & Moll, 2005).

But are humans alone in our capacity to represent the minds of others? Or do we share at least some of our mentalizing capacities with our closest living relatives, the nonhuman primates (hereafter, primates). Like humans, most primate species live in large social groups, and thus it would be adaptive as for socially living primates to share many of the same theory of mind abilities of humans (Byrne & Bates, 2010). For the past four decades, researchers have devoted much empirical effort to testing whether primates share human-like mentalizing abilities (see reviews in Call & Tomasello, 2008; Krupenye & Call, 2019; Rosati, Santos, & Hare, 2010). Here, we explore what this research has taught us a date, with the goal of providing a unified account of what primates do and do not understand about other agents' mental states.

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M. Gilead, K. N. Ochsner (eds.), *The Neural Basis of Mentalizing*,
https://doi.org/10.1007/978-3-030-51890-5_7

Four Decades of Primate Theory of Mind

Over 40 years ago, Premack and Woodruff (1978) were the first to ask whether chimpanzees possess a theory of mind. Their seminal work attempted to investigate the mentalizing abilities of a single chimpanzee, Sarah, using a series of tasks involving videos of a human facing a problem (e.g., being stuck in a locked cage) and subsequent photographs of possible solutions to the problem. Sarah chose the photograph that depicted the correct solution to the problem, which Premack and Woodruff interpreted as evidence that Sarah recognized both the experimenter's mental state (i.e., his intentions), as well as what was needed in order to fulfill the experimenter's goal.

Although many have debated Premack & Woodruff's initial interpretation of these findings (e.g., Dennett, 1978; Pylyshyn, 1978), their seminal paper launched several decades of work on the development of these abilities across human infancy and childhood (e.g., Astington & Gopnik, 1991; Flavell, 1999; Gopnik & Wellman, 1992; Wellman & Woolley, 1990; Wellman, Cross & Watson, 2001), which has revealed much about how mentalizing arises over the lifecourse and the different component processes that human children develop in order to represent the mental states of others (e.g., Wellman & Liu, 2004; Scott & Baillargeon, 2017; Sodian, 2011). Simultaneously, Premack and Woodruff launched a long line of work investigating the mentalizing capacities of nonhuman primates as well (see reviews in Call & Tomasello, 2011; Krupenye & Call, 2019; Rosati et al., 2010). Here, we explore what that work has shown about primate mentalizing. Throughout, we'll argue that understanding the combined (and often confusing) pattern of primates' successes and failures on these tasks will help us better understand not just how primates think about other minds but what primates can tell us about human mentalizing representations as well.

Representing that Agents Are Aware

Much of our human theory of mind reasoning involves tracking what other individuals are *aware* of: we track whether others share the same information we have, whether someone has noticed our indiscretions, and whether we need to inform our friends of new heretofore unknown gossip. Much research in human development has shown that this capacity to track what others are aware of emerges surprisingly early in human development. Human infants are able to track what others are looking at (Hains & Muir, 1996; Hood, Willen, & Driver, 1998; Symons, Hains, & Muir, 1998) or have seen in the past (Luo & Johnson, 2009; Song & Baillargeon, 2007; Song, Baillargeon, & Fisher, 2005) and use this information to make informed predictions about how an agent will act in the future (e.g., Onishi & Baillargeon, 2005). But do nonhuman primates share this capacity to represent awareness in others? As we review below, a number of studies using a variety of different kinds of tasks appears to converge on clear evidence that primates share this awareness representation capacity with humans (Crockford, Wittig, Mundry, & Zuberbühler, 2012; Flombaum & Santos, 2005; Hare, Call, Agnetta, & Tomasello, 2000; Hare, Call, & Tomasello, 2001, 2006; Hattori, Kano, & Tomonaga, 2010; Hirata & Matsuzawa, 2001; Hostetter, Russell, Freeman, & Hopkins, 2007; Kaminski et al., 2008; Karg, Schmelz, Call, & Tomasello, 2015; Marticorena et al., 2011; Melis, Call, & Tomasello, 2006; Santos, Nissen, & Ferrugia, 2006; Schmelz, Call, & Tomasello, 2011).

Gaze Following Tasks

Eyes serve as the window to what other social agents' are aware of. As such, researchers have long considered attention to others' faces and direction of gaze to be a foundational skill needed for a rich understanding of others' awareness (Wellman, 2011). For this reason, much of the early empirical work testing primates understanding of others' awareness began by exploring whether primates are able to follow the gaze of another individual. This work has shown that gaze following is widespread across the primate order, with many species of primates naturally following the gaze of conspecifics and human experimenters (apes: Povinelli & Eddy, 1996; Tomasello, Call, & Hare, 1998; Old World monkeys: Emery, Lorincz, Perrett, Oram, & Baker, 1997; Tomasello et al., 1998; New World monkeys: Burkart & Heschl, 2006; Neiworth, Burman, Basile, & Lickteig, 2002; prosimians: Sandel, MacLean, & Hare, 2011; Shepherd & Platt, 2008; Ruiz, Gómez, Roeder, & Byrne, 2009; Botting et al. (2011), for a review, see Rosati & Hare, 2009). Nevertheless, as many scholars have pointed out (Friesen & Kingstone, 1998; Penn & Povinelli, 2007), success on a gaze following task may not be indicative of a sophisticated understanding of others' awareness and may instead be nothing more than a reflexive process (i.e., co-orienting without any sort of meaningful representation of the content of the gaze). For this reason, primate researchers have developed more complex gaze following tasks, ones that require subjects to follow gaze towards a specific target object, often around a barrier or through a window. Such new geometric gaze following tasks require subjects to recognize that there is a *referent* to an agent's gaze (i.e., that the agent is *aware of something*, not just looking in some direction). While early work with great apes demonstrated our closest living relatives shared our human-like ability to geometrically gaze follow (Bräuer, Call, & Tomasello, 2005; MacLean & Hare, 2012; Okamoto-Barth, Call, & Tomasello, 2007; Tomasello, Hare, & Agnetta, 1999), more recent work has found evidence for this capacity in more distantly related monkeys as well (Amici, Aureli, Visalberghi, & Call, 2009; Bettle & Rosati, 2019).

In an even more direct use of gaze following to test whether primates represent others' awareness, MacLean and Hare (2012) tested chimpanzees on a modified gaze task where they directly varied whether the agent was aware of a target object. Specifically, the researchers varied whether the object a surprised agent looked at was novel (a toy she was unaware of and had never seen before) or familiar (one she had just seen, and thus should be uninterested in). If subjects understand that individuals rarely get surprised by objects they are aware of, then they should assume that the target object is the referent of the agent's gaze in the novel condition but not the familiar condition. Chimpanzees (and in later studies, rhesus monkeys, see Drayton & Santos, 2017) showed just this pattern of performance—they assumed that the agent was looking at the object in the ignorant condition (and just followed her gaze to the object) but assumed the agent must have a different referent when she was familiar with the object (and thus tracked her gaze beyond the object and out into open space). In this way, gaze following work shows that several primate species seem to gaze follow based on what a human experimenter is aware of and is not solely a reflexive reaction.

Competitive Tasks

Researchers have also observed evidence of primates' understanding of others' awareness using competitive tasks, where subjects must take into account what other agents are aware of when competing for resources in naturalistic situations (Bräuer et al., 2006; Flombaum & Santos, 2005; Hare et al., 2000, 2001; Kaminski et al., 2008; Santos et al., 2006, see Hare & Tomasello, 2004 and Lyons & Santos, 2006 for a review of these competitive tasks).

In the first of such tasks, Hare et al. (2000) placed dominant and subordinate chimpanzees into competition over two food rewards. The subordinate subject was able to see the position of both food rewards, while the dominant individual could only see one. If subordinates are able to track what dominant chimpanzees are aware of, then they should be more likely to steal food that the dominant individuals can't see. Hare et al. (2000) found that subordinate chimpanzees performed well on this task, successfully using information about what others were aware of during competition (see also Hare et al., 2001; Kaminski, Call, & Tomasello, 2008). Flombaum and Santos (2005) used a similar competitive design with free-ranging rhesus monkeys; they found that monkeys preferentially stole food from a human agent whose visual access was obscured (e.g., by turning away from the food, occluding the experimenter's face) but not from an agent who was aware of the location of the food.

Santos et al. (2006) tested the same macaque population on an auditory version of this stealing task. Monkeys could steal from one of two boxes in front of a human competitor: a *silent* box that opened and closed quietly or a *noisy* box covered in jingle bells that made noise when touched. If monkeys understand that noise can cause an unaware agent become aware, then they should preferentially steal from the silent box. Monkey showed just this pattern of performance, suggesting they are able to incorporate an additional sensory modality (audition) when considering another agent's awareness state (see also Melis et al., 2006 for similar results in apes).

Looking Time Tasks

Evidence that primates can accurately predict how another agent will act based on their awareness also comes from violation of expectation tasks (Drayton & Santos, 2018; Arre, Stumph, & Santos, 2021; Horschler, Santos, & MacLean, 2019; Arre, Clark, & Santos, 2020; Marticorena et al., 2011; Martin & Santos, 2014; for a review, see Drayton & Santos, 2016). Modeled off similar tasks used in human infants (e.g., Onishi & Baillargeon, 2005), the logic of these studies is that subject will look longer at events that violate their expectations compared to control scenes where no expectations are violated. In one study (Marticorena et al., 2011), rhesus monkeys watched as a human agent saw an object slide into one of two boxes. The agent then performed one of two actions: she reached into the box with the object (which should be consistent with her awareness that the object is in the box) or she reached into the empty box (and thus acted inconsistently with respect to her awareness of the object's location). Martincorena and colleagues found that macaques looked longer at the unexpected condition in which the experimenter reached towards the empty box, suggesting that they expect agents to act in accord with their visual awareness.

In another example, Drayton and Santos (2018) used a rotational displacement display to test whether subjects expected an agent to update their awareness of where an object was located. In this task, subjects saw an experimenter hide a piece of food in one of two boxes and then both the subject and the experimenter watched the two boxes rotate 180°. If monkeys understand that people can flexibly update what they're aware of, then they should expect the agent to reach in the object's newly displaced location rather than the original location. Monkeys showed just this expectation, looking longer when the agent reached in the original box. Importantly, rhesus monkeys only expected the agent to know the location of the hidden object when she herself had witnessed the difficult rotational displacement. These results suggest that primates recognize that awareness comes from perceptual access to a relevant event, and further, that primates' perceptual awareness representations are malleable when the context calls for it.

Taken together, a number of comparative studies using a variety of different methodologies presents clear evidence that primates are able to track what others are aware of. In addition, this work also suggests that primates' representations of other agents' perceptual awareness are multimodal and flexible, suggesting a robust mechanism that can update online as the subject gains more information about the other agent. Moreover, there is clear evidence that primates are further able to use these awareness representations both to make predictions about how agents will act in the future, and to determine their own best course of action in the social world.

Representing Others' Beliefs

Adult humans spend considerable time thinking about how another agent's subjective (and sometimes incorrect) worldview might influence their behavior. This striking ability to represent other individuals' *belief* states in this way requires that we generate both our own representation about the world, as well as another agent's potentially untrue or unfounded belief. Perhaps surprisingly given the complexity of these representations, researchers have observed such belief state representational abilities in infants younger than 15 months (for a review, see Scott & Baillargeon, 2017, although see Baillargeon et al., 2018, Poulin-Dubois et al., 2018, and Powell et al., 2018 which review some controversy about these findings). Using a nonverbal looking time version of the famous Sally Anne Task (Wimmer & Perner, 1983), Onishi and Baillargeon (2005) tested whether infant make predictions about how an experimenter should act based on what she believes. Fifteen-month-olds watched as a human agent witnessed a toy disappear into one of two locations. The agent then had her visual perspective occluded so that she could not see the presentation stage. While the agent was occluded, the infant saw the toy then move from its original location to the opposite location. Onishi and Baillargeon found that 15-month-olds looked longer when the agent reached into the *actual* location of the toy. In this way, infants seemed to expect that the agent should falsely believe that the object was in the first original location. Infants as young as 10 months old (Luo, 2011) have shown success on this and related tests of false beliefs (see review in Scott & Baillargeon, 2017), but what about primates? Do they also successfully represent others' beliefs?

Competitive Tasks

The earliest work exploring false belief capacities in primates tested these abilities in the context of a competitive food task. Kaminski et al. (2008) tested two chimpanzees on a turn-taking game in which they manipulated how much information each subject had about the content of three buckets on the table. Specifically, the researchers tested whether one chimpanzee (the subject) would change their choice behavior in response to what a competitor chimpanzee was aware of (Study 1) and believed (Study 2). In the first study, subjects watched as the competitor chimpanzee either saw or didn't see a high-quality food reward being hidden. Subjects then had a choice between that high-quality food reward or a low-quality alternative. Critically, the experimenters varied *when* subjects made their choice. When the competitor chose before the subject (and thus was likely to have already taken the high-quality food if they were aware of where it was), subjects selectively chose the low-quality option, but only if the competitor witnessed the baiting. Study 2 then built on this original design but included a false belief condition. Subjects in Study 2 failed to represent the false belief of the competitor, and instead, treated the agent as if they had no information about the content of the buckets at all. In this and other competitive studies (e.g., Krachun, Carpenter, Call, & Tomasello, 2009), primates fail to use others' false beliefs to successfully outcompete their foes.

Interactive Helping Tasks

Researchers have also attempted to test primate false belief understanding using interactive helping tasks, a method originally designed for use with human infants (Buttelmann et al., 2009). In the original infant version of this study, Buttelmann et al. (2009) allowed 16-, 18-, and 30-month-olds to watch as an agent placed an object in a box (A) which was then moved by another experimenter to a second box (B). Buttelmann and colleagues varied whether the agent saw the object's movement from box A to box B. The agent then intentionally tried to open box A. In the case where the agent had a true belief and therefore knew what was in both boxes, helping the agent achieve his goal would involve opening the box the agent was trying to open (box A). But when the agent had a false belief, helping to open box is no longer the best way to fulfill the agent's goal; instead, infants should selectively help the experimenter by opening box B, the one with the object actually inside. Infants show just this pattern of performance, helping the experimenter open box B on the false belief condition (77% of participants opening box B) but critically showing the opposite pattern of performance on the true belief condition (only 29% of participants opening box B).

Buttelmann and colleagues (2017) adapted this same task for use with great apes. Although apes mirrored infants' performance on the false belief condition (76% of trials opened box B), they showed a very different pattern of performance on the true belief condition, failing to distinguish between either of the two boxes (53% of trials opening box B). Although this result has been interpreted by some as evidence that apes distinguish between true and false belief states (Buttelmann et al., 2017), the difference in apes' performance from that of human infants raises doubts that primates interpret this task in the same way as humans do, and thus has made many scholars worry that this experiment cannot provide robust evidence that primates track others' beliefs.

Looking Time Studies

Researchers have also tested primate false belief understanding using expectancy violation looking time studies, including some measures borrowed from classic tests of theory of mind in human infants (e.g., Onishi & Baillargeon, 2005). Marticorena and colleagues (2011) presented rhesus monkeys with a scene in which an agent watched an object move between two possible locations. After the agent saw the object enter one of the two boxes, her visual perspective was blocked and the subject monkey alone watched as the object switched locations. If subjects represent that the agent now has a false belief, they should be surprised and subsequently look longer when the agent reaches into the box containing the object than when she reaches towards the box where she last saw the object (i.e., acting consistently with her false belief). In contrast to the performance of human infants (Onishi & Baillargeon, 2005), monkeys seem to show no prediction about where the experimenter will reach, looking for the same duration of time when she reaches to either box. Other looking time studies of false beliefs (Martin & Santos, 2014) have found similar failures when primates are allowed to automatically encode others' false beliefs (see Kovács et al. 2010 for a human infant version of this study). Taken together, the looking time studies match what has been observed in other kinds of primate false belief tasks—to date, there is no evidence that primates track what others believe. Indeed, when an agent has a false belief, primates for the most part seem to have no prediction about how that agent will behave.

Anticipatory Looking Methods

The single study to date providing positive evidence that apes may track others' false beliefs used anticipatory looking as a dependent measure (Krupenye, Kano, Hirata, Call, & Tomasello, 2016). In this task, apes watched videos of a human in an ape suit moving between different locations (or moving an object to different locations). Krupenye and colleagues then manipulated the amount of information a second agent in the video knew about the location of the first agent (or object). Critically, when the second agent in the video possessed a false belief about the location of the first agent (or the object), subjects made more anticipatory looks to the location where the second agent falsely believed the first agent (or object) to be. The researchers took this pattern of performance as evidence that apes indeed have false belief representational abilities, but that these abilities are fragile, elicited only in complex social situations and requiring a novel methodology to tap into the appropriate behavioral response (Krupenye et al., 2016; Krupenye & Call, 2019).

Conclusions

Although apes' performance on one single anticipatory looking task (Krupenye et al., 2016) has been interpreted by some as strong evidence that chimpanzees may understand the false beliefs of others (Krupenye & Call, 2019, see Krupenye, 2020, this volume), several scholars have criticized the paper on the grounds of small sample sizes and other methodological issues (for problems on the replicability of anticipatory looking methods for testing false beliefs in human development, see Baillargeon et al., 2018). Indeed, one co-author of the Krupenye et al. (2016) paper remains skeptical of that paper's interpretation, noting that this single piece of evidence has only "changed our conclusion somewhat … but in many studies, they still do not make behavioral decisions based on others' beliefs." (Tomasello, 2018, p. 180).

Apart from a single published report, primates have tended to perform poorly (Call & Tomasello, 1999; Kaminski et al., 2008; Krachun et al., 2009; O'Connell &

Dunbar, 2003) and differently than human infants (Buttelmann et al., 2017) on tests of false beliefs, even when tested with automatic processing tasks (Martin & Santos, 2014) and looking paradigms that require minimal task demands (Marticorena et al., 2011). Based on the preponderance of the evidence to date, we argue there is still relatively little reason to suspect that most primates successfully represent others' beliefs, at least in the way humans do.

Representing Unawareness in Others

While much of the existing comparative research tests whether primates understand what others are aware of and believe, there is less work specifically examining whether primates share another critical aspect of human-like mentalizing: what it means for someone to be ignorant or *unaware*. Understanding when others don't know something is an important aspect of human theory of mind. People successfully track other agents' ignorance across many contexts (e.g., when keeping or divulging secrets, when deciding what information to teach, when making communicative utterances intended to provide information, etc.). But do primates share this ability to reason about when others are unaware?

At first glance, the work reviewed previously might seem to show evidence that primates can track others' unawareness. For example, rhesus monkeys avoid stealing food from a person who is aware of their actions, but selectively take food from a person who is unaware (Flombaum & Santos, 2005, see also Hare et al., 2001 for similar evidence in chimpanzees). Similarly, macaques expect an aware agent to search for an object where she last saw it, but show no prediction about where an unaware person will search (Marticorena et al., 2011). These results have historically led researchers to argue that primates have an understanding of what it means for an agent to be unaware (Call & Santos, 2012; Call & Tomasello, 2008; Rosati et al., 2010; Whiten, 2013). Nevertheless, we and colleagues have recently proposed a different account of this pattern of performance (Horschler et al., 2019; Martin & Santos, 2016). While available results clearly suggest that primates treat aware agents *differently* from unaware agents, there is no clear evidence that primates make clear positive predictions about what an unaware agent should do. That is, when primates are asked to reason about an unaware agent, they often *no prediction* about what the agent will do (Marticorena et al., 2011) or simply react in a way consistent with their usual baseline behavior (e.g., taking food they want: Flombaum & Santos, 2005; taking the highest-value of two food items: Kaminski et al., 2008). Indeed, to our knowledge, there is only one published study in which primates are required to make a specific positive prediction about how an unaware experimenter should behave. In this study (Karg et al., 2015), chimpanzees played a foraging game with one of two experimenters: a cooperative experimenter who shared food and a competitive experimenter who stole food. Chimpanzees sat in front of an array of food rewards that were inaccessible to them but could be covered with an opaque screen before the other experimenter arrived. The logic was that chimpanzees should want to make the food rewards as visible to the cooperative experimenter as possible: food rewards that were not already covered should remain that way, and any covered food rewards should be revealed. In contrast, chimpanzees should show different performance when playing with the competitive experimenter; in this case, they should leave any covered food rewards hidden and cover up any visible food rewards to make the competitor ignorant. Karg and colleagues found that chimpanzees successfully opened the covered food rewards when playing with the cooperator (i.e., they knew that they could reveal foods to make the cooperator *aware*) but they failed to cover up the visible food rewards when playing with the competitor (i.e., they didn't seem to realize that they needed to make the competitor *unaware*). Apes therefore don't seem to realize what it means to make someone unaware. Yet again, when faced with an unaware experimenter, they default to the most obvious behavior (in this case, not moving any of the covers). We have argued that results like these suggest that in addition to lacking representations of others' beliefs, primates may also lack representations of others' unawareness (see Martin & Santos, 2016). That is, primates may not show a human-like understanding of others' belief or others' ignorance, despite their success in understanding others' awareness.

A Unified Theory for Nonhuman Theory of Mind

Given the complicated pattern of findings observed above, what can we conclude currently about the nature of primate mentalizing capacities? First, we argue that the results to date suggest clear evidence that primates can represent others' awareness. Many primate species successfully make predictions about what other agents see and know in a variety of different tasks. Moreover, primates use information about what agents are aware of to succeed in naturalistic competitive tasks. In this way, primates seem to possess one of the important aspects of human theory of mind capacities: the capacity to represent what others see and know (see also Martin & Santos, 2016 for a review of this awareness relations account).

In contrast, there is rather limited evidence that primates share our understanding of others' beliefs. Despite decades of experimental attempts, there is only one published report demonstrating that apes can succeed in a standard false belief test (Krupenye et al., 2016). This study also used an anticipatory looking measure that has recently generated some controversy in the developmental literature concerning whether human infants robustly show false belief reasoning on this task (e.g., Baillargeon et al., 2018). While the jury is still out about how to interpret these new ape anticipatory looking successes, the preponderance of false belief failures observed in comparative studies suggests that either primates cannot represent others' beliefs at all or that such representations are incredibly fragile and task specific. Taken together, then, there appears to be one area in which adult primates mentalize quite differently from adult humans: they seem (mostly) unable to represent other individuals' beliefs.

Finally, there is growing evidence of a second domain in which primate mentalizing may differ from that of humans: primates may lack the capacity to track unawareness in others. To date, most primate studies of unawareness show that primates make no positive predictions when faced with ignorant agents; they show no prediction when an agent who lacks awareness searches for a hidden object (Marticorena et al., 2011) and switch to default behaviors whenever a competitor is ignorant (Flombaum & Santos, 2005; Kaminski et al., 2008). The one study in which chimpanzees had the opportunity to actively make a competitor ignorant (Karg et al., 2015) found that primates fail to do so. Overall, primates' emerging pattern of performance suggests that they may represent others' awareness, but not others' unawareness (see also Martin & Santos, 2016 for a review).

What Is Missing?: Future Directions

Given the current evidence for primates' successes and failures in mentalizing, there are a few obvious next steps both for understanding the representations that primates use to make sense of other agents and for determining which aspects of human mentalizing are unique. First, more work is needed to better clarify if and when (some) primates do indeed track others' beliefs. As noted above, primates have long shown a consistent pattern of failures on false belief tasks (Call & Tomasello, 1999; Kaminski et al., 2008; Krachun et al., 2009; Marticorena et al., 2011; Martin & Santos, 2014; O'Connell & Dunbar, 2003), but one new study has argued that apes may be able to represent others' beliefs at least under very specific conditions (Krupenye et al., 2016). At the present time, it's not clear how to rectify these new findings with previous failures and thus future work could profit from replicating chimpanzees' performance on anticipatory looking tasks as well as testing other primates on related tasks. Moreover, researchers must think more about why some looking methods (e.g., anticipatory looking) are more likely to demonstrate successful belief reasoning than others (e.g., violation of expectation, as in Marticoriena et al., 2011; competitive tasks, as in Kaminski et al., 2008) where primates have previously shown task successes in different mentalizing abilities.

A second avenue of future research is to further test whether primates successfully make positive predictions about unaware agents. To date, few comparative researchers have designed studies of unawareness representations that require primates positive predictions about how an unaware agent will be have (see Karg et al., 2015 for an exception). Such studies would help us determine what (if anything) primates understand about others' ignorance. It's also worth noting that relatively little is known about human infants' unawareness representations; this too is a ripe area for future study, as we know little about infants' understanding of ignorance interacts with their early belief representations.

Third, and perhaps most importantly, future research must aim to better understand the nature of the representations that primates *do* possess: an understanding of others' states of awareness. For example, how and under what conditions do primates decide that a person is aware and turn on these awareness representations? And what kinds of situations cause primates to stop tracking an agent's awareness? Recent work has begun focusing on this latter question. In one recent study, Horschler et al. (2019) used an expectancy violation paradigm to test whether they could "break" a subject monkey's representation that an agent was aware of the location of an object. In the task, subjects saw a human agent watch a piece of fruit hidden in one of two boxes. After the agent's view was occluded, the fruit quickly moved outside of the box and back in. The agent then reached into one of the two boxes. If monkeys' representations of the agent's awareness are robust to irrelevant changes (e.g., a small irrelevant motion of the fruit), then subjects should look longer when the experimenter searches in the wrong location for the object. In contrast, if monkeys' representations are fragile enough to be disrupted by simple spatial manipulation of the object, then subjects should show no expectation about where the agent will search. Horschler and colleagues found this latter pattern of looking, suggesting that primates' awareness representations can be disrupted even by a quick movement of the target object while the person is looking away. Importantly, not all changes outside of a person's awareness seem to affect primates' awareness representations. Horschler and colleagues added a control in which a change irrelevant to the location of the object happened when the person wasn't paying attention (e.g., the box covering the fruit flipped open and immediately closed but the object remained stationary). In this case, monkeys were able to make a positive prediction about where the agent would search for the object, looking longer when the agent looked in the wrong (i.e., empty) box. These findings suggest that monkeys stop representing an agent as aware of an object's location when the object makes an irrelevant movement but not when there are changes to the target environment. In this regard, it seems that primates' awareness representations may be more nuanced than previously thought. Moving forward, future work should critically test whether other state changes of the target object (e.g., location, physical appearance) are enough to break these awareness representations. A better understanding of these mechanisms will thus be important not only for a full account of primate mentalizing but also for gaining more clarity on which aspects of human mentalizing are unique.

There is also a need to better explore how primates develop these awareness representations in the first place. Although much is known about the early development of human theory of mind representations (e.g., Helming et al., 2014; Wellman & Liu, 2004; Scott & Baillargeon, 2017; Sodian, 2011), to date there are few studies exploring the ontogenetic origins of primate mentalizing. This is unfortunate, as understanding the developmental history of primates' theory of mind representations would provide critical hints as to whether they emerge along the same timeline as early human mentalizing capacities (see review in Rosati, Wobber, Hughes, & Santos, 2014).

Indeed, recent empirical work hints that some primates may show a different developmental pattern in their early mentalizing than humans do; specifically, one species of primates (the rhesus macaque) appears to develop awareness representations in a delayed time course (Arre, Clark, & Santos, 2020; Rosati, Arre, Platt, &

Santos, 2016) relative to humans. This new work suggests that some primates may require more experience interacting with other social agents in order to develop sophisticated awareness representations. Moving forward, the field of comparative cognitive development may provide critical tests for the types of experiences required for different mentalizing capacities to come online.

Finally, having established that primates share some aspects of human-like mentalizing capacities, it is important to explore the neural basis of these socio-cognitive abilities. While human social cognitive neuroscience has made great strides in understanding the mechanisms by which humans mentalize about their future selves and others (Leshinskaya, Contreras, Caramazza, & Mitchell, 2017; Macrae et al., 2017; Tamir, Thornton, Contreras, & Mitchell, 2016; Thornton & Mitchell, 2017), very little is known about the neural mechanisms primates use to track what others know and perceive. Although it is often hypothesized that there is a high level of conservation between human and nonhuman primate functional neuroanatomy (Chang et al., 2013, 2015; Ghazanfar & Santos, 2004; Platt, Seyfarth, & Cheney, 2016; Platt & Spelke, 2009), little research has investigated whether similar neural mechanisms underlie mentalizing in our primate relatives. Excitingly, comparative researchers have now developed a number of experimental methodologies that can be adapted into neurophysiological preparations. In addition, we now know much more about the mentalizing abilities of those primate species specifically used in neuroscientific investigations (e.g., rhesus macaques, for a review see Drayton & Santos, 2016). In this way, the empirical stage is now set to begin exploring the neural mechanisms underlying theory of mind capacities in primates.

The past four decades have revealed much about the nature of primate' understanding of other agents. Our continued hope is that a better understanding of primates' successes and failures on mentalizing tasks can help cognitive and neural scientists to better understand not just how primates think about other minds but what primates mentalizing reveals about the cognitive and neural basis of our own species' mentalizing as well.

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