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Review

What Cognitive Representations Support Primate Theory of Mind?

Alia Martin[1,*] and Laurie R. Santos[2]

Much recent work has examined the evolutionary origins of human mental state representations. This work has yielded strikingly consistent results: primates show a sophisticated ability to track the current and past perceptions of others, but they fail to represent the beliefs of others. We offer a new account of the nuanced performance of primates in theory of mind (ToM) tasks. We argue that primates form awareness relations tracking the aspects of reality that other agents are aware of. We contend that these awareness relations allow primates to make accurate predictions in social situations, but that this capacity falls short of our human-like representational ToM. We end by explaining how this new account makes important new empirical predictions about primate ToM.

Trends

Previous research suggests that nonhuman primates, unlike human adults and children, do not track the beliefs of others.

However, primates do track the current and past perceptual awareness of others when predicting their behavior or competing with them.

We argue that primates succeed in ToM tasks by representing awareness relations between agents and true (but not false) information.

In contrast to other accounts arguing that primates represent knowledge and ignorance, this awareness relations account is consistent with failures in false belief tasks and with recent findings that primates competitively keep information concealed but do not actively conceal it.

The awareness relations account makes new predictions for the performance of primates in tasks that require a full-fledged understanding of the mental state of ignorance.

A Framework for Thinking about Cognitive Representations for ToM

Humans expect that agents will act on the basis of their unobservable mental states: their beliefs, desires, and intentions. Are humans alone in positing that others have internal mental states representing the external world? Or do nonhuman primates (hereafter primates) share our human-like representational ToM? Here, we explore these age-old (e.g., [1]) questions by reviewing recent ToM experiments in primates. We offer a new theoretical proposal for the performance of primates in ToM tasks, one that makes new empirical predictions about the origins of human mental state understanding.

The goal of ToM research is to figure out whether and how organisms make predictions about the behavior of other agents based on a model of the mental states of those agents. One way an organism could predict the behavior of other agents is by tracking particular agents (e.g., mom), particular bits of information that the organism knows about the world (e.g., the apple is on the table), and the relation between the two based on cues relevant to the mental state of the agent (e.g., mom sees the apple on the table). Such representations of the relation between an agent and information could then be used to predict or interpret the actions of the agent. For example, if I see that mom is looking at an apple that I see on the table, I can represent that mom now has a connection to this information that I know to be true. I could then use this 'awareness relation' between mom and the information I know to predict how mom will behave (e.g., mom will walk to the table to grab the apple).

Awareness relations can allow organisms to make many accurate predictions about the behavior of other agents. However, organisms sometimes interact with agents who represent different information than they themselves represent; agents will act on the basis of their own personal beliefs, which in some cases might be false. As such, an organism needs a way to represent the relation between an agent and a piece of information that the organism itself does not represent as reality. Human adults use this type of 'representational relation' all the time: we understand that other people believe information that we ourselves do not currently think is true,

[1]Victoria University of Wellington, Wellington, New Zealand
[2]Yale University, New Haven, CT, USA

*Correspondence:
alia.martin@vuw.ac.nz (A. Martin).

think about information that will happen in the future, and so on. The act of representing a relation between an agent and a piece of information that is not part of our current reality is a computational challenge. To predict behavior using representational relations rather than just awareness relations, organisms first need the capacity to conceive of states of the world that are different or 'decoupled' from their own current reality (e.g., [2]). Examples of such 'decoupled' states include hypothetical or counterfactual situations (what if the apple was on the floor, not the table), pretend contexts (let's pretend the apple is on a spaceship), or even past or future states of the world (yesterday, the apple was in the cupboard). Only an organism that succeeds in conceiving of these sorts of decoupled information states can form relations between these alternative pieces of information and particular agents. For example, to represent mom's outdated belief that the apple is in the cupboard, I would have to represent what I myself know about the world (the apple is on the table) as well as a separate decoupled counterfactual state of the world (the apple is in the cupboard) to which the agent in question (mom) has a relation (mom thinks the apple is in the cupboard). The ability to form representational relations allows an organism to predict how an agent will behave when that agent's representation of the world conflicts with the organism's own idea of reality. In this way, representational relations allow for much of the richness of adult human ToM.

The Development of Humans' Ability to Use ToM Relations

Much of the focus on ToM research to date has explored how humans develop the ability to form representational relations. Specifically, researchers have examined how humans develop the capacity to form one common representational relation: that an agent has a false belief. In so-called 'false belief studies' [3–6], a character typically hides an object in one location and the object moves to a new location while the character is gone. The question of interest is where participants predict the character will search for the object. Successful performance on this task requires that participants do more than merely establish an awareness relation between the character and the object; participants who treat the character as unaware about the location of the object should expect the character to search at random. By contrast, participants who are able to form a representational relation between the character and the object should realize that the character is not merely unaware: the character should search for the object in its original location, where the character falsely believes the object to be. Although earlier research suggested that children do not begin to form representational relations until 4 years of age [3], recent work suggests that human infants show some evidence of using representational relations within the first 2 years [6–20]. For example, infants correctly predict where agents with a false belief will look for a hidden object [7–16], and successfully take into account agents' beliefs when helping [17,18] and communicating with them [19,20]. Infants' performance in these false belief tasks have led some [6,7,21,22], although not all [23–26], researchers to argue that humans have innate cognitive machinery for forming representational relations between agents and decoupled (e.g., false) states of the world.

No Evidence that Nonhuman Primates Use Representational Relations in ToM Tasks

Over the past few decades, researchers have also tested whether primates have the capacity to form representational relations [27–32]. Although some aspects of the performance of primates in these tasks are still debated [33–39], most researchers agree on one thing: there is currently no evidence that any nonhuman primate forms representational relations in the same way as humans. More specifically, there is no evidence that primates attribute decoupled representational states, such as false beliefs, to other agents [27–32]. In one experiment [29], chimpanzees watched as a competitor either did or did not see a high-quality food being hidden. Subjects then chose between that hidden food and a safe low-quality food. Crucially, subject chimpanzees made their own choice only after the competitor made a choice. Chimpanzees went to the hidden location for the high-quality food when the competitor had not seen that food being

baited, but switched to the safe low-quality food in cases where the competitor had seen the baiting. These results suggest that chimpanzees understood that the competitor would choose the high-quality food only when the competitor had perceptual access to the baiting. However, chimpanzees did not distinguish between a condition where the experimenter moved the high-quality food to a new container when the competitor was not looking (the competitor had a false belief) and a condition where the experimenter simply lifted and lowered the same container over food when the competitor was not looking; in both cases, chimpanzees chose the high-quality food at high rates. Therefore, chimpanzees treated a competitor with a false belief about the location of the food identically to a competitor that had a true belief about the location of the food but that was unaware that the food had briefly moved (see also [30]).

In another experiment [27], rhesus macaques were tested on a looking-time false belief task (see [7] for a similar test in human infants). In a true belief condition, monkeys watched an experimenter see a lemon slide into a green box, then slide back out and into a white box. Monkeys looked longer when the experimenter subsequently reached into the green box than into the white box, suggesting that they expected the experimenter to search for the lemon where she last saw it. In a false belief condition, monkeys watched a series of events identical to those of the true belief condition except that the experimenter's view was occluded as the lemon slid from the green box into the white box. Unlike human infants, monkeys showed no evidence of attributing a false belief to the experimenter. Instead, monkeys showed similar durations of looking no matter which box the experimenter searched. Similar to chimpanzees [29], rhesus macaques treated an agent with a false belief about the location of the food as though the agent was totally unaware of where the food could be, making no prediction about the behavior of the agent.

To date, evidence from primate false belief experiments suggests that primates do not understand that other agents have distinct representations of the world that can be decoupled from reality. It is also worth noting that the failures of primates to represent false beliefs in experimental contexts nicely match what has been observed in field reports [40–42]. Indeed, the tactical deception literature has, at least to date, lacked evidence that primates attempt to mislead competitors by actively giving false information (i.e., implanting a false belief).

But Nonhuman Primates Can Use Awareness Relations in ToM Tasks

Despite the current lack of evidence that primates can form representational relations between agents and information decoupled from reality, there is consistent evidence that primates are sensitive to whether other individuals are aware of information that primates themselves represent as true about the world ([43–50]; reviewed in [35–37]). When competing for food, primates are sensitive to what potential competitors can see [43–48], hear [46,47], have recently seen or heard [48,49], and can infer based on physical clues to food location [50]. Primates also use information about what a competitor could become aware of when obtaining food; for example, primates prefer to take a silent rather than a loud path when approaching contested food [46,47]. In this way, primates do not merely respond to visible cues of awareness (e.g., the presence of eyes), but avoid producing cues that may lead to awareness across multiple perceptual sources. Together, this pattern suggests that primates have a flexible understanding of the link between perceptual access and awareness.

In line with these experimental findings, many field observations demonstrate that primates often prevent competitors from becoming aware of useful information, for instance by keeping relevant information concealed [40–42]. In addition, primates can use information about the awareness of others to learn about what is relevant in their environment. In one experiment [49], researchers placed a novel object on a platform between a chimpanzee and an experimenter so that both could see it. The experimenter then left the room, and either the same experimenter or a new experimenter entered and vocalized excitedly while looking in the general direction of the object.

When a new experimenter vocalized in the direction of the object, subjects assumed that this new experimenter must be looking at the object and followed the experimenter's attention to the object. By contrast, when the old experimenter entered, subjects behaved as though the experimenter must be reacting to something new, and looked for a novel target of the experimenter's attention rather than the original object. In this way, chimpanzees infer that the gaze of an agent is directed at something, even if chimps themselves can not yet see what that target is.

A New Cognitive Proposal of Primate ToM Performance

What representations underlie primate performance in these ToM tasks? Put differently, what representations would allow primates to succeed in predicting the behavior of agents in some ToM tasks, yet would cause them to make inaccurate predictions in cases where agents have false beliefs?

Nonhuman Primates Do Not Represent Knowledge and Ignorance

Some researchers [34] have proposed low-level behavior-based accounts of primate performance in ToM tasks, and others [51] have proposed that primates represent something belief-like but that falls short of full-blown beliefs (reviewed in Box 1). However, a middle-ground view that many researchers have converged on [33,35–38], and that we ourselves have argued for previously [27], is that primates succeed in many ToM tasks by representing the knowledge and ignorance of other agents. Under this knowledge-ignorance account, primates are able to represent what others know and do not know (i.e., ignorance) and can use these representations to make predictions and guide their own actions toward other agents.

The core problem with this sort of knowledge-ignorance account of the performance of primates concerns the kind of representation needed to truly understand another agent as ignorant *per se*. Recognizing that an agent is in state of ignorance requires an organism to form a relation between an agent and a state of the world that is, in an important sense, decoupled from the

Box 1. Other Accounts of Primate Performance in ToM Tasks

Abstract Behavioral Rules

Some researchers (e.g., [34,54]) have argued that the success of primates in ToM tasks does not suggest any mental state understanding. Instead, they argue that this success can be explained by an ability to represent abstract behavioral rules (e.g., if the competitor has oriented toward the food, do not approach it). These proposed rules are abstract in the sense that they can generalize across a variety of agent-information relations, and causal in the sense that primates can use them to predict the behavior of an agent.

The problem with this behavioral rules account is that primates track the awareness of other agents across several perceptually dissimilar situations (e.g., hearing, seeing, inferring; see [43–50]). Furthermore, primates successfully predict when an agent will be aware in novel situations with unfamiliar stimuli and no training (e.g., [47,55]). Given that behavioral rules fail to account for the performance of primates in these novel scenarios, we and others [33,37] worry that the behavioral rules account can explain neither the flexibility with which primates represent the behaviors of other agents, nor the range of contexts in which primates successfully act on the basis of agent-information relations.

Minimal Theory of Mind

Other researchers [23,51] have argued that human infants and nonhuman animals share a 'minimal ToM' that allows them to represent certain belief-like relations between agents and objects, called 'registrations'. In this view, an individual who registers information attributes a relation between an agent and the location where the agent sees an object (e.g., agent registers 'apple is in the green box'), and this content ('apple is in the green box') can be maintained as part of the representation even when the information is no longer true. These researchers developed their idea of registration to account for infants' performance in false belief tasks [23].

The problem with the registration account is that it fails to explain the poor performance of primates in false belief tasks [27–32]. The registration account proposes that primates should perform like human infants [7,9] on false belief tasks, but they do not [27,28]. Therefore, we consider minimal ToM to be an interesting account of the infant findings, but disagree with the authors' extension of these same representations to primates [23].

organism's own reality. To truly understand that an agent is ignorant, an organism must attribute to that agent a state of uncertainty or not knowing, even though the organism itself knows exactly where the food is. In this way, representing agents as truly ignorant likely requires the same cognitive resources as representing agents with false beliefs, namely, forming a representational relation, which so far primates appear not to do [27–32].

Nonhuman Primates Use Awareness Relations to Track the Access of Others

Given these issues with the knowledge-ignorance account of the performance of primates, we propose a new account: primates succeed in some ToM tasks because they are able to attribute awareness relations between different agents and information about the world that primates themselves are already representing as true of reality. In this view, primates track particular agents (the competitor) and particular bits of information (there is food in the box) and can represent whether there is a relation between the two based on cues relevant to the mental state of the agent (e.g., the competitor sees the food in the box). Such representations of the relation between an agent and information allow primates to track whether an agent is aware of the same things that the primates themselves are aware of, and can be used to predict or interpret the actions of the agent. Importantly, this account posits that the awareness attributions of primates have an 'on/off' quality: the primate subject either represents a relation between an agent and some piece of information, or represents no relation at all (see Box 2 for an explanation of how an on/off system also accounts for the lack of egocentric errors in primate false belief tasks).

The Awareness Relations View Is Consistent with the Successful Performance of Primates in ToM Tasks

Once primates represent an awareness relation between an agent and some target bit of information, they can use this relation to predict how the agent will act on the information. For example, primates can make predictions about what another agent that is aware will do (the agent will search in the green box, the agent will react if I try to approach the green box), and can

Box 2. Awareness Relations and Egocentric Errors in False Belief Tasks

Interestingly, primates do not fail false belief tasks in the way one might expect: they do not assume that the character will look for the object in its true location (e.g., [27,29]). Such 'egocentric errors' are common in children's performance on verbal false belief tasks; before their fourth birthday, children tend to respond that a character with a false belief will search for the toy in its true location [3]. Similar egocentric errors continue well into human adulthood in complex perspective-taking and judgment tasks [56,57].

Some researchers have proposed that humans show egocentric errors because successfully representing someone's false belief requires inhibiting a 'reality bias' [58], 'curse of knowledge' [59], or 'true belief default' [60], all of which would lead to a default prediction that others will act on the basis of reality. Evidence for the importance of inhibiting a reality bias stems from the connection between false belief task performance and inhibitory control capacities (see [61,62]). However, primates do not show egocentric errors in false belief tasks despite their relatively poor inhibitory control (e.g., [63,64], although see [65]).

The lack of egocentric errors in primate false belief tasks also raises the question of whether primates have default expectations about what information another agent has in the absence of cues to the perceptual access of that agent. Little work has addressed this question, although at least one study suggests that primates treat agents that have not yet had perceptual access as unaware. Hare and colleagues [44] allowed chimpanzee subjects to see food hidden while a dominant chimpanzee competitor looked on. This dominant competitor was then replaced by a new dominant competitor that had no information about the hiding event. Subjects were willing to approach the contested food with the new dominant present, suggesting that primates treat agents with no information as unaware (i.e., they hold no awareness relation and make no prediction about the behavior of these agents). However, do primates ever expect agents to be aware in the absence of perceptual access cues? Humans often assume that others share information without direct evidence of perceptual access (e.g., [66]). We, for example, expect others to share knowledge of word meanings [67] and how artifacts work [68] without evidence that that the individuals in question have had the access necessary to gain that knowledge. It is an interesting open question whether primates can form similar expectations of shared awareness in some cases.

use these predictions to guide their behavior (I should not steal food if a competitor is aware, I should not produce auditory cues that might make a competitor aware). Awareness relations can also account for the performance of chimpanzees reported in [49]: chimpanzees in this task formed a relation between the experimenter and the object as soon as the experimenter looked at the object. When the experimenter acted surprised, chimpanzees inferred that the experimenter's reaction could not be toward an object with which the experimenter already had a relation. Thus, chimpanzees assumed that the experimenter's increased attention could not be directed at the original object, and searched for an alternative target.

The Awareness Relations View Is Consistent with the Limitations of Primates in ToM Tasks

Our awareness relations account also leads to a novel interpretation of primates' failures in false belief tasks, the same performance that led researchers to argue that primates represent an agent with a false belief as 'ignorant'. While there is robust evidence that primates make positive predictions about how agents will act on based on their knowledge of some piece of information [27,29,43–50], there is less clear evidence that primates make positive predictions about how agents will act when they do not know some piece of information. Consider again the performance of monkeys reported in [27]. When the lemon moved to a new location when the agent was not looking, monkeys looked equally regardless of whether the agent searched in either the correct or incorrect location. One interpretation of this pattern of performance is that monkeys recognized that the agent was ignorant (that the agent did not know where the food was) and, thus, predicted that the agent would search at random. However, another interpretation of this pattern of performance is that primates had no prediction about what the agent would do. That is, monkeys had no representation of this agent in relation to any relevant information and, thus, had no expectation about the agent's behavior.

This same alternative interpretation can be applied to the performance of chimpanzees in the false belief condition reported in [29]. The authors claimed that chimpanzees treated the competitor as ignorant and, thus, understood that they could take the high-quality food because the competitor would not know where it was. However, the performance of chimpanzees is also consistent with the possibility that they made no prediction about what the competitor would do when the competitor did not see the movement of the food and, thus, chose the food that they themselves preferred originally. In both cases, one can just as easily interpret the performance of the primates as consistent with them having no representation of a relation between the agent and the food. The idea that primates make no prediction when they have no representation of a relation between an agent and information fits with recent evidence suggesting that primates do not attempt to actively create states of ignorance in others. For example, chimpanzees keep already hidden food from the view of a competitor, but do not actively hide food that is not currently hidden [52]. Again, these findings raise the possibility that chimpanzees cannot represent another agent in a state of ignorance.

The Awareness Relations View Makes Novel Empirical Predictions

To date, most evidence from primate ToM studies are consistent with both the awareness relations proposal we have argued for here and the knowledge-ignorance account that others have argued for previously. Nevertheless, these two accounts make different predictions in situations in which primates have not yet been tested, ones that require representations of ignorance as a subjective mental state. Our awareness relations account uniquely explains a finding that should be puzzling from a knowledge-ignorance account: competitive primates understand that they should prevent cues that would lead their competitors to gain awareness (e.g., do not reveal hidden food), but not that they should break existing cues that would cause their competitors to become ignorant (e.g., hide visible food). Consider again the performance of chimpanzees reported in [52]. Chimpanzees understood the consequences of making a competitor aware (they knew to keep food that was already hidden from a competitor out

of sight) but not how to break the future state of awareness of the competitor: they did not try to actively hide food in advance so that the competitor would not later see it. Under our awareness relations account, this dissociation makes sense: chimpanzees can not anticipate a state of ignorance in others because they have no way to represent a state of ignorance *per se*. Thus, our awareness relations account predicts this observed dissociation between the capacity to hide food and the capacity to leave food hidden.

The awareness relations and knowledge-ignorance accounts also differ on a second empirical prediction: whether primates will show positive expectations about ignorant agents. If primates represent others as ignorant, then they should predict that ignorant agents will engage in information-seeking behaviors to find food. In addition, if primates represent others as ignorant, they should find it particularly surprising if an ignorant agent finds a target object when a guess is improbable. Finally, primates who represent others as ignorant should expect an ignorant agent to react with surprise rather than indifference upon finding a target object. Note that each of these predictions requires researchers to assess primates' expectations of the behavior of others rather than only primates' responses. Fortunately, researchers have developed new methods for assessing such expectations [27,28], including new methods that can even probe what primates expect before agents begin acting [53]. Although it is an (exciting) open question how primates would behave in these novel experimental situations (see Outstanding Questions), we predict they will perform poorly: representing a subjective mental state of ignorance would require primates to use representational relations, which primates' performance in false belief tasks suggests they are unable to do [27–32].

Concluding Remarks

As we have reviewed here, primates understand something critical about the relation between agents and information: primates can represent relations between agents and information that is true from their own perspective. Such awareness relations allow primates to functionally exploit what others know and do not know, and to make correct predictions about others' future behavior. Importantly, however, there is also a critical limit to the awareness relations that primates can represent: primates cannot represent relations between agents and untrue or decoupled states of the world. These more computationally sophisticated representational relations allow human ToM to go beyond that of other primates. In doing so, we may have become the only species that is able to track the contents of others' minds even when the contents of those other minds differ from our own.

Outstanding Questions

What situations make primates establish an awareness relation between an agent and some piece of information? Human infants and adults can establish representations of others' beliefs even in circumstances in which doing so is irrelevant to their own behavior, but do primate information relations representations automatically turn on in the same way?

How do the awareness relation representations of primates develop? Are primates able to form these representations from early in infancy?

Does the awareness relations account explain the performance that nonprimate animals show in ToM tasks? Little direct empirical work has tested how nonprimate animals perform in false belief tests. Are humans unique in forming representational relations and, thus, in the ability to track others' beliefs?

Do humans represent others' action in terms of awareness relations, or do they only use representational relations? Unfortunately, testing this question is likely to be difficult: research suggests that humans automatically generate representations of others' beliefs and, once a belief representation has been generated, it will likely mask any of the empirical signatures of the awareness representations that have been observed in primates. One way to get around this issue would be to develop ToM tasks involving cognitive load, which inhibit humans' ability to generate belief representations, to tease apart whether humans fall back on the sorts of awareness relations that primates use.

What evolutionary pressures led to our human-like ability to represent other agents' relations to false or pretend information in ways that no other primates seem to do?

References

1. Premack, D. and Woodruff, G. (1978) Does the chimpanzee have a theory of mind? *Behav. Brain Sci.* 1, 515–526
2. Leslie, A.M. (1987) Pretense and representation: the origins of 'theory of mind'. *Psychol. Rev.* 94, 412–426
3. Wellman, H. *et al.* (2001) Meta-analysis of theory-of-mind development: the truth about false belief. *Child Dev.* 72, 655–684
4. Perner, J. *et al.* (1987) Three-year-olds' difficulty with false belief: the case for a conceptual deficit. *Brit. J. Dev. Psychol.* 5, 125–137
5. Wimmer, H. and Perner, J. (1983) 'Beliefs about beliefs: representation and constraining function of wrong beliefs in young children's understanding of deception'. *Cognition* 13, 103–128
6. Baillargeon, R. *et al.* (2010) False-belief understanding in infants. *Trends Cogn. Sci.* 14, 110–118
7. Onishi, K.H. and Baillargeon, R. (2005) Do 15-month-old infants understand false beliefs? *Science* 308, 255–258
8. Luo, Y. and Baillargeon, R. (2010) Toward a mentalistic account of early psychological reasoning. *Curr. Dir. Psychol. Sci.* 19, 301–307
9. Kovács, Á.M. *et al.* (2010) The social sense: susceptibility to others' beliefs in human infants and adults. *Science* 330, 1830–1834
10. Luo, Y. (2011) Do 10-month-old infants understand others' false beliefs? *Cognition* 121, 289–298
11. Surian, L. *et al.* (2007) Attribution of beliefs by 13-month-old infants. *Psychol. Sci.* 18, 580–586
12. Yott, J. and Poulin-Dubois, D. (2012) Breaking the rules: do infants have a true understanding of false belief? *Brit. J. Dev. Psychol.* 30, 156–171
13. Scott, R.M. and Baillargeon, R. (2009) Which penguin is this? Attributing false beliefs about object identity at 18 months. *Child Dev.* 80, 1172–1196
14. Song, H.J. and Baillargeon, R. (2008) Infants' reasoning about others' false perceptions. *Dev. Psychol.* 44, 1789–1795
15. Scott, R.M. *et al.* (2010) Attributing false beliefs about non-obvious properties at 18 months. *Cogn. Psychol.* 61, 366–395
16. He, Z. *et al.* (2011) False-belief understanding in 2.5-year-olds: evidence from violation-of-expectation change-of-location and unexpected-contents tasks. *Dev. Sci.* 14, 292–305
17. Buttelmann, D. *et al.* (2014) Eighteen-month-olds understand false beliefs in an unexpected-contents task. *J. Exp. Child Psychol.* 119, 120–126
18. Buttelmann, D. *et al.* (2009) Eighteen-month-old infants show false belief understanding in an active helping paradigm. *Cognition* 112, 337–342

19. Knudsen, B. and Liszkowski, U. (2012) 18-month-olds predict specific action mistakes through attribution of false belief, not ignorance, and intervene accordingly. *Infancy* 17, 672–691
20. Southgate, V. *et al.* (2010) Seventeen-month-olds appeal to false beliefs to interpret others' referential communication. *Dev. Sci.* 13, 907–912
21. Carruthers, P. (2013) Mindreading in infancy. *Mind Lang.* 28, 141–172
22. Leslie, A.M. (2005) Developmental parallels in understanding minds and bodies. *Trends Cogn. Sci.* 9, 459–462
23. Apperly, I.A. and Butterfill, S.A. (2009) Do humans have two systems to track beliefs and belief-like states? *Psychol. Rev.* 116, 953–970
24. Heyes, C. (2014) Submentalizing I am not really reading your mind. *Perspect. Psychol. Sci.* 9, 131–143
25. Perner, J. and Roessler, J. (2012) From infants' to children's appreciation of belief. *Trends Cogn. Sci.* 16, 519–525
26. Ruffman, T. (2014) To belief or not belief: children's theory of mind. *Dev. Rev.* 34, 265–293
27. Marticorena, D.C.W. *et al.* (2011) Monkeys represent others' knowledge but not their beliefs. *Dev. Sci.* 14, 1406–1416
28. Martin, A. and Santos, L.R. (2014) The origins of belief representation: monkeys fail to automatically represent others' beliefs. *Cognition* 130, 300–308
29. Kaminski, J. *et al.* (2008) Chimpanzees know what others know, but not what they believe. *Cognition* 109, 224–234
30. Krachun, C. *et al.* (2009) A competitive nonverbal false belief task for children and apes. *Dev. Sci.* 12, 521–535
31. O'Connell, S. and Dunbar, R.I.M. (2003) A test for comprehension of false belief in chimpanzees. *Evol. Cogn.* 9, 131–140
32. Call, J. and Tomasello, M. (1999) A nonverbal false belief task: the performance of children and great apes. *Child Dev.* 70, 381–395
33. Whiten, A. (2013) Humans are not alone in computing how others see the world. *Anim. Behav.* 86, 213–221
34. Penn, D.C. and Povinelli, D.J. (2007) On the lack of evidence that non-human animals possess anything remotely resembling a 'theory of mind'. *Philos. Trans. R. Soc. B* 362, 731–744
35. Rosati, A. *et al.* (2010) Primate social cognition: thirty years after Premack and Woodruff. *Primate Neuroethol.* 1, 117–144
36. Tomasello, M. *et al.* (2005) Understanding and sharing intentions: the origins of cultural cognition. *Behav. Brain Sci.* 28, 675–691
37. Call, J. and Tomasello, M. (2008) Does the chimpanzee have a theory of mind? 30 years later. *Trends Cogn. Sci.* 12, 187–192
38. Call, J. and Santos, L.R. (2012) Understanding other minds. In *The Evolution of Primate Societies* (Mitani, J.C. and Call, J., eds), pp. 664–681, University of Chicago Press
39. Lurz, R.W. (2011) *Mindreading Animals: The Debate over what Animals Know about other Minds,* MIT Press
40. Byrne, R.W. and Whiten, A. (1990) *Tactical Deception in Primates: The 1990 Database,* German Primate Center
41. Byrne, R.W. and Whiten, A. (1991) Computation and mindreading in primate tactical deception. In *Natural Theories of Mind: Evolution, Development, and Simulation of Everyday Mindreading* (Whiten, A., ed.), pp. 127–141, Blackwell
42. Whiten, A. and Byrne, R.W. (1988) Tactical deception in primates. *Behav. Brain Sci.* 11, 233–244
43. Flombaum, J.I. and Santos, L.R. (2005) Rhesus monkeys attribute perceptions to others. *Curr. Biol.* 15, 447–452
44. Hare, B. *et al.* (2000) Chimpanzees know what conspecifics do and do not see. *Anim. Behav.* 59, 771–785
45. Hare, B. *et al.* (2006) Chimpanzees deceive a human competitor by hiding. *Cognition* 101, 495–514
46. Melis, A.P. *et al.* (2006) Chimpanzees (*Pan troglodytes*) conceal visual and auditory information from others. *J. Comp. Psychol.* 120, 154–162
47. Santos, L.R. *et al.* (2006) Rhesus monkeys, *Macaca mulatta*, know what others can and cannot hear. *Anim. Behav.* 71, 1175–1181
48. Hare, B. *et al.* (2001) Do chimpanzees know what conspecifics know? *Anim. Behav.* 61, 139–151
49. MacLean, E.L. and Hare, B. (2012) Bonobos and chimpanzees infer the target of another's attention. *Anim. Behav.* 83, 345–353
50. Schmelz, M. *et al.* (2011) Chimpanzees know that others make inferences. *Proc. Natl. Acad. Sci. U.S.A.* 108, 3077–3079
51. Butterfill, S.A. and Apperly, I.A. (2013) How to construct a minimal theory of mind. *Mind Lang.* 28, 606–637
52. Karg, K. *et al.* (2015) Chimpanzees strategically manipulate what others can see. *Anim. Cogn.* 18, 1069–1076
53. Kano, F. and Hirata, S. (2015) Great apes make anticipatory looks based on long-term memory of single events. *Curr. Biol.* 25, 2513–2517
54. Penn, D.C. and Povinelli, D.J. (2013) The comparative delusion: the 'behavioristic/mentalistic' dichotomy in comparative theory of mind research. In *Agency and Joint Attention* (Metcalfe, J. and Terrace, H.S., eds), pp. 62–78, Oxford University Press
55. Karg, K. *et al.* (2015) The goggles experiment: can chimpanzees use self-experience to infer what a competitor can see? *Anim. Behav.* 105, 211–221
56. Keysar, B. *et al.* (2003) Limits on theory of mind use in adults. *Cognition* 89, 25–41
57. Epley, N. (2008) Solving the (real) other minds problem. *Soc. Personal. Psychol. Compass* 2, 1455–1474
58. Mitchell, P. and Lacohée, H. (1991) Children's early understanding of false belief. *Cognition* 39, 107–127
59. Birch, S.A.J. and Bloom, P. (2003) Children are cursed: an asymmetric bias in mental-state attribution. *Psychol. Sci.* 14, 283–286
60. Leslie, A.M. *et al.* (2004) Core mechanisms in 'theory of mind'. *Trends Cogn. Sci.* 8, 528–533
61. Perner, J. and Lang, B. (1999) Development of theory of mind and executive control. *Trends Cogn. Sci.* 3, 337–344
62. Schneider, D. *et al.* (2014) Task instructions and implicit theory of mind. *Cognition* 133, 43–47
63. Boysen, S.T. and Berntson, G.G. (1995) Responses to quantity: Perceptual versus cognitive mechanisms in chimpanzees (*Pan troglodytes*). *J. Exp. Psychol. Anim. Behav. Process.* 21, 82
64. Tobin, H. *et al.* (1996) Self-control in the monkey *Macaca fascicularis*. *Anim. Learn. Behav.* 24, 168–174
65. Rosati, A.G. *et al.* (2007) The evolutionary origins of human patience: temporal preferences in chimpanzees, bonobos, and human adults. *Curr. Biol.* 17, 1663–1668
66. Clark, H.H. (1996) *Using Language,* Cambridge University Press
67. Diesendruck, G. (2005) The principles of conventionality and contrast in word learning: an empirical examination. *Dev. Psychol.* 41, 451
68. Schmidt, M.F. *et al.* (2011) Young children attribute normativity to novel actions without pedagogy or normative language. *Dev. Sci.* 14, 530–539