Theory of Mind in Nonhuman Primates

Laura S. Lewis[1,2,*] & Christopher Krupenye[3,4,*]

1. Department of Human Evolutionary Biology, Harvard University, Cambridge, MA, USA
2. School of Psychology & Neuroscience, University of St Andrews, St Andrews, UK
3. Department of Psychological & Brain Sciences, Johns Hopkins University, Baltimore, MD, USA
4. Department of Psychology, Durham University, Durham, UK

This chapter is currently in press and will be published at Cambridge University Press in the volume “Primate Cognitive Studies”, edited by Michael J. Beran and Bennett L. Schwartz. Please use the following citation:

Lewis, L. S. and Krupenye, C. (in press). Theory of mind in nonhuman primates. In B. L. Schwartz & M. J. Beran (Eds.), *Primate Cognitive Studies*. Cambridge University Press.

Correspondence: laura.lewis889@gmail.com (LSL) and krupenye@jhu.edu (CK)

Abstract:

Social life demands complex strategies for coordinating and competing with others. In humans, these strategies are supported by rich cognitive mechanisms, such as theory of mind. Theory of mind (i.e., mental state attribution, mentalizing, or mindreading) is the ability to track the unobservable mental states, like desires and beliefs, that guide others' actions. Deeply social animals, like most nonhuman primates, would surely benefit from the adept capacity to interpret and predict others' behavior that theory of mind affords. Yet, after forty years of investigation, the extent to which nonhuman primates represent the minds of others remains a topic of contentious debate. In the present chapter, we review evidence consistent with the possibility that monkeys and apes are capable of inferring others' goals, perceptions, and beliefs. We then evaluate the quality of that evidence and point to the most prominent alternative explanations to be addressed by future research. Finally, we take a more broadly phylogenetic perspective, to identify evolutionary modifications to social cognition that have emerged throughout primate evolutionary history and to consider the selective pressures that may have driven those modifications. Taken together, this approach sheds light on the complex mechanisms that define the social minds of humans and other primates.

Keywords: Theory of mind, mentalizing, mental state attribution, mindreading, perspective-taking, social cognition, cognitive evolution, human evolution, comparative cognition, primates

Section 1: What is Theory of Mind?

Humans are remarkable within the animal kingdom for many reasons, but our extreme sociality and intricately complex social lives are some of the most prominent and unique features of our species (Richerson & Boyd, 2020; Sterelny, 2019; Tomasello, 1999). The ability to communicate, cooperate, teach, and make moral judgments are deeply ingrained within our complex cultural systems, and rely on the capacity to reason about the minds of others (Premack & Woodruff, 1978). This cognitive skill, termed theory of mind (or mind-reading, mentalizing, mental state attribution), is defined as the ability to ascribe mental states to others. As humans, we are able to understand that others have mental states such as desires, goals, perceptions, and beliefs, that guide their actions and that can be different from our own (Baillargeon et al., 2016; Baron-Cohen et al., 1985; Wimmer & Perner, 1983). This ability has profound impacts on the ways in which we interact with others, as it allows us to interpret, predict, and manipulate the behavior of others. By using theory of mind, we are able to teach our children, foster communication between nations, and identify cultural boundaries based on shared and differing belief systems.

It has long been believed that theory of mind is a capacity unique to humans. A prominent hypothesis suggests that humans' exceptional mentalizing abilities are responsible for other unique features of human sociality, and that the absence of theory of mind in our closest phylogenetic relatives, the nonhuman great apes, explains the absence of hyper-sociality in these species (Boyd, 2006; Byrne & Bates, 2007; Hammerstein, 2003; Herrmann et al., 2007). As a result, for more than 40 years researchers have investigated the extent to which non-human primates and other animals are able to reason about the minds of others.

Research into animal theory of mind contributes unique insights into its evolutionary origins and the cognitive mechanisms that support it (Krupenye & Call, 2019). Studies of humans' closest relatives, chimpanzees and bonobos, clarify which foundations of human theory of mind are shared and were likely present 6-9 million years ago in our common evolutionary ancestor, and which traits are unique to our species. Research on more distantly related taxa helps us to infer the cognitive phenotypes of more basal ancestors (Krupenye, 2020), and broad phylogenetic comparisons can identify cases of convergent evolution and point to socioecological pressures that are consistently associated with pronounced social cognitive skills and likely drove their evolution (Emery & Clayton, 2004; MacLean et al., 2013).

Animal research can also answer questions about the cognitive underpinnings of theory of mind that are intractable when studied in humans alone. For example, human research suggests that theory of mind may depend on language (Lohmann & Tomasello, 2003; Milligan et al., 2007; Pyers & Senghas, 2009), but only research in nonhumans can fully determine whether theory of mind can operate in its absence (because even preverbal human infants and nonverbal human adults may possess some incipient features of language not shared by nonhumans). Similarly, animal research can shed light on the extent to which human culture and socialization shape theory of mind (Heyes & Frith, 2014; Liu et al., 2008). Exploring whether nonhuman animals have theory of mind can also determine how much it depends on or is simply enhanced by secondary mechanisms like inhibitory control and memory (Carlson et al., 2002; Powell & Carey, 2017). For example, the discovery of theory of mind abilities in animals with more limited inhibitory control or memory capacities would help to reveal the minimum cognitive requirements for the emergence of theory of mind. Finally, research with nonhuman primates can help to elucidate the cognitive architecture of theory of mind by identifying the relationships between its various evolutionary precursors. Capacities that arose earlier in primate evolution (i.e., those shared across a wider range of related taxa, with an older common ancestor) may also arise earlier in human development and provide the foundation for later-evolving and later-developing capacities. Thus, exploring theory of mind in nonhuman animals contributes insights into both the evolutionary precursors as well as the proximate, mechanistic underpinnings of this capacity (Krupenye, MacLean, et al., 2017; Meunier, 2017).

In the ensuing sections, we first provide some historical context for research into primate theory of mind. Next, we survey the diversity of experimental research that has been conducted over the last four decades. We evaluate the quality of this evidence, in light of persistent disagreements in interpretation, and we highlight the most prominent alternative explanations to be tested. Finally, we address the evolutionary origins of human theory of mind before pointing to important future directions. Together, these investigations illuminate how richly nonhuman primates can peer into others’ minds, and how their remarkable social intelligence evolved.

Section 2: The History of the Study of Theory of Mind

Despite substantial variation in social systems (Kappeler & Schaik, 2002; Shultz et al., 2011), primates are, by and large, deeply social species. In many primate taxa, social life is hugely dynamic, involving regular competition and cooperation with groupmates. Individuals build stable relationships, including coalitionary alliances, that complicate competition and shape health and fitness (de Waal, 1982; Foerster et al., 2015; Gilby et al., 2013; Silk et al., 2010; Snyder-Mackler et al., 2020). In such a context, it is evident that primates would benefit from a detailed understanding of the minds of others. Wild primates also engage in apparent acts of deception that *might* reflect rich capacities like theory of mind, providing an impetus for exploring the underlying mechanisms in experimental contexts (Whiten & Byrne, 1988). Given primates' obvious social sophistication, it is no wonder that experimental psychologists have long been curious about the cognitive mechanisms that support their complex sociality.

Intriguingly, the study of theory of mind as we know it today began in 1978 not with humans but with chimpanzees. The term was first used when Premack and Woodruff historically posed the question "Does the chimpanzee have a theory of mind?"(Premack & Woodruff, 1978), and it was responses to that seminal paper that catalyzed work on theory of mind in both comparative and developmental psychology, including the emergence of classic tasks like the false belief task (Baron-Cohen et al., 1985; Dennett, 1978; Pylyshyn, 1978; Wimmer & Perner, 1983). This original study explored whether chimpanzees could identify the image of a correct solution after observing a scene of a human encountering a problem, like a broken heater or a desired but inaccessible food item. A decade later, Povinelli and colleagues (1990) demonstrated that chimpanzees were able to discriminate between a knowledgeable and ignorant informant to successfully find hidden food (Povinelli et al., 1990). This finding, however, was hotly debated, and in 1993, Celia Heyes offered convincing alternative explanations for the theory of mind abilities previously reported in nonhuman animals (Heyes, 1993). Although there was anecdotal evidence that wild nonhuman primates engaged in behaviors, such as deception, that could be supported by mentalizing capacities, there came to be wide consensus by the 1990's that theory of mind was unique to humans (Anderson et al., 1996; Byrne & Whiten, 1988; Cheney & Seyfarth, 1990; de Waal, 1982; Heyes, 1998; Kummer et al., 1996; Leavens, 1998; Povinelli et al., 1990, 1991, 1994; Povinelli & Eddy, 1996; Tomasello & Call, 1997; Whiten & Byrne, 1997).

However, at the turn of the century, research with chimpanzees (as well as macaques and corvids) began to accumulate evidence consistent with the possibility that some species are sensitive to some mental states of others (Bugnyar & Kotrschal, 2002; Emery & Clayton, 2001; Flombaum & Santos, 2005; Hare et al., 2000; Tomasello et al., 2003). This drastic change was spurred by the introduction of competitive elements into experimental paradigms, with the realization that competition is central to primate social life and may be particularly motivating (Hare, 2001; Hare & Tomasello, 2004). The impressive success of competitive paradigms led some to wonder whether complex social cognition might be specific to the competitive domain in primates (Lyons & Santos, 2006). However, with increasing demonstration of primates' capacity to flexibly cooperate (e.g., Melis et al., 2006; see Mayerhoff, Saldaña, & Brosnan, this volume), in more recent years researchers have called for enhanced effort to examine the versatility of primate theory of mind and whether capacities demonstrated in competitive contexts can also be deployed in cooperative ones (Schmelz & Call, 2016). Thus, there are important and sometimes subtle considerations that require attention when investigating theory of mind capacities in nonhuman animals. Motivation on a task can greatly shape performance, as can the context of an experiment (e.g., cooperative versus competitive paradigm). Researchers exploring theory of mind must be sensitive to how intuitive the set-up is for the study species, recognizing that the same set-up will not always be effective across species. Finally, it is critical to create a paradigm that can avoid alternative explanations, like those we will discuss in section 4.

Today, research on primate theory of mind is characterized by a continued effort to adjudicate amongst a growing array of lean and rich theoretical accounts, and to precisely characterize the cognitive representations that support primate social cognition (Krupenye & Call, 2019; Martin & Santos, 2016). Owing to the introduction of novel methodologies (Kano et al., 2017; Marticorena et al., 2011), there is also renewed interest in the most sophisticated dimensions of mentalizing, such as understanding of false beliefs, which we will address in the next section (Martin, 2019). Additionally, some researchers are beginning to examine theory of mind in the natural contexts in which it may have evolved (Crockford et al., 2012, 2017), and in a greater range of species (Krupenye & Call, 2019).

Section 3: Evidence for theory of mind in lemurs, monkeys, and apes

In the present section, we survey evidence for theory of mind across primate taxa (see also Table 1). Theory of mind is likely composed of a large suite of interrelated cognitive capacities that can be parsed in many different ways. For the purposes of the present exposition, however, we organize our review around particular mental states, restricting our scope to primates' understanding of others' cognitive states (see Brooker, Webb & Clay, this volume, for discussion of affective perspective-taking). We first detail evidence consistent with the possibility that primates see others as goal-directed intentional agents before examining, in turn, their sensitivity to what others can perceive, what others know, and what others believe. In the present section, our aim is to describe existing evidence, reserving deeper discussions about cognitive mechanisms and alternative explanations for Section 4.

[Table 1 here]

Section 3a: Sensitivity to others' goals and intentions

Agents typically act in pursuit of desired outcomes, or goals. Understanding that others are goal-driven can aid in flexibly predicting their actions across social and nonsocial contexts (Buttelmann et al., 2012; Tomasello & Call, 1997). All primates, including our most distant relatives, the strepsirrhines (lemurs, galagos, and lorises), seem capable of recognizing and discriminating amongst familiar agents (Boysen & Berntson, 1986; Lewis et al., 2021; Marechal et al., 2010; Palagi & Dapporto, 2006; Pokorny & de Waal, 2009; Pokorny & de Waal, 2009). Do they also track agents' goals? Although we currently lack sufficient research in strepsirrhines, other primates (haplorrhines: monkeys and apes) have shown sensitivity to agents' goals across a wide array of tasks.

Lemurs, monkeys, and apes are capable of copying the goal-directed actions of others (Buttelmann et al., 2007; Horner & Whiten, 2005; Schnoell & Fichtel, 2012; Van de Waal et al., 2015; Voelkl & Huber, 2000; Van de Waal & Whiten, 2012). Furthermore, capuchin monkeys (*Cebus apella*) have demonstrated a willingness to help an experimenter satisfy her goals, by repeatedly providing an out-of-reach object that the experimenter was trying to obtain (Barnes et al., 2008; Drayton & Santos, 2014). Both capuchin monkeys and Tonkean macaques (*Macaca tokeana*) also distinguish whether an experimenter intends to give them food but is unable to or is simply unwilling to (Canteloup & Meunier, 2017; Phillips et al., 2009). Monkeys are also able to differentiate helping versus hindering agents, and whether the actions of others are intentional or accidental (Anderson et al., 2013; Anderson et al., 2013; Brügger et al., 2021; Costes-Thiré et al., 2015; Kawai et al., 2014, 2019; Wood et al., 2007). In addition, violation-of-expectation paradigms have further clarified marmosets' (*Callithrix jacchus*) and rhesus macaques' (*Macaca mulatta*) sensitivity to others' goals. Marmosets expect the actions of other agents, but not a black box, to be goal-directed (Burkart et al., 2012; Kupferberg et al., 2013), and Rochat et al. (2008) demonstrated that macaques expect agents to pursue the most efficient routes to their goals.

Furthermore, research with nonhuman great apes has determined that they, too, are sensitive to the goals and intentions that guide the actions of others. For example, chimpanzees are able to determine when an agent is unwilling versus unable to give them food (Call et al., 2004). In this study, chimpanzees produced more begging, assertive, and coercive behaviors and left the testing room earlier when a human experimenter was unwilling to give them food than when the experimenter was purely unable to give them food. In addition, great apes are able to complete the failed actions of others, discriminate when an action is intentional versus accidental, detect cues of agency, distinguish helpers from hinderers, imitate rationally, and both anticipate and help facilitate the outcomes of others' goal-directed behaviors (Buttelmann et al., 2007, 2012, 2017; Josep Call & Tomasello, 1998; Kano & Call, 2014; Krupenye et al., 2018; Krupenye & Hare, 2018; Melis et al., 2011; Melis & Tomasello, 2013, 2019; Myowa-Yamakoshi et al., 2012; Myowa-Yamakoshi & Matsuzawa, 2000; Michael Tomasello & Carpenter, 2005; Uller, 2004; Warneken et al., 2007; Warneken & Tomasello, 2006; Yamamoto et al., 2009, 2012). The aggregation of this research over the past three decades confirms that many monkey and ape species are able to track the goals and intentions of others. However, debate remains about whether primates use a bona fide understanding of mental states to do so, or more basic principles of rational action (e.g., Gergely & Csibra, 2003). Future work must also confirm whether these skills extend to strepsirrhine primates or are unique to haplorrhines.

Section 3b: Sensitivity to others' perception

Understanding another's perspective requires not only recognizing her motivations but also constructing a model of the world as she knows it. Agents come to know their world on the basis of perception and inferences, which ultimately produce knowledge and beliefs. The capacity to understand what other individuals can see, hear, and otherwise perceive is therefore a fundamental building block for theory of mind. Sensitivity to others' perception has been examined through a variety of methodologies in primates.

First, members of all groups of primates have been shown to gaze-follow — that is, to orient to the target of another's gaze. Gaze-following can aid in the detection of mates, food, predators, and competitors (Krupenye, 2020; Ruiz et al., 2009; Sandel et al., 2011; Shepherd & Platt, 2007; Tomasello et al., 1998). Gaze-following is therefore a highly adaptive behavior potentially underlain by a variety of cognitive mechanisms, from true understanding of the nature of seeing to less sophisticated mechanisms like reflexive orienting produced by attention-grabbing gaze cues (Rosati & Hare, 2009). In the last decade, comparative cognition research has aimed to compare and contrast the underlying cognitive mechanisms of gaze-following across primates.

Several lemur species spontaneously follow the gaze of others, which suggests that gaze-following has deep evolutionary roots in the primate order (Ruiz et al., 2009; Shepherd & Platt, 2007; but see Anderson & Mitchell, 1999). Monkeys and apes are also able to follow and understand the gaze of others, in ways seemingly richer than lemurs. Several species of monkey and every great ape species gaze-follow geometrically and around barriers, and check back with an individual if they cannot pinpoint the target of their gaze (*Monkeys*: Amici et al., 2009; Bettle & Rosati, 2019; Goossens et al., 2012; Goossens et al., 2008; Scerif et al., 2004; Spadacenta et al., 2019; Tomasello et al., 2001; *Great apes*: Bräuer et al., 2005; Call et al., 1998; Okamoto et al., 2004; Okamoto-Barth et al., 2007; Povinelli & Eddy, 1996; Tomasello et al., 1998, 1999, 2007). Interestingly, lesser apes, the gibbons, also follow gaze but in one study did not check back with the actor (Horton & Caldwell, 2006; Liebal & Kaminski, 2012). Other nonprimates, like dogs, goats, corvids and tortoises, follow others' gaze as well, indicating either extremely deep evolutionary roots or multiple instances of convergent evolution (Bugnyar et al., 2004; Kaminski et al., 2005; Met et al., 2014; Schloegl et al., 2007; Téglás et al., 2012; Wilkinson et al., 2010).

In addition to gaze following, lemurs have been shown to respond to other coarse cues of attention and social orientation. They preferentially choose a food item that a competitor is oriented away from over a food item that is in the competitor's clear line of sight, and steal food from competitors who cannot see them (Bray et al., 2014; Sandel et al., 2011). However, lemurs do not seem to be sensitive to what others can hear, and do not integrate information about what others can hear and see, unlike other haplorrhine species (Bray et al., 2014). The authors suggest that this difference in sensitivity between the visual vs. auditory domains may be due to an absence of persistent social cues in this task and an inability to mentally represent the perceptually significant features of the apparatus, the mental state of the experimenter, or both. Therefore, although lemurs are able to respond appropriately to basic cues of attention and social orientation, there is no evidence that they possess a richer understanding of others' perspectives.

However, monkeys and apes have demonstrated more nuanced sensitivity to the visual and auditory perspectives of others as compared to lemurs. In competitive tasks they are able to exploit this information to their advantage (Canteloup et al., 2016, 2017; Hare et al., 2000a; Melis, Call, et al., 2006; Santos et al., 2006). Monkeys, gibbons, and great apes conceal their approach or the visibility of food, and selectively choose a food item that is not visible to their competitor (Bräuer et al., 2005; J. Burkart & Heschl, 2007; Canteloup et al., 2016; Hare et al., 2001, 2006; Karg et al., 2015; Melis, Call, et al., 2006; Sánchez-Amaro et al., 2020). For example, Hare and colleagues (2006) demonstrated that in a competitive food choice paradigm, captive chimpanzees preferentially chose to approach a food item from which an experimenter was facing away as compared to one they were facing. Chimpanzees similarly chose to approach a food item that was behind a barrier and not visible to the experimenter versus a food item placed in front of the occluder and thus visible to the experimenter (Hare et al., 2006). Monkeys and apes also selectively choose a reward that is not audible to a competitor over one that is noisy to access, and integrate information about what a competitor can see and hear; that is, they show a preference for a silent reward only when the competitor cannot already see them (Melis et al., 2006b; Santos et al., 2006). In addition, monkeys and great apes consider a recipient's orientation for communication, positioning themselves within a recipient's visual plane before beginning a gesture or collaborative act, or selecting auditory versus visual communication depending on whether the recipient was oriented toward or away from them (Anderson et al., 2010; Aychet et al., 2020; Botting & Bastian, 2019; Bourjade et al., 2014; Josep Call & Tomasello, 1994; Canteloup et al., 2015; Grueneisen et al., 2017; Hattori et al., 2006, 2009; Hostetter et al., 2001; Kaminski, 2011; Kaminski et al., 2004; Leavens et al., 2004; Liebal et al., 2004; Maille et al., 2012; Tempelmann et al., 2011). Chimpanzees also understand that an agent's choices will reflect his preferences only when he can see (Eckert et al., 2018). Thus, a large body of research suggests that haplorrhine primates are able to track *what* others can perceive. Interestingly, to date, no work has provided evidence that primates understand *how* that object looks from another's perspective (Karg et al., 2016).

Section 3c: Sensitivity to others' knowledge

Further research suggests that monkeys and apes are not just sensitive to others' perception and attentional states; they may also grasp that attention leads to knowledge, or "seeing" leads to "knowing." This includes comprehending both when an actor is knowledgeable about the state of something in the world and also when an actor is ignorant (Kuroshima et al., 2002, 2003). Rhesus macaques, chimpanzees, and bonobos consider whether an object is familiar or unfamiliar to an agent when inferring whether that object is likely to be the target of the agent's excited attention (Drayton & Santos, 2017; MacLean & Hare, 2012). Monkeys also expect an agent to reach for an object in a place where the agent saw it hidden, and even to track the object's location if the hiding places are rotated (Arre et al., 2019, 2021; Drayton & Santos, 2018; Horschler et al., 2019; Marticorena et al., 2011). These findings suggest that monkeys may expect agents to maintain, and dynamically update, representations of objects even when those objects are not currently visible. Similarly, several studies suggest that chimpanzees can track where others have seen food hidden. Chimpanzees were more likely to approach, or search for, a hidden food item when their conspecific competitor was ignorant or misinformed about the placement of the food item than when he was knowledgeable about its location (Hare et al., 2001; Kaminski et al., 2008). Critically, chimpanzees were also more likely to approach a hidden food item when their knowledgeable competitor was switched out for a new, ignorant competitor, suggesting that their ascriptions of knowledge or awareness are agent-specific (Hare et al., 2001). Finally, a field experiment with wild chimpanzees demonstrated that chimpanzees were more likely to vocalize, apparently to inform an approaching groupmate about the presence of a snake, if their groupmate had not yet seen the snake as compared to if she was already knowledgeable about its presence (Crockford et al., 2012, 2017). This finding suggests both that chimpanzees' social cognition operates in natural conspecific interactions, and that it can serve prosocial ends. However, it remains unclear whether nonhuman apes are able to differentiate between knowledgeable and ignorant informants (Call et al., 2000; Kuroshima et al., 2002, 2003;

Povinelli et al., 1990, 1991, 1994). This collection of evidence indicates that at least some monkey and ape species maintain a relatively rich sensitivity to others' knowledge.

Section 3d: Sensitivity to others' beliefs

Agents not only know (or don't know) things that they have (or have not) perceived. They also have beliefs about states of the world, which may or may not reflect reality. Because another agent's beliefs can be dissociated from one's own knowledge, understanding others' beliefs has long been seen as a core feature, and litmus test, of a metarepresentational theory of mind (Baron-Cohen et al., 1985; Dennett, 1978; Pylyshyn, 1978; Wellman et al., 2001). A false belief is an epistemic state that is in conflict with reality (e.g., believing that there are crayons in a box when in reality the contents are chocolate candies). It is characterized as a core feature of theory of mind because it requires the simultaneous representation of two conflicting states – one's own, which aligns with reality, and another's, which does not. The canonical test for the capacity to comprehend others' false beliefs is the change-of-location false belief task. This task typically involves an actor placing an object in one location and then turning away from the object or leaving the scene. In the absence of the first actor's gaze, a second actor moves the object to a different location, and therefore the first actor's belief (that the object remains in its original location) becomes false (Dennett, 1978; Wimmer & Perner, 1983). Studies tend to ask, through various verbal or nonverbal metrics, whether participants can correctly predict that the actor will search for the object in its original location, even though participants know that it is no longer there (Clements & Perner, 1994).

Early research on false belief understanding in nonhuman primates found no clear evidence that macaques or great apes were sensitive to the beliefs of others. For example, in violation of expectation paradigms, although monkeys expected an agent to search for an object where she had seen it hidden, they did not expect the agent to search for the object in that location if it was moved at all while the agent was not present (Horschler et al., 2019; Marticorena et al., 2011). Martin and Santos (2014) also found no evidence that monkeys automatically represent others' beliefs in a task in which human children appear to do so: monkeys did not require longer attention to process events that violated an agent's false beliefs (Kovacs et al., 2010; Martin & Santos, 2014).

Great apes have also struggled on a variety of false beliefs tasks, all of which were action-based tasks centered around food. In one of the first studies to test false-belief understanding in nonhuman great apes, Call and Tomasello (1999) presented apes with a hidden reward task. Apes watched a human "hider" hide a reward in one of two identical containers. A human "communicator" also watched this hiding process and helped the participant by placing a marker on the container that held the reward. However, in the crucial false belief condition, the "communicator" saw the original hiding action but then left the area, and did not see the "hider" switch the location of the container with the reward. Therefore, the "communicator" held a false belief about the location of the reward, and placed the marker on the incorrect container. If the apes understood the "communicator's" false belief, they should have chosen the other container (without the marker). However, apes continued to follow the marker, leading the authors to conclude that they did not understand false beliefs. Krachun and co-authors (2009) devised a similar competitive paradigm where chimpanzees and bonobos watched an experimenter hide a reward in the presence of a human competitor, and the competitor reached effortfully toward the location where she believed the food to be (Krachun et al., 2009). Apes tended to follow the reaching cue, even in the false belief condition where it was directed at the incorrect location (see also (Krachun et al., 2010).

In tasks involving competition with conspecifics, results are more ambiguous. Hare and colleagues (2001) found that chimpanzees were more likely to acquire food when competing with a misinformed competitor (who had witnessed the food's initial baiting but not its subsequent relocation) than a knowledgeable one. Chimpanzees were also marginally - though nonsignificantly - more likely to enter the testing arena to compete at all when the competitor was misinformed rather than knowledgeable (Hare et al., 2001). However, these findings were paralleled in conditions in which the competitor was ignorant (i.e. when the competitor did not know that a food reward had been hidden at all). As a result, it is difficult to determine whether chimpanzees actually tracked the competitor's belief that the food remained in its initial location, or only the competitor's ignorance of the food's final location. In a similar food competition task in which chimpanzee participants took turns choosing cups with food rewards, chimpanzees preferentially targeted food whose location their competitor was misinformed about (Kaminski et al., 2008). However, they also preferentially targeted food that their competitor had an incidentally true belief about (the partner had seen the food hidden but had not seen it temporarily removed and placed back in the same location). At the time, the authors concluded that chimpanzees could identify when their competitor had become (at least temporarily) ignorant and were potentially applying the same strategy of exploiting ignorance even in false belief conditions (see also Horschler et al., 2019). A more recently proposed alternative is that chimpanzees succeeded on the false belief condition and failed on the incidental true belief condition for different reasons: they tracked their competitor's false beliefs but were overwhelmed by the additional cognitive demands of the incidental true belief condition, in which it is necessary to reconcile contrasting mental states (an initial attribution of knowledge and a later attribution of ignorance) with identical content (food is in location 1) (Durdevic & Krupenye, 2021). In the incidental true belief condition, if chimpanzees failed to correctly update their representation, they would likely be left with an incorrect (more recent) representation that their competitor was ignorant.

Although early work led many to conclude that humans have a unique capacity to represent the false beliefs of others, recent evidence (in paradigms that do not involve food) raises the possibility that some nonhuman primate species do in fact share this capacity. Several eye-tracking studies have now shown that great apes and Japanese macaques (*Macaca fuscata*) visually anticipate that an actor will search for an object where he falsely believes it to be (Hayashi et al., 2020; Kano et al., 2019; Krupenye et al., 2016). Although there are some questions about the reproducibility of similar paradigms in human infants, to date these primate findings appear to be robust (Kano et al., 2020). These studies capitalized on novel methodological tools, in combination with highly engaging third-party social stimuli. Although it remains to be directly tested, the authors have argued that the use of socially dynamic stimuli may be fundamental to eliciting high engagement and reproducible results (Kano et al., 2020). Using a chemogenetic neuronal manipulation to block neuronal activity in the medial prefrontal cortices of Japanese macaques, Hayashi and colleagues (2020) further demonstrated that the medial prefrontal cortex, a key component of humans' social brain network, supports primates' capacity to predict agents' belief-based actions. Finally, Buttelmann et al. (2017) provided evidence that apes can act on their representations of others' beliefs: apes provided different help in response to an experimenter's action depending on whether that action was informed by a true or false belief. Although the evidence in monkeys remains particularly mixed, a growing body of work now suggests that at least some primates may represent others' beliefs.

Section 4: Interpreting the evidence: Do primates have a theory of mind?

As section 3 demonstrated, there is substantial evidence, particularly in monkeys and apes, consistent with the possibility that these animals track a variety of mental states. However, pinning down the mechanisms, and precisely specifying the representations that support this apparently sophisticated capacity remains a challenge, with persistent and staunch disagreement about how to interpret the evidence. Since the first comparative tests of theory of mind, alternative explanations for positive evidence have abounded, as have experimental efforts to test them.

In recent years, Celia Heyes has proposed that many (human and nonhuman) social cognitive tasks, particularly those employing spontaneous nonverbal metrics (e.g., gaze, reaction time), may not be measuring anything like mental state representation at all (Heyes, 2014a, 2014b, 2017). Instead, they might be measuring submentalizing. Submentalizing describes a constellation of low-level, domain-general mechanisms, such as "the processes that mediate involuntary attentional orienting, spatial coding of response locations, object-centered spatial coding of stimulus locations, retroactive interference, and distraction" (Heyes, 2014a). Many of these processes are akin to perceptual cueing effects and, collectively, Heyes argues, they can account for a great many experimental results. Since these processes can help us to anticipate outcomes, including in social settings, they may constitute fundamental mechanisms that feed into true mentalizing. However, on their own, they do not involve the representation of mental states, or of anything social. Heyes has challenged researchers studying theory of mind to control for the influence of submentalizing with inanimate control conditions. For example, in video-based eye-tracking tasks, the human or conspecific agent can be replaced by an inanimate shape. Inanimate control conditions should mirror the perceptual features of experimental conditions but minimize the sorts of agency cues that are necessary for proper mentalizing. Provided that they elicit comparable levels of attention, submentalizing predicts that inanimate controls will yield comparable performance to experimental conditions, if experimental results indeed derive from domain-general mechanisms.

Several studies speak against the argument that submentalizing alone can explain primates' performance in theory of mind tasks (Kano et al., 2017). For example, Kano and Call

(2014) showed that great apes visually anticipate the goal-directed reaching behavior of a human hand but not an inanimate claw, after first observing the hand or claw interact with objects in the same way (Kano & Call, 2014). Second, Krupenye et al. (2017) implemented an inanimate control that was closely matched to a previous eye-tracking false belief experiment (Experiment 2 of Krupenye et al., 2016; Krupenye et al., 2017): instead of a human agent observing an object and returning to search for it, apes watched a green shape exhibiting matched movements in an animated version of the same scene. Although apes showed similar attention to both versions, the control did not elicit the successful anticipatory looking that was documented in the original experiment. Similar results were recently reported with human infants (Surian & Franchin, 2020). Although future work, particularly in other taxa, should continue to control for submentalizing, existing findings (including others discussed in more detail by Kano et al., 2017) suggest that submentalizing alone cannot account for performance on theory of mind tasks, at least in apes.

However, other alternative explanations persist. Over the last few decades, the dominant debate in the animal theory of mind literature has concerned whether animals are really reading minds, or just reading behavior (Heyes, 2015; Penn & Povinelli, 2007). The problem stems from the fact that mental states are often inferred based on observed behavioral cues (e.g., an agent's facial orientation is a cue to what she can see). However, organisms might also learn rules, or associations, linking behavioral cues to outcomes that frequently follow them (e.g., that agents tend to pursue objects within their unobstructed line-of-gaze). In experiments in which behavioral cues are available, it is impossible to determine whether subjects are responding to those cues alone or are additionally inferring from them a bona fide mental state, or at least what Whiten has called an intervening variable (an abstraction that commonly links a variety of behavioral cues to a variety of predicted future behaviors) (Whiten, 1996, 1994, 2013).

Researchers have gone to a variety of lengths to control for individual behavior rules or behavioral cues (see, e.g., Table 1 of Hare, 2011). For example, some studies have presented primates with identical behavior across conditions, except for subtle differences linked to mental states, in an effort to minimize behavior-reading explanations (e.g., Drayton & Santos, 2017; MacLean & Hare, 2012). Others have dissociated particular cues, such as 'line of gaze', from particular mental states, such as seeing, by using mirrors in clever ways: showing that chimpanzees selectively beg for food from experimenters who can see them, including in cases in which the experimenter can see the subject through a mirror but has her back turned to the subject so that her line-of-gaze is actually directed away from the subject (Lurz et al., 2018). In several other studies, the agent was removed entirely in an effort to exclude all available cues (Bugnyar et al., 2016; Schmelz et al., 2011; Schmelz et al., 2013).

The strongest test of mindreading, called the goggles test, was proposed by Heyes (2015, 1998) who was inspired by Novey (1979), and it has since been promoted by a number of scholars (e.g., Penn & Povinelli, 2007; Whiten, 2013). Heyes (1998) noted that an unusually powerful way to exclude behavior-reading explanations would be to engineer a scenario in which behavioral cues are kept constant, and subjects are likely able to solve the task only if they can project onto an agent a novel mental state that they themselves have only just experienced (Heyes, 1998). The paradigmatic example involves two sets of identical goggles. Both appear to be opaque but, through experience, subjects learn that one is in fact transparent. Mindreading subjects who then witness an experimenter wearing the goggles should determine whether the experimenter can see by projecting onto the experimenter the subject’s own experience of seeing or not seeing through those same goggles. Heyes argued that, because the goggles do not differ in appearance, they are distinguished only by the subject’s internal mental experience of them, and that this, rather than any behavioral cue, is the only available information the subject can use to correctly predict the experimenter’s actions.

This paradigm has been successfully adapted for apes in two studies (see also related work with human infants: Meltzoff & Brooks, 2008; Senju et al., 2011). Karg and colleagues (2015) presented chimpanzees with a competitive setting (similar to Hare et al., 2006; Melis, et al., 2006), in which subjects could approach either of two compartments to steal food from a human competitor. From the subject’s perspective, the lids of the two compartments appeared to be opaque but, from the competitor’s perspective, one was actually transparent. In an initial phase, the lids were raised so that subjects could view them from the same perspective as the experimenter, allowing subjects to experience their divergent occlusive properties. In the test, chimpanzees preferentially stole food from the opaque container; that is, they used their self-experience with the perceptual properties of the two containers to determine how best to exploit the competitor. In an anticipatory looking eye-tracking study, Kano and colleagues (2019) similarly showed that great apes apply their self-experience with the occlusive properties of a barrier (i.e., opaque or see-through) to predict whether an agent will behave as though he can see through that same barrier. Excitingly, in this study, apes responded differentially to the exact same video stimulus depending on whether they had previously experienced the barrier in real life as opaque or see-through. Some researchers have argued that the goggles task can be solved non-mentalisticly if subjects integrate the information they learn about the occlusive properties of the experimental substrate (i.e., that it does or does not obstruct line-of-gaze) with existing behavior rules (rather than by projecting their experience of seeing or not seeing onto the agent) (Henley & Povinelli, 2020; Lurz, 2009; Perner, 2012); others have challenged this deflationary account (e.g., Heyes, 2015). In either case, the goggles task remains the strongest identified nonverbal test of mindreading currently on the market, and it is one that at least great apes have passed.

The broader body of work has been interpreted in contradictory ways. Some scholars have emphasized that no single experiment provides unequivocal evidence of mindreading (e.g., Penn & Povinelli, 2007). Others have argued that, although it is challenging to control for all possible alternatives in any one experiment, positing a common mindreading capacity is more parsimonious than the diverse suite of behavior rules that would be necessary to explain primates' success across the full range of theory of mind tasks (e.g., Tomasello & Call, 2008). Whereas we think that researchers should continue their efforts to adjudicate amongst mentalistic and nonmentalistic explanations of primate social behavior, we also want to relay a key point made by Barrett (2018): that the mechanisms underlying mindreading or behavior-reading in primates remain underspecified. The key task moving forward then, at least for the cognitivist, is to precisely characterize the representations that support primate social cognition and the mechanisms that compute, store, and utilize those representations (see, e.g., Butterfill & Apperly, 2013; Krupenye, 2020; Martin & Santos, 2016; Penn et al., 2008; Phillips & Norby, 2019).

Section 5: The evolution of theory of mind

As we described earlier, another major goal of animal theory of mind research is to reconstruct its evolutionary history and identify selective pressures that may have driven its evolution (Krupenye, 2020). In this section, we will address these issues in turn. By comparing theory of mind abilities across primates, as we have done in Section 3, we can identify traits that are widespread and that were likely present in a basal common ancestor – and we can also identify those that likely appeared in a later common ancestor and are only found in the narrower range of species that descended from it. Before attempting to chart the evolutionary history of theory of mind within primates, we first note that biases exist in sampling effort, with greater experimental attention to the capacities of species more closely related to humans, and that future work should broaden its phylogenetic focus to further test this preliminary model and to fill gaps in our understanding.

That being said, current data suggest that primates from all major clades (strepsirrhines, platyrrhines, cercopithecoids, and hominoids) share a coarse sensitivity to social cues, like gaze direction. Limitations among strepsirrhines hint that the most basic foundations of theory of mind may have been primitive heuristics that allowed our ancestors to respond adaptively to the visual orientation of conspecifics and predators (Bray et al., 2014; Sandel et al., 2011). These capacities were likely present in an ancestor common to all major primate clades that lived about 77 million years ago (Steiper & Young, 2006).

It is unclear whether that ancestor had any appreciation of others as goal-directed agents, as research into this capacity is limited in strepsirrhines. However, by 43 million years ago, the common ancestor of platyrrhines, cercopithecoids, and hominoids appears to have possessed this appreciation in some fundamental sense. There is evidence from members of all descendent clades that they treat others' actions as goal-directed. This common ancestor may also have had a richer capacity for perspective-taking than earlier ancestors (e.g., Burkart & Heschl, 2007; Defolie et al., 2015), although the evidence for this is particularly plentiful among cercopithecoid and hominoid primates who share a common ancestor that lived 30 million years ago. By this time, our common ancestor was likely capable of tracking, in some sense, what others could see (e.g., Flombaum & Santos, 2005; Hare et al., 2000), and what they could know (e.g., Drayton & Santos, 2017; MacLean & Hare, 2012). It is also possible that this ancestor may have represented something about what others believe, although the evidence in cercopithecoids is even more mixed (e.g., Hayashi et al., 2020; Marticorena et al., 2011) than in hominoids (e.g., Buttelmann et al., 2017; Kano et al., 2019; Krupenye et al., 2016). Among hominoids, whose ancestors lived closer to 20 million years ago, there is also more substantial evidence to support the view that these animals' representations may be mentalistic (e.g., Kano et al., 2019; Karg et al., 2015; Lurz et al., 2018), although complementary experiments have not been performed in other primates. Human theory of mind, of course, is defined by numerous features and capabilities not demonstrated in other species, such as *explicit* representation of others' mental states, understanding of *how* things look from another's perspective, and the capacity to structure cooperation around a shared mental framework of common goals (for a more full list, see Krupenye, 2020). Further work will be necessary to determine how closely the social cognitive abilities of our closest relatives, chimpanzees and bonobos, approximate those of humans. However, our phylogenetic reconstruction suggests an elaboration of social cognition throughout primate evolutionary history, with the most notable differences occurring between strepsirrhines and haplorhines and, presumably, between nonhuman apes and humans.

What drove the evolution of social cognition? Although it is possible that some capacities arose through evolutionary mechanisms beyond natural selection, or as byproducts of selection on other related traits, several adaptive hypotheses have been put forward. These hypotheses are largely of three varieties, proposing that cognitive and brain evolution were driven by selective pressures for navigating either foraging challenges (ecological intelligence hypothesis), social challenges (social intelligence hypothesis), or a combination of the two (cultural intelligence hypothesis) (Reader et al., 2011). Within each family of hypotheses, variants further specify whether these selective pressures are thought to have driven increases in overall brain size and general cognitive skill as a whole, or whether they selected for elaboration of specific brain structures or cognitive capacities.

Given the high metabolic costs of brain tissue, adaptations to diet and gut morphology may help to meet those costs and release evolutionary constraints on brain size and cognitive capacities (Aiello & Wheeler, 1995; Pontzer et al., 2016; Wrangham, 2009). Foraging challenges may also directly select for cognitive adaptations, because certain feeding strategies (e.g., finding sparse and ephemeral resources like fruits) may demand particular cognitive abilities (e.g., spatial cognition and memory) (Clutton-Brock & Harvey, 1980; Milton, 1998; Rosati, 2018). Comparisons across primate species provide support for the role of feeding ecology in shaping the evolution of brain size and general cognitive capacities: species with more demanding ecologies tend to have larger brains and better performance on inhibitory control tasks (DeCasien et al., 2017; MacLean et al., 2014; Powell et al., 2017).

However, research also provides evidence that the challenges associated with navigating the social world – competing (and coordinating) with groupmates for reproductive opportunities – may confer adaptive benefits to the most socially savvy and select for social-cognitive adaptations (Byrne & Whiten, 1988; Byrne & Bates, 2007; Dunbar & Shultz, 2007; Humphrey, 1976; Jolly, 1966). Distantly related taxa that exhibit complex social systems—such as primates, cetaceans, and corvids—appear to have convergently evolved sophisticated social cognition (Emery & Clayton, 2004). Among closely related taxa in at least two lineages, species with more complex social systems also perform better on social cognitive tasks than those with less complex social systems (Bond et al., 2003; MacLean et al., 2008, 2013; Sandel et al., 2011). Observational anecdotes (Byrne & Whiten, 1988; de Waal, 1982) and controlled experiments (reviewed above, see also: Cheney & Seyfarth, 2007) also point to a number of potential adaptive functions of social cognition, in competition, deception, communication, and coordination. Although more work will be needed to probe the adaptive origins of theory of mind, research to date points to a mixture of ecological drivers enabling brain expansion and social factors selecting for social cognitive skill.

Section 6: Future Directions

Comparative cognition has seen countless advances in theory of mind research since its inception over four decades ago. Clever experiments have demonstrated that a range of species are sensitive to others' goals, perception, and beliefs. Studies have begun to clarify underlying mechanisms, determine the phylogenetic origins of specific traits, and identify selective drivers of social cognitive evolution. Despite such progress, as we have shown here, open questions abound, as do disagreements about how best to interpret existing evidence. In this final section, we point to what we see as particularly fruitful avenues for future research.

One fundamental priority should be honing our (lean and rich) hypotheses about the mechanisms that support primate social behavior. Central to this effort will be specifying the cognitive representations that primates generate when tracking others' perspectives, clarifying the extent to which their representational formats are innate or constructed through processes of learning and development, and determining how they are generated in real-time, encoded in memory, and deployed in prediction and decision-making. To date, a range of representational formats have been hypothesized, from awareness relations (Martin & Santos, 2016) to belief-like states (Butterfill & Apperly, 2013) to propositional attitudes, offering testable predictions for future work.

Alongside this effort, researchers should continue to take seriously, and directly test, the alternative explanations that have proliferated over the years. They should also seek to triangulate and conceptually replicate findings of theoretical significance, and to leverage both new and old methodologies to confirm existing findings and to seek novel frontiers. Tasks in which the goal is not to obtain food but rather to understand or engage in social interactions (e.g., Krupenye et al., 2016) could also help to elucidate primates' capacities, as a focus on food may inhibit the capacity to fully attribute mental states to others (Kano et al., 2017; Völter et al., 2019). Primate social cognition research would also greatly benefit from the addition of computational work to elucidate the mathematics behind theory of mind abilities. By building computational models, cognitive scientists can generate plausible and mathematically sound accounts of the computations involved in specific theory of mind processes (Baker et al., 2017; Lake et al., 2017; Ullman et al., 2009). Alternative models can be pitted against one another, producing sets of competing predictions, and experiments can be designed to adjudicate amongst competing models.

Correlational studies and cognitive test batteries, encompassing suites of social and nonsocial tasks, are another fundamental tool for understanding the mechanisms and broader cognitive architecture that support primate theory of mind (Krachun et al., 2019; Völter et al., 2018). Large test batteries can help to identify individual as well as species differences in cognitive performance and, through correlated variation, point to links between social and nonsocial capacities that are commonly involved in social cognitive tasks. Further, the administration of multiple rounds of such test batteries at various intervals across the participants' life span would also help to identify ontogenetic patterns of theory of mind development and to compare them across species. A better understanding of the developmental trajectories of theory of mind abilities across species would produce a clearer picture of the underlying mechanisms and their relationships to each other (i.e., which early mechanisms may support the development of which later ones). This would also aid in clarifying the unique developmental patterns that ultimately lead to differences in adult cognition and theory of mind abilities across species (Hare et al., 2012; Krupenye et al., 2017; Krupenye & Call, 2019; Wobber et al., 2010).

Finally, testing for theory of mind capacities in a greater number of nonhuman species would expand our understanding of both the phylogenetic origins of these capacities as well as the selective pressures that shaped them across taxa (Krupenye & Call, 2019; Tomasello et al., 2001). To date, the vast majority of theory of mind research has focused on chimpanzees (and to some extent other great apes) and macaques, with other species receiving comparatively much less attention. When comparing samples across development, across species, or across populations within species, researchers should be mindful of the many factors that shape cognitive performance, from motivation to rearing history, life history stage, testing environment, and the suitability of the task (Leavens et al., 2019). Attention to such sources of variation can fuel more powerful tests as well as more judicious interpretations of research findings and the evolutionary and ontogenetic origins of differences across populations.

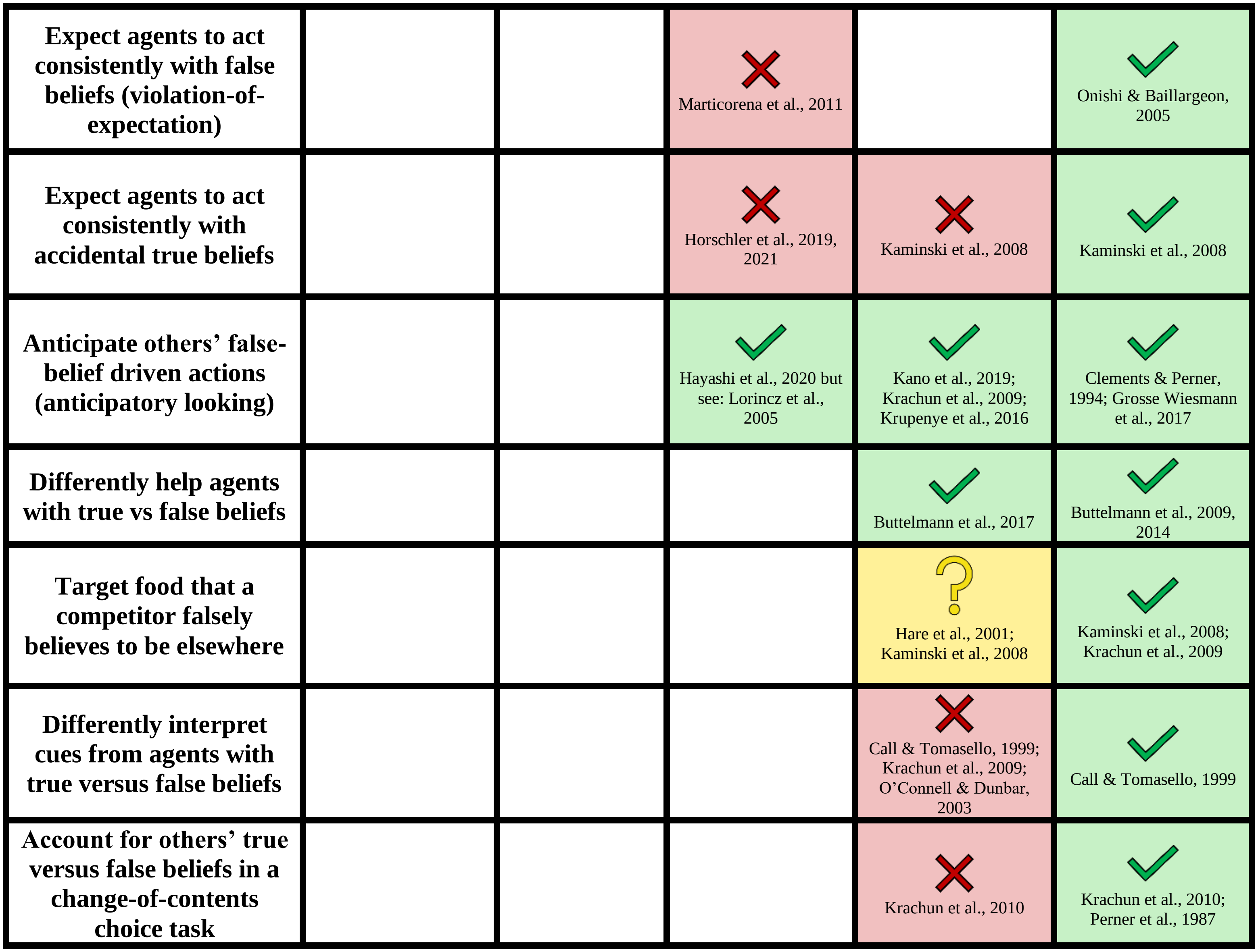
As we have alluded throughout this paper, there are many emerging frontiers and open questions in theory of mind research. How do primates understand false beliefs? Do primates know *how* something looks from another's perspective (level II perspective-taking), or only *what* another has perceived (level I perspective-taking)? Are primates conscious of their mental state representations, or do they just track them implicitly? Can primates embed mental state representations in higher levels of recursion (for example, tracking not just that agent 1 knows something, but also that agent 1 knows that agent 2 knows something)? Can primates track shared goals or common ground or engage in shared intentional mental frameworks to facilitate coordination (e.g., Heesen et al., 2020; Tomasello et al., 2005)? How did theory of mind evolve? With powerful new tools and myriad avenues for investigation, the future promises exciting discoveries that will move us ever closer to answering many of these questions, and ultimately to understanding the origins and psychology of theory of mind in humans and other primates.

					
Theory of Mind Evidence	**Strepsirrhines: Lemurs, lorises, & galagos**	**Platyrrhines: Monkeys of the Americas**	**Catarrhines: Monkeys of Afro-Eurasia**	**Hominoids: Nonhuman Great Apes**	**Hominins: Humans**
Sensitivity to others' goals					
Expect agents to pursue goals consistently		✓ Burkart et al., 2012; Kupferberg et al., 2013		✓ Kano & Call, 2014; Myowa-Yamakoshi et al., 2012	✓ Woodward, 1998
Expect agents to pursue goals efficiently			✓ Rochat et al., 2008	✓ Uller, 2004	✓ Gergely et al., 1995
Help others achieve their goals		✓ Barnes et al., 2008; Burkart et al., 2007; Drayton & Santos, 2014		✓ Buttelmann et al., 2017; Krupenye et al., 2018; Melis et al., 2011; Melis & Tomasello, 2013, 2019; Warneken et al., 2007; Warneken & Tomasello, 2006; Yamamoto et al., 2009, 2012	✓ Moll & Tomasello, 2004; Warneken & Tomasello, 2006
Complete others' intended (but failed) actions				✓ Myowa-Yamakoshi & Matsuzawa, 2000; Tomasello & Carpenter, 2005	✓ Carpenter et al., 2002; Meltzoff, 1995; Myowa-Yamakoshi & Matsuzawa, 2000
Exploit competitive reaches in object choice tasks			✗ Joly et al., 2017	✓ Hare & Tomasello, 2004; Herrmann et al., 2007, 2010	✓ Herrmann et al., 2007

Copy goal-directed actions	✓ Schnoell & Fichtel, 2012	✓ J. Burkart et al., 2012; Voelkl & Huber, 2000	✓ Van de Waal et al., 2015; Van de Waal & Whiten, 2012	✓ Buttelmann et al., 2007; Horner & Whiten, 2005	✓ Gergely et al., 2002
Rationally imitate				✓ Buttelmann et al., 2007; Horner & Whiten, 2005	✓ Gergely et al., 2002; Carpenter et al., 2005 Carpenter et al., 2005; Gergely et al., 2002
Differentiate others' intentional versus accidental actions		✓ Wood et al., 2007	? Wood et al., 2007; but see Costes-Thiré et al., 2015	✓ Call & Tomasello, 1998; Tomasello & Carpenter, 2005; but see Povinelli et al., 1998	✓ Call & Tomasello, 1998; Carpenter et al., 1998; Olineck & Poulin-Dubois, 2005
Differentiate unwilling versus unable others		✓ Phillips et al., 2009; but see: Drayton et al., 2016	✓ Canteloup & Meunier, 2017	✓ Buttelmann et al., 2012; Call et al., 2004	✓ Behne et al., 2005
Differentiate helping versus hindering agents		✓ Anderson et al., 2013; Anderson et al., 2013; Brügger et al., 2021; Kawai et al., 2014, 2019	✗ Kawai et al., 2019	✓ Herrmann et al., 2013; Krupenye & Hare, 2018; Russell et al., 2008; Subiaul et al., 2008	✓ Hamlin et al., 2007
Sensitivity to others' perception					
Follow others' gaze	✓ Ruiz et al., 2009; Sandel et al., 2011; Shepherd & Platt, 2007; but see Anderson & Mitchell, 1999; Itakura, 1996	✓ Amici et al., 2009; Burkart & Heschl, 2007; Spadacenta et al., 2019	✓ Anderson & Mitchell, 1999; Bettle & Rosati, 2019; Goossens et al., 2012; Goossens et al., 2008; Micheletta & Waller, 2012; Tomasello et al., 1998, 2001	✓ Bräuer et al., 2005; Call et al., 1998; Herrmann et al., 2010; Horton & Caldwell, 2006; Itakura, 1996; Kano & Call, 2014; Okamoto et al., 2004; Okamoto-Barth et al., 2007; Povinelli & Eddy, 1996, 1997; Tomasello et al., 1998, 1999, 2001	✓ Butterworth & Jarrett, 1991; Tomasello et al., 2007
Follow others' gaze around barriers		✓ Amici et al., 2009	✓ Bettle & Rosati, 2019; Goossens et al., 2012	✓ Bräuer et al., 2005; Okamoto-Barth et al., 2007; Povinelli & Eddy, 1996; Tomasello et al., 1999	✓ Moll & Tomasello, 2004

Check back with actor when target of gaze is unclear		? Burkart & Heschl, 2006; but see Amici et al., 2009	✓ Goossens et al., 2008; Scerif et al., 2004	✓ Bräuer et al., 2005; Call et al., 1998; Horton & Caldwell, 2006; Okamoto-Barth et al., 2007	✓ Scaife & Bruner, 1975
Consider recipient's orientation for communication		✓ Anderson et al., 2010; Defolie et al., 2015; Hattori et al., 2007, 2010	✓ Aychet et al., 2020; Bourjade et al., 2014; Canteloup et al., 2015b; Deshpande et al., 2018; Lamaury et al., 2019; Maille et al., 2012; Meunier et al., 2013	✓ Bania & Stromberg, 2013; Botting & Bastian, 2019b, 2019c; Josep Call & Tomasello, 1994; Hostetter et al., 2001; Kaminski et al., 2004; Leavens et al., 2004; Liebal et al., 2004; Lurz et al., 2018; Poss et al., 2006; Povinelli et al., 1996, 2003; Tempelmann et al., 2011; Michael Tomasello et al., 1994; but see Theall & Povinelli, 1999	✓ Liszkowski et al., 2008
Exploit information about what another can or cannot see in competition	✓ Bray et al., 2014; MacLean et al., 2013; Sandel et al., 2011	? Burkart & Heschl, 2007; but see Hare et al., 2003	✓ Canteloup et al., 2016, 2017; Flombaum & Santos, 2005; Overduin - de Vries et al., 2013; Vick & Anderson, 2003	✓ Bräuer et al., 2007; Grueneisen et al., 2017; Hare et al., 2000, 2001, 2006; Karg et al., 2015; Karin-D'Arcy & Povinelli, 2002; Melis et al., 2006; Sánchez-Amaro et al., 2020	✓ Grueneisen et al., 2017; Melis et al., 2010
Exploit information about what another can or cannot hear in competition	✗ Bray et al., 2014		✓ Santos et al., 2006; but see Costes-Thiré et al., 2015	✓ Melis et al., 2006; Slocombe & Zuberbuhler, 2007; but see Bräuer et al., 2008	✓ Melis et al., 2010
Integrate information about seeing and hearing in competition	✗ Bray et al., 2014		✓ Santos et al., 2006	✓ Melis et al., 2006	✓ Melis et al., 2010
Exploit others' presumed inferences in competition				✓ Schmelz et al., 2011	✓ Pillow & Pearson, 2012
Consider information about what another can see in cooperation				✓ Grueneisen et al., 2017	✓ Grueneisen et al., 2017
Use agent's visual orientation to make inferences about preferences				✓ Eckert et al., 2018	✓ Luo & Baillargeon, 2007

Manipulate what others can see				✓ Grueneisen et al., 2017; Hall et al., 2017; Hare et al., 2006; Karg et al., 2015	✓ Grueneisen et al., 2017
Use personal perceptual experience to exploit others' perception				✓ Kano et al., 2019; Karg et al., 2015	✓ Meltzoff & Brooks, 2008
Consider *how* something looks from another's perspective				✗ Karg et al., 2016	✓ Moll & Meltzoff, 2011
Sensitivity to others' knowledge and ignorance					
Expect agents to search where they have seen something hidden			✓ Arre et al., 2019, 2021; Drayton & Santos, 2018; Horschler et al., 2019; Marticorena et al., 2011	✓ Kaminski et al., 2008	✓ Onishi & Baillargeon, 2005
Target food that a competitor has not seen hidden				✓ Hare et al., 2001; Kaminski et al., 2008	✓ Kaminski et al., 2008
Communicate differentially with knowledgeable versus ignorant others (presumably, to inform)				✓ Crockford et al., 2012, 2017	✓ Liszkowski et al., 2008
Consider agent's awareness of object when seeking the target of her attention			✓ Drayton & Santos, 2017	✓ MacLean & Hare, 2012	✓ Tomasello & Haberl, 2003 Tomasello & Haberl, 2003
Discriminate knowledgeable versus ignorant informants		? Kuroshima et al., 2002, 2003	✗ Povinelli et al., 1991	? Povinelli et al., 1990 but see Call et al., 2000; Povinelli et al., 1994	✓ Povinelli & DeBlois, 1992
Sensitivity to others' beliefs					
Experience interference from others' beliefs			✗ Martin & Santos, 2014		✓ Kovacs et al., 2010



Expect agents to act consistently with false beliefs (violation-of-expectation)			✗ Marticorena et al., 2011		✓ Onishi & Baillargeon, 2005
Expect agents to act consistently with accidental true beliefs			✗ Horschler et al., 2019, 2021	✗ Kaminski et al., 2008	✓ Kaminski et al., 2008
Anticipate others' false-belief driven actions (anticipatory looking)			✓ Hayashi et al., 2020 but see: Lorincz et al., 2005	✓ Kano et al., 2019; Krachun et al., 2009; Krupenye et al., 2016	✓ Clements & Perner, 1994; Grosse Wiesmann et al., 2017
Differently help agents with true vs false beliefs				✓ Buttelmann et al., 2017	✓ Buttelmann et al., 2009, 2014
Target food that a competitor falsely believes to be elsewhere				? Hare et al., 2001; Kaminski et al., 2008	✓ Kaminski et al., 2008; Krachun et al., 2009
Differently interpret cues from agents with true versus false beliefs				✗ Call & Tomasello, 1999; Krachun et al., 2009; O'Connell & Dunbar, 2003	✓ Call & Tomasello, 1999
Account for others' true versus false beliefs in a change-of-contents choice task				✗ Krachun et al., 2010	✓ Krachun et al., 2010; Perner et al., 1987

Fig. 1: Theory of mind capacities and precursors across primate clades. Evidence or lack thereof is organized around sensitivity to particular classes of mental studies, broken down by coarse varieties of evidence. A red X reflects negative evidence, a green checkmark reflects positive evidence, a yellow question mark indicates contradicting evidence (with positive evidence listed first, and negative evidence listed second), and empty cells reflect no evidence thus far. Contradicting evidence (yellow boxes) may also reflect clades where some species uniformly succeed and others do not. While we have attempted to aggregate all nonhuman primate evidence, human examples are illustrative but not comprehensive. Photo copyrights: Liran Samuni (bonobo image) and creative commons licenses (all other images).

References

Aiello, L. C., & Wheeler, P. (1995). The Expensive-Tissue Hypothesis: The Brain and the Digestive System in Human and Primate Evolution. *Current Anthropology*, *36*(2), 199–221. https://doi.org/10.1086/204350

Amici, F., Aureli, F., Visalberghi, E., & Call, J. (2009). Spider monkeys (Ateles geoffroyi) and capuchin monkeys (Cebus apella) follow gaze around barriers: Evidence for perspective taking? *Journal of Comparative Psychology*, *123*(4), 368–374. https://doi.org/10.1037/a0017079

Anderson, J. R., Kuroshima, H., Hattori, Y., & Fujita, K. (2010). Flexibility in the use of requesting gestures in squirrel monkeys (Saimiri sciureus). *American Journal of Primatology*, *72*(8), 707–714. https://doi.org/10.1002/ajp.20827

Anderson, J. R., Kuroshima, H., Takimoto, A., & Fujita, K. (2013). Third-party social evaluation of humans by monkeys. *Nature Communications*, *4*(1), 1561. https://doi.org/10.1038/ncomms2495

Anderson, J. R., & Mitchell, R. W. (1999). Macaques but Not Lemurs Co-Orient Visually with Humans. *Folia Primatologica*, *70*(1), 17–22. https://doi.org/10.1159/000021670

Anderson, J. R., Montant, M., & Schmitt, D. (1996). Rhesus monkeys fail to use gaze direction as an experimenter-given cue in an object-choice task. *Behavioural Processes*, *37*(1), 47–55. https://doi.org/10.1016/0376-6357(95)00074-7

Anderson, J. R., Takimoto, A., Kuroshima, H., & Fujita, K. (2013). Capuchin monkeys judge third-party reciprocity. *Cognition*, *127*(1), 140–146. https://doi.org/10.1016/j.cognition.2012.12.007

Arre, A. M., Clark, C. S., & Santos, L. R. (2019). Do young rhesus macaques know what others see?: A comparative developmental perspective. *American Journal of Primatology*, *82*(11), e23054. https://doi.org/10.1002/ajp.23054

Arre, A. M., Stumph, E., & Santos, L. R. (2021). Macaque species with varying social tolerance show no differences in understanding what other agents perceive. *Animal Cognition*. https://doi.org/10.1007/s10071-021-01485-5

Aychet, J., Pezzino, P., Rossard, A., Bec, P., Blois-Heulin, C., & Lemasson, A. (2020). Red-capped mangabeys (Cercocebus torquatus) adapt their interspecific gestural communication to the recipient's behaviour. *Scientific Reports*, *10*(1), 12843. https://doi.org/10.1038/s41598-020-69847-6

Baillargeon, R., Scott, R. M., & Bian, L. (2016). Psychological Reasoning in Infancy. *Annual Review of Psychology*, *67*(1), 159–186. https://doi.org/10.1146/annurev-psych-010213-115033

Baker, C. L., Jara-Ettinger, J., Saxe, R., & Tenenbaum, J. B. (2017). Rational quantitative attribution of beliefs, desires and percepts in human mentalizing. *Nature Human Behaviour*, *1*(4), 1–10. https://doi.org/10.1038/s41562-017-0064

Bania, A., & Stromberg, E. (2013). The Effect of Body Orientation on Judgments of Human Visual Attention in Western Lowland Gorillas (Gorilla gorilla gorilla). *Journal of Comparative Psychology (Washington, D.C. : 1983)*, *127*. https://doi.org/10.1037/a0027261

Barnes, J. L., Hill, T., Langer, M., Martinez, M., & Santos, L. R. (2008). Helping behaviour and regard for others in capuchin monkeys (Cebus apella). *Biology Letters*, *4*(6), 638–640. https://doi.org/10.1098/rsbl.2008.0410

Baron-Cohen, S., Leslie, A. M., & Frith, U. (1985). Does the autistic child have a “theory of mind” ? *Cognition*, *21*(1), 37–46. https://doi.org/10.1016/0010-0277(85)90022-8

Barrett, L. (2018). Picturing Primates and Looking at Monkeys: Why 21st Century Primatology Needs Wittgenstein. *Philosophical Investigations*, *41*(2), 161–187. https://doi.org/10.1111/phin.12189

Behne, T., Carpenter, M., Call, J., & Tomasello, M. (2005). Unwilling Versus Unable: Infants’ Understanding of Intentional Action. *Developmental Psychology*, *41*(2), 328–337. https://doi.org/10.1037/0012-1649.41.2.328

Beliefs about beliefs: Representation and constraining function of wrong beliefs in young children’s understanding of deception. (1983). *Cognition*, *13*(1), 103–128. https://doi.org/10.1016/0010-0277(83)90004-5

Bettle, R., & Rosati, A. (2019). Flexible gaze-following in rhesus monkeys. *Animal Cognition*, *22*. https://doi.org/10.1007/s10071-019-01263-4

Bond, A. B., Kamil, A. C., & Balda, R. P. (2003). Social complexity and transitive inference in corvids. *Animal Behaviour, 65*(3), 479–487. https://doi.org/10.1006/anbe.2003.2101

Botting, J., & Bastian, M. (2019a). Orangutans (Pongo pygmaeus and Hybrid) and Gorillas (Gorilla gorilla gorilla) Modify Their Visual, but Not Auditory, Communicative Behaviors, Depending on the Attentional State of a Human Experimenter. *International Journal of Primatology, 40*(2), 244–262. https://doi.org/10.1007/s10764-019-00083-0

Botting, J., & Bastian, M. (2019b). Orangutans (Pongo pygmaeus and Hybrid) and Gorillas (Gorilla gorilla gorilla) Modify Their Visual, but Not Auditory, Communicative Behaviors, Depending on the Attentional State of a Human Experimenter. *International Journal of Primatology*, *40*(2), 244–262. https://doi.org/10.1007/s10764-019-00083-0

Botting, J., & Bastian, M. (2019c). Examining the Use of Auditory Signals as “Attention-Getters” in Zoo-Housed Gorillas (Gorilla gorilla gorilla) and Orangutans (Pongo pygmaeus and Hybrid). *International Journal of Primatology*, *40*(4), 573–586. https://doi.org/10.1007/s10764-019-00100-2

Bourjade, M., Meguerditchian, A., Maille, A., Gaunet, F., & Vauclair, J. (2014). Olive baboons, Papio anubis, adjust their visual and auditory intentional gestures to the visual attention of others. *Animal Behaviour*, *87*, 121–128. https://doi.org/10.1016/j.anbehav.2013.10.019

Boyd, R. (2006). The Puzzle of Human Sociality. *Science*, *314*(5805), 1555–1556. https://doi.org/10.1126/science.1136841

Boysen, S. T., & Berntson, G. G. (1986). Cardiac correlates of individual recognition in the chimpanzee (Pan troglodytes). *Journal of Comparative Psychology*, *100*(3), 321–324. https://doi.org/10.1037/0735-7036.100.3.321

Bräuer, J., Call, J., & Tomasello, M. (2005). All Great Ape Species Follow Gaze to Distant Locations and Around Barriers. *Journal of Comparative Psychology*, *119*(2), 145–154. https://doi.org/10.1037/0735-7036.119.2.145

Bräuer, J., Call, J., & Tomasello, M. (2007). Chimpanzees really know what others can see in a competitive situation. *Animal Cognition*, *10*, 439–448. https://doi.org/10.1007/s10071-007-0088-1

Bräuer, J., Call, J., & Tomasello, M. (2008). Chimpanzees do not take into account what others can hear in a competitive situation. *Animal Cognition*, *11*(1), 175–178. https://doi.org/10.1007/s10071-007-0097-0

Bray, J., Krupenye, C., & Hare, B. (2014a). Ring-tailed lemurs (Lemur catta) exploit information about what others can see but not what they can hear. *Anim Cogn*, 10.

Bray, J., Krupenye, C., & Hare, B. (2014b). Ring-tailed lemurs (Lemur catta) exploit information about what others can see but not what they can hear. *Animal Cognition*, *17*(3), 735–744. https://doi.org/10.1007/s10071-013-0705-0

Brügger, R. K., Willems, E. P., & Burkart, J. M. (2021). Do marmosets understand others' conversations? A thermography approach. *Science Advances*, *7*(6), eabc8790. https://doi.org/10.1126/sciadv.abc8790

Bugnyar, T., & Kotrschal, K. (2002). Observational learning and the raiding of food caches in ravens, Corvus corax: Is it 'tactical' deception? *Animal Behaviour*, *64*(2), 185–195. https://doi.org/10.1006/anbe.2002.3056

Bugnyar, T., Reber, S. A., & Buckner, C. (2016). Ravens attribute visual access to unseen competitors. *Nature Communications*, *7*(1), 10506. https://doi.org/10.1038/ncomms10506

Bugnyar, T., Stöwe, M., & Heinrich, B. (2004). Ravens, Corvus corax, follow gaze direction of humans around obstacles. *Proceedings of the Royal Society B: Biological Sciences*, *271*(1546), 1331–1336. https://doi.org/10.1098/rspb.2004.2738

Burkart, J., & Heschl, A. (2006). Geometrical gaze following in common marmosets (Callithrix jacchus). *Journal of Comparative Psychology (Washington, D.C. : 1983)*, *120*, 120–130. https://doi.org/10.1037/0735-7036.120.2.120

Burkart, J., & Heschl, A. (2007). Understanding visual access in common marmosets, Callithrix jacchus: Perspective taking or behaviour reading? *Animal Behaviour*, *73*(3), 457–469. https://doi.org/10.1016/j.anbehav.2006.05.019

Burkart, J., Kupferberg, A., Glasauer, S., & van Schaik, C. (2012). Even simple forms of social learning rely on intention attribution in marmoset monkeys (Callithrix jacchus). *Journal of Comparative Psychology, 126*(2), 129–138. https://doi.org/10.1037/a0026025

Burkart, J. M., Fehr, E., Efferson, C., & Schaik, C. P. van. (2007). Other-regarding preferences in a non-human primate: Common marmosets provision food altruistically. *Proceedings of the National Academy of Sciences*, *104*(50), 19762–19766. https://doi.org/10.1073/pnas.0710310104

Buttelmann, D., Buttelmann, F., Carpenter, M., Call, J., & Tomasello, M. (2017). Great apes distinguish true from false beliefs in an interactive helping task. *PLOS ONE*, *12*(4), e0173793. https://doi.org/10.1371/journal.pone.0173793

Buttelmann, D., Carpenter, M., Call, J., & Tomasello, M. (2007). Enculturated chimpanzees imitate rationally. *Developmental Science*, *10*(4), F31–F38. https://doi.org/10.1111/j.1467-7687.2007.00630.x

Buttelmann, D., Carpenter, M., & Tomasello, M. (2009). Eighteen-month-old infants show false belief understanding in an active helping paradigm. *Cognition*, *112*(2), 337–342. https://doi.org/10.1016/j.cognition.2009.05.006

Buttelmann, D., Over, H., Carpenter, M., & Tomasello, M. (2014). Eighteen-month-olds understand false beliefs in an unexpected-contents task. *Journal of Experimental Child Psychology*, *119*, 120–126. https://doi.org/10.1016/j.jecp.2013.10.002

Buttelmann, D., Schütte, S., Carpenter, M., Call, J., & Tomasello, M. (2012). Great apes infer others’ goals based on context. *Animal Cognition*, *15*(6), 1037–1053. https://doi.org/10.1007/s10071-012-0528-4

Butterfill, S. A., & Apperly, I. A. (2013). How to Construct a Minimal Theory of Mind. *Mind & Language*, *28*(5), 606–637. https://doi.org/10.1111/mila.12036

Butterworth, G., & Jarrett, N. (1991). What minds have in common is space: Spatial mechanisms serving joint visual attention in infancy. *British Journal of Developmental Psychology*, *9*(1), 55–72. https://doi.org/10.1111/j.2044-835X.1991.tb00862.x

Byrne, R. W., & Whiten, A. (1988). Toward the next generation in data quality: A new survey of primate tactical deception. *Behavioral and Brain Sciences*, *11*(2), 267–273. https://doi.org/10.1017/S0140525X00049955

Byrne, R., & Whiten, A. (1988). Toward the next generation in data quality: A new survey of primate tactical deception. *Behavioral and Brain Sciences*, *11*(2), 267–273. https://doi.org/10.1017/S0140525X00049955

Byrne, Richard W., & Bates, L. A. (2007). Sociality, Evolution and Cognition. *Current Biology*, *17*(16), R714–R723. https://doi.org/10.1016/j.cub.2007.05.069

Call, J., Agnetta, B., & Tomasello, M. (2000). Cues that chimpanzees do and do not use to find hidden objects. *Animal Cognition*, *3*(1), 23–34. https://doi.org/10.1007/s100710050047

Call, Josep, Hare, B. A., & Tomasello, M. (1998). Chimpanzee gaze following in an object-choice task. *Animal Cognition*, *1*(2), 89–99. https://doi.org/10.1007/s100710050013

Call, Josep, Hare, B., Carpenter, M., & Tomasello, M. (2004). “Unwilling” versus “unable”: Chimpanzees’ understanding of human intentional action. *Developmental Science*, *7*(4), 488–498. https://doi.org/10.1111/j.1467-7687.2004.00368.x

Call, Josep, & Tomasello, M. (1994). Production and comprehension of referential pointing by orangutans (Pongo pygmaeus). *Journal of Comparative Psychology*, *108*(4), 307–317. https://doi.org/10.1037/0735-7036.108.4.307

Call, Josep, & Tomasello, M. (1998). Distinguishing intentional from accidental actions in orangutans (Pongo pygmaeus), chimpanzees (Pan troglodytes) and human children (Homo sapiens). *Journal of Comparative Psychology*, *112*(2), 192–206. https://doi.org/10.1037/0735-7036.112.2.192

Call, Josep, & Tomasello, M. (1999). A Nonverbal False Belief Task: The Performance of Children and Great Apes. *Child Development*, *70*(2), 381–395. https://doi.org/10.1111/1467-8624.00028

Canteloup, C., Bovet, D., & Meunier, H. (2015a). Intentional gestural communication and discrimination of human attentional states in rhesus macaques (Macaca mulatta). *Animal Cognition*, *18*(4), 875–883. https://doi.org/10.1007/s10071-015-0856-2

Canteloup, C., Bovet, D., & Meunier, H. (2015b). Intentional gestural communication and discrimination of human attentional states in rhesus macaques (Macaca mulatta). *Animal Cognition*, *18*(4), 875–883. https://doi.org/10.1007/s10071-015-0856-2

Canteloup, C., & Meunier, H. (2017). ‘Unwilling’ versus ‘unable’: Tonkean macaques’ understanding of human goal-directed actions. *PeerJ*, *5*, e3227. https://doi.org/10.7717/peerj.3227

Canteloup, C., Piraux, E., Poulin, N., & Meunier, H. (2016). Do Tonkean macaques (Macaca tonkeana) perceive what conspecifics do and do not see? *PeerJ*, *4*, e1693. https://doi.org/10.7717/peerj.1693

Canteloup, C., Poitrasson, I., Anderson, J. R., Poulin, N., & Meunier, H. (2017). Factors influencing deceptive behaviours in Tonkean macaques (Macaca tonkeana). *Behaviour*, *154*(7–8), 765–784. https://doi.org/10.1163/1568539X-00003443

Carlson, S. M., Moses, L. J., & Breton, C. (2002). How specific is the relation between executive function and theory of mind? Contributions of inhibitory control and working memory. *Infant and Child Development*, *11*(2), 73–92. https://doi.org/10.1002/icd.298

Carpenter, M., Akhtar, N., & Tomasello, M. (1998). Fourteen- through 18-month-old infants differentially imitate intentional and accidental actions. *Infant Behavior and Development*, *21*(2), 315–330. https://doi.org/10.1016/S0163-6383(98)90009-1

Carpenter, M., Call, J., & Tomasello, M. (2002). Understanding “Prior Intentions” Enables Two-Year-Olds to Imitatively Learn a Complex Task. *Child Development*, *73*(5), 1431–1441. https://doi.org/10.1111/1467-8624.00481

Carpenter, M., Call, J., & Tomasello, M. (2005). Twelve- and 18-month-olds copy actions in terms of goals. *Developmental Science*, *8*(1), F13–F20. https://doi.org/10.1111/j.1467-7687.2004.00385.x

Cheney, D. L., & Seyfarth, R. M. (2007). *Baboon metaphysics: The evolution of a social mind*. University of Chicago Press.

Cheney, D., & Seyfarth, R. (1990). Attending to behaviour versus attending to knowledge: Examining monkeys’ attribution of mental states. *Animal Behaviour*, *40*(4), 742–753. https://doi.org/10.1016/S0003-3472(05)80703-1

Clements, W. A., & Perner, J. (1994). Implicit understanding of belief. *Cognitive Development*, *9*(4), 377–395. https://doi.org/10.1016/0885-2014(94)90012-4

Clutton-Brock, T. H., & Harvey, P. H. (1980). Primates, brains and ecology. *Journal of Zoology*, *190*(3), 309–323. https://doi.org/10.1111/j.1469-7998.1980.tb01430.x

Costes-Thiré, M., Levé, M., Uhlrich, P., Pasquaretta, C., De Marco, A., & Thierry, B. (2015). Evidence that monkeys (Macaca tonkeana and Sapajus apella) read moves, but no evidence that they read goals. *Journal of Comparative Psychology*, *129*(3), 304–310. https://doi.org/10.1037/a0039294

Crockford, C., Wittig, R. M., Mundry, R., & Zuberbühler, K. (2012). Wild Chimpanzees Inform Ignorant Group Members of Danger. *Current Biology*, *22*(2), 142–146. https://doi.org/10.1016/j.cub.2011.11.053

Crockford, C., Wittig, R. M., & Zuberbühler, K. (2017). Vocalizing in chimpanzees is influenced by social-cognitive processes. *Science Advances*, *3*(11), e1701742. https://doi.org/10.1126/sciadv.1701742

de Waal, F. (1982). *Chimpanzee Politics: Power and Sex Among Apes*. The Johns Hopkins University Press. https://books.google.com/books?hl=en&lr=&id=XsrhU2vV5PIC&oi=fnd&pg=PR9&dq=chimpanzee+politics+1982&ots=93I648ipwi&sig=LX1dxyE1R0iyQ0yqDHI-ucjo8UA#v=onepage&q=chimpanzee%20politics%201982&f=false

DeCasien, A. R., Williams, S. A., & Higham, J. P. (2017). Primate brain size is predicted by diet but not sociality. *Nature Ecology & Evolution*, *1*(5), 1–7. https://doi.org/10.1038/s41559-017-0112

Defolie, C., Malassis, R., Serre, M., & Meunier, H. (2015). Tufted capuchins (Cebus apella) adapt their communicative behaviour to human’s attentional states. *Animal Cognition*, *18*(3), 747–755. https://doi.org/10.1007/s10071-015-0841-9

Dennett, D. (1978). Beliefs about beliefs [P&W, SR&B]. *Behavioral and Brain Sciences*, *1*, 568–570. https://doi.org/10.1017/S0140525X00076664

Deshpande, A., Gupta, S., & Sinha, A. (2018). Intentional communication between wild bonnet macaques and humans. *Scientific Reports*, *8*(1), 5147. https://doi.org/10.1038/s41598-018-22928-z

Drayton, L. A., & Santos, L. R. (2014). Capuchins' (Cebus apella) sensitivity to others' goal-directed actions in a helping context. *Animal Cognition*, *17*(3), 689–700. https://doi.org/10.1007/s10071-013-0700-5

Drayton, L. A., & Santos, L. R. (2017a). Do rhesus macaques, Macaca mulatta, understand what others know when gaze following? *Animal Behaviour*, *134*, 193–199. https://doi.org/10.1016/j.anbehav.2017.10.016

Drayton, L. A., & Santos, L. R. (2017b). Do rhesus macaques, Macaca mulatta, understand what others know when gaze following? *Animal Behaviour*, *134*, 193–199. https://doi.org/10.1016/j.anbehav.2017.10.016

Drayton, L. A., & Santos, L. R. (2017c). Do rhesus macaques, Macaca mulatta, understand what others know when gaze following? *Animal Behaviour*, *134*, 193–199. https://doi.org/10.1016/j.anbehav.2017.10.016

Drayton, L. A., & Santos, L. R. (2018). What do monkeys know about others' knowledge? *Cognition*, *170*, 201–208. https://doi.org/10.1016/j.cognition.2017.10.004

Drayton, L. A., Varman, L., & Santos, L. R. (2016). Capuchins (Cebus apella) are limited in their ability to infer others' goals based on context. *Journal of Comparative Psychology*, *130*(1), 71–75. https://doi.org/10.1037/com0000016

Dunbar, R. I. M., & Shultz, S. (2007). Evolution in the Social Brain. *Science, 317*(5843), 1344–1347. https://doi.org/10.1126/science.1145463

Durdevic, K., & Krupenye, C. (2021). Representing knowledge, belief, and everything in between: Representational complexity in humans and other apes. Behavioral and Brain Sciences. *In Press.*

Eckert, J., Rakoczy, H., Call, J., Herrmann, E., & Hanus, D. (2018). Chimpanzees Consider Humans' Psychological States when Drawing Statistical Inferences. *Current Biology*, *28*(12), 1959-1963.e3. https://doi.org/10.1016/j.cub.2018.04.077

Emery, N. J., & Clayton, N. S. (2001). Effects of experience and social context on prospective caching strategies by scrub jays. *Nature*, *414*(6862), 443–446. https://doi.org/10.1038/35106560

Emery, Nathan J., & Clayton, N. S. (2004). The Mentality of Crows: Convergent Evolution of Intelligence in Corvids and Apes. *Science*, *306*(5703), 1903–1907. https://doi.org/10.1126/science.1098410

Flombaum, J. I., & Santos, L. R. (2005). Rhesus Monkeys Attribute Perceptions to Others. *Current Biology*, *15*(5), 447–452. https://doi.org/10.1016/j.cub.2004.12.076

Foerster, S., McLellan, K., Schroepfer-Walker, K., Murray, C. M., Krupenye, C., Gilby, I. C., & Pusey, A. E. (2015). Social bonds in the dispersing sex: Partner preferences among adult female chimpanzees. *Animal Behaviour*, *105*, 139–152. https://doi.org/10.1016/j.anbehav.2015.04.012

Gergely, György, Bekkering, H., & Király, I. (2002). Rational imitation in preverbal infants. *Nature*, *415*(6873), 755–755. https://doi.org/10.1038/415755a

Gergely, György, & Csibra, G. (2003). Teleological reasoning in infancy: The naïve theory of rational action. *Trends in Cognitive Sciences*, *7*(7), 287–292. https://doi.org/10.1016/S1364-6613(03)00128-1

Gergely, Gyorgy, Nadasdy, Z., Csibra, G., & Bíró, S. (1995). *Taking the intentional stance at 12 months of age*. *56.2*, 165–193. https://doi.org/doi.org/10.1016/0010-0277(95)00661-H

Gilby, I. C., Brent, L. J. N., Wroblewski, E. E., Rudicell, R. S., Hahn, B. H., Goodall, J., & Pusey, A. E. (2013). Fitness benefits of coalitionary aggression in male chimpanzees. *Behavioral Ecology and Sociobiology*, *67*(3), 373–381. https://doi.org/10.1007/s00265-012-1457-6

Goossens, B. M. A., Dekleva, M., Reader, S. M., Sterck, E. H. M., & Bolhuis, J. J. (2008). Gaze following in monkeys is modulated by observed facial expressions. *Animal Behaviour*, *75*(5), 1673–1681. https://doi.org/10.1016/j.anbehav.2007.10.020

Goossens, B., Reader, S. M., van den Berg, L., & Sterck, E. H. M. (2012). An analysis of gaze following to a hidden location in long-tailed macaques (Macaca fascicularis). *Behaviour*, *149*(13–14), 1319–1337. https://doi.org/10.1163/1568539X-00003017

Grosse Wiesmann, C., Friederici, A. D., Singer, T., & Steinbeis, N. (2017). Implicit and explicit false belief development in preschool children. *Developmental Science*, *20*(5), e12445. https://doi.org/10.1111/desc.12445

Grueneisen, S., Duguid, S., Saur, H., & Tomasello, M. (2017). Children, chimpanzees, and bonobos adjust the visibility of their actions for cooperators and competitors. *Scientific Reports*, *7*(1), 8504. https://doi.org/10.1038/s41598-017-08435-7

Hall, K., Oram, M. W., Campbell, M. W., Eppley, T. M., Byrne, R. W., & de Waal, F. B. M. (2017). Chimpanzee uses manipulative gaze cues to conceal and reveal information to foraging competitor. *American Journal of Primatology*, *79*(3), e22622. https://doi.org/10.1002/ajp.22622

Hamlin, J. K., Wynn, K., & Bloom, P. (2007). Social evaluation by preverbal infants. *Nature*, *450*(7169), 557–559. https://doi.org/10.1038/nature06288

Hammerstein, P. (Ed.). (2003). *Genetic and cultural evolution of cooperation*. MIT Press.

Hare, B. (2001). Can competitive paradigms increase the validity of experiments on primate social cognition? *Animal Cognition*, *4*(3), 269–280. https://doi.org/10.1007/s100710100084

Hare, B. (2011). From Hominoid to Hominid Mind: What Changed and Why? *Annual Review of Anthropology*, *40*(1), 293–309. https://doi.org/10.1146/annurev-anthro-081309-145726

Hare, B., Addessi, E., Call, J., Tomasello, M., & Visalberghi, E. (2003). Do capuchin monkeys, Cebus apella, know what conspecifics do and do not see? *Animal Behaviour*, *65*(1), 131–142. https://doi.org/10.1006/anbe.2002.2017

Hare, B., Call, J., Agnetta, B., & Tomasello, M. (2000a). Chimpanzees know what conspecifics do and do not see. *Animal Behaviour*, *59*(4), 771–785. https://doi.org/10.1006/anbe.1999.1377

Hare, B., Call, J., Agnetta, B., & Tomasello, M. (2000b). Chimpanzees know what conspecifics do and do not see. *Animal Behaviour*, *59*(4), 771–785. https://doi.org/10.1006/anbe.1999.1377

Hare, B., Call, J., & Tomasello, M. (2001). Do chimpanzees know what conspecifics know? *Animal Behaviour*, *61*(1), 139–151. https://doi.org/10.1006/anbe.2000.1518

Hare, B., Call, J., & Tomasello, M. (2006). Chimpanzees deceive a human competitor by hiding. *Cognition*, *101*(3), 495–514. https://doi.org/10.1016/j.cognition.2005.01.011

Hare, B., & Tomasello, M. (2004). Chimpanzees are more skilful in competitive than in cooperative cognitive tasks. *Animal Behaviour*, *68*(3), 571–581. https://doi.org/10.1016/j.anbehav.2003.11.011

Hare, B., Wobber, V., & Wrangham, R. (2012). The self-domestication hypothesis: Evolution of bonobo psychology is due to selection against aggression. *Animal Behaviour*, *83*(3), 573–585. https://doi.org/10.1016/j.anbehav.2011.12.007

Hattori, Y., Kuroshima, H., & Fujita, K. (2006). I know you are not looking at me: Capuchin monkeys' (Cebus apella) sensitivity to human attentional states. *Animal Cognition*, *10*(2), 141. https://doi.org/10.1007/s10071-006-0049-0

Hattori, Y., Kuroshima, H., & Fujita, K. (2007). I know you are not looking at me: Capuchin monkeys' (Cebus apella) sensitivity to human attentional states. *Animal Cognition*, *10*(2), 141–148. https://doi.org/10.1007/s10071-006-0049-0

Hattori, Y., Kuroshima, H., & Fujita, K. (2009). Tufted capuchin monkeys (Cebus apella) show understanding of human attentional states when requesting food held by a human. *Animal Cognition*, *13*(1), 87. https://doi.org/10.1007/s10071-009-0248-6

Hattori, Y., Kuroshima, H., & Fujita, K. (2010). Tufted capuchin monkeys (Cebus apella) show understanding of human attentional states when requesting food held by a human. *Animal Cognition*, *13*(1), 87–92. https://doi.org/10.1007/s10071-009-0248-6

Hayashi, T., Akikawa, R., Kawasaki, K., Egawa, J., Minamimoto, T., Kobayashi, K., Kato, S., Hori, Y., Nagai, Y., Iijima, A., Someya, T., & Hasegawa, I. (2020). Macaques Exhibit Implicit Gaze Bias Anticipating Others' False-Belief-Driven Actions via Medial Prefrontal Cortex. *Cell Reports*, *30*(13), 4433-4444.e5. https://doi.org/10.1016/j.celrep.2020.03.013

Heesen, R., Bangerter, A., Zuberbühler, K., Rossano, F., Iglesias, K., Guéry, J.-P., & Genty, E. (2020). Bonobos engage in joint commitment. *Science Advances*, *6*(51), eabd1306. https://doi.org/10.1126/sciadv.abd1306

Henley, T., & Povinelli, D. J. (2020). Seeing through: An Analysis of Kano et al. (2019). *Animal Behavior and Cognition*, *7*(4), 658–660. https://doi.org/10.26451/abc.07.04.11.2020

Herrmann, E., Call, J., Hernandez-Lloreda, M. V., Hare, B., & Tomasello, M. (2007). Humans Have Evolved Specialized Skills of Social Cognition: The Cultural Intelligence Hypothesis. *Science*, *317*(5843), 1360–1366. https://doi.org/10.1126/science.1146282

Herrmann, E., Hernández-Lloreda, M. V., Call, J., Hare, B., & Tomasello, M. (2010). The Structure of Individual Differences in the Cognitive Abilities of Children and Chimpanzees. *Psychological Science*, *21*(1), 102–110. https://doi.org/10.1177/0956797609356511

Herrmann, E., Keupp, S., Hare, B., Vaish, A., & Tomasello, M. (2013). Direct and indirect reputation formation in nonhuman great apes (Pan paniscus, Pan troglodytes, Gorilla gorilla, Pongo pygmaeus) and human children (Homo sapiens). *Journal of Comparative Psychology, 127*(1), 63–75. https://doi.org/10.1037/a0028929

Heyes, C. (2014a). Submentalizing: I Am Not Really Reading Your Mind. *Perspectives on Psychological Science, 9*(2), 131–143. https://doi.org/10.1177/1745691613518076

Heyes, C. (2014b). False belief in infancy: A fresh look. *Developmental Science*, *17*(5), 647–659. https://doi.org/10.1111/desc.12148

Heyes, C. (2015). Animal mindreading: What’s the problem? *Psychonomic Bulletin & Review*, *22*(2), 313–327. https://doi.org/10.3758/s13423-014-0704-4

Heyes, C. (2017). Apes Submentalise. *Trends in Cognitive Sciences*, *21*(1), 1–2. https://doi.org/10.1016/j.tics.2016.11.006

Heyes, C. M. (1993). Anecdotes, training, trapping and triangulating: Do animals attribute mental states? *Animal Behaviour*, *46*(1), 177–188. https://doi.org/10.1006/anbe.1993.1173

Heyes, C. M. (1998). Theory of mind in nonhuman primates. *Behavioral and Brain Sciences*, *21*(1), 101–114.

Heyes, C. M., & Frith, C. D. (2014). The cultural evolution of mind reading. *Science*, *344*(6190), 1243091–1243091. https://doi.org/10.1126/science.1243091

Horner, V., & Whiten, A. (2005). Causal knowledge and imitation/emulation switching in chimpanzees (Pan troglodytes) and children (Homo sapiens). *Animal Cognition*, *8*(3), 164–181. https://doi.org/10.1007/s10071-004-0239-6

Horschler, D. J., Santos, L. R., & MacLean, E. L. (2019). Do non-human primates really represent others' ignorance? A test of the awareness relations hypothesis. *Cognition*, *190*, 72–80. https://doi.org/10.1016/j.cognition.2019.04.012

Horschler, D. J., Santos, L. R., & MacLean, E. L. (2021). How do non-human primates represent others' awareness of where objects are hidden? *Cognition*, *212*, 104658. https://doi.org/10.1016/j.cognition.2021.104658

Horton, K. E., & Caldwell, C. A. (2006). Visual co-orientation and expectations about attentional orientation in pileated gibbons (Hylobates pileatus). *Behavioural Processes*, *72*(1), 65–73. https://doi.org/10.1016/j.beproc.2005.12.004

Hostetter, A. B., Cantero, M., & Hopkins, W. D. (2001). Differential use of vocal and gestural communication by chimpanzees (Pan troglodytes) in response to the attentional status of a human (Homo sapiens). *Journal of Comparative Psychology*, *115*(4), 337–343. https://doi.org/10.1037/0735-7036.115.4.337

Humphrey, N. (1976). The social function of intellect. In *Growing points in ethology* (Vol. 37, pp. 303–317).

Itakura, S. (1996). An exploratory study of gaze-monitoring in nonhuman primates1. *Japanese Psychological Research*, *38*(3), 174–180. https://doi.org/10.1111/j.1468-5884.1996.tb00022.x

Jolly, A. (1966). Lemur Social Behavior and Primate Intelligence. *Science*, *153*(3735), 501–506. https://doi.org/10.1126/science.153.3735.501

Joly, M., Micheletta, J., De Marco, A., Langermans, J. A., Sterck, E. H. M., & Waller, B. M. (2017). Comparing physical and social cognitive skills in macaque species with different degrees of social tolerance. *Proceedings of the Royal Society B: Biological Sciences*, *284*(1862), 20162738. https://doi.org/10.1098/rspb.2016.2738

Kaminski, J. (2011). Communicative Cues Among and Between Human and Non-human Primates: Attending to Specificity in Triadic Gestural Interactions. In M. Boos, M. Kolbe, P. M. Kappeler, & T. Ellwart (Eds.), *Coordination in Human and Primate Groups* (pp. 245–261). Springer Berlin Heidelberg. https://doi.org/10.1007/978-3-642-15355-6_14

Kaminski, J., Call, J., & Tomasello, M. (2004). Body orientation and face orientation: Two factors controlling apes' begging behavior from humans. *Animal Cognition*, *7*(4), 216–223. https://doi.org/10.1007/s10071-004-0214-2

Kaminski, J., Call, J., & Tomasello, M. (2008). Chimpanzees know what others know, but not what they believe. *Cognition*, *109*(2), 224–234. https://doi.org/10.1016/j.cognition.2008.08.010

Kaminski, J., Riedel, J., Call, J., & Tomasello, M. (2005). Domestic goats, Capra hircus, follow gaze direction and use social cues in an object choice task. *Animal Behaviour*, *69*(1), 11–18. https://doi.org/10.1016/j.anbehav.2004.05.008

Kano, F., & Call, J. (2014a). Cross-species variation in gaze following and conspecific preference among great apes, human infants and adults. *Animal Behaviour*, *91*, 137–150. https://doi.org/10.1016/j.anbehav.2014.03.011

Kano, F., & Call, J. (2014b). Great Apes Generate Goal-Based Action Predictions: An Eye-Tracking Study. *Psychological Science*, *25*(9), 1691–1698. https://doi.org/10.1177/0956797614536402

Kano, F., Call, J., & Krupenye, C. (2020). Primates Pass Dynamically Social Anticipatory-Looking False-Belief Tests. *Trends in Cognitive Sciences*, *24*(10), 777–778. https://doi.org/10.1016/j.tics.2020.07.003

Kano, F., Krupenye, C., Hirata, S., & Call, J. (2017). Eye tracking uncovered great apes' ability to anticipate that other individuals will act according to false beliefs. *Communicative & Integrative Biology*, *10*(2), e1299836. https://doi.org/10.1080/19420889.2017.1299836

Kano, F., Krupenye, C., Hirata, S., Call, J., & Tomasello, M. (2017). Submentalizing cannot explain belief-based action anticipation in apes. *Trends in Cognitive Sciences*, *21*(9), 633–634. https://doi.org/10.1016/j.tics.2017.06.011

Kano, F., Krupenye, C., Hirata, S., Tomonaga, M., & Call, J. (2019). Great apes use self-experience to anticipate an agent's action in a false-belief test. *Proceedings of the*

National Academy of Sciences, *116*(42), 20904–20909. https://doi.org/10.1073/pnas.1910095116

Kappeler, P., & Schaik, C. (2002). Evolution of Primate Social Systems. *International Journal of Primatology*, *23*, 707–740. https://doi.org/10.1023/A:1015520830318

Karg, K., Schmelz, M., Call, J., & Tomasello, M. (2015a). The goggles experiment: Can chimpanzees use self-experience to infer what a competitor can see? *Animal Behaviour*, *105*, 211–221. https://doi.org/10.1016/j.anbehav.2015.04.028

Karg, K., Schmelz, M., Call, J., & Tomasello, M. (2015b). Chimpanzees strategically manipulate what others can see. *Animal Cognition*, *18*(5), 1069–1076. https://doi.org/10.1007/s10071-015-0875-z

Karg, K., Schmelz, M., Call, J., & Tomasello, M. (2016). Differing views: Can chimpanzees do Level 2 perspective-taking? *Animal Cognition*, *19*(3), 555–564. https://doi.org/10.1007/s10071-016-0956-7

Karin-D'Arcy, R. M., & Povinelli, D. J. (2002). Do Chimpanzees Know What Each Other See? A Closer Look. *International Journal of Comparative Psychology*, *15*(1). https://escholarship.org/uc/item/8hb9f6xs

Kawai, N., Nakagami, A., Yasue, M., Koda, H., & Ichinohe, N. (2019). Common marmosets (Callithrix jacchus) evaluate third-party social interactions of human actors but Japanese monkeys (Macaca fuscata) do not. *Journal of Comparative Psychology*, *133*(4), 488–495. https://doi.org/10.1037/com0000182

Kawai, N., Yasue, M., Banno, T., & Ichinohe, N. (2014). Marmoset monkeys evaluate third-party reciprocity. *Biology Letters*, *10*(5), 20140058. https://doi.org/10.1098/rsbl.2014.0058

Kovacs, A. M., Teglas, E., & Endress, A. D. (2010a). The Social Sense: Susceptibility to Others' Beliefs in Human Infants and Adults. *Science*, *330*(6012), 1830–1834. https://doi.org/10.1126/science.1190792

Kovacs, A. M., Teglas, E., & Endress, A. D. (2010b). The Social Sense: Susceptibility to Others' Beliefs in Human Infants and Adults. *Science*, *330*(6012), 1830–1834. https://doi.org/10.1126/science.1190792

Krachun, C., Carpenter, M., Call, J., & Tomasello, M. (2009). A competitive nonverbal false belief task for children and apes. *Developmental Science*, *12*(4), 521–535. https://doi.org/10.1111/j.1467-7687.2008.00793.x

Krachun, C., Carpenter, M., Call, J., & Tomasello, M. (2010). A New Change-of-Contents False Belief Test: Children and Chimpanzees Compared. *International Journal of Comparative Psychology*, *23*(2). https://escholarship.org/uc/item/68c0p8dk

Krachun, C., Lurz, R., Mahovetz, L. M., & Hopkins, W. D. (2019). Mirror self-recognition and its relationship to social cognition in chimpanzees. *Animal Cognition*, *22*(6), 1171–1183. https://doi.org/10.1007/s10071-019-01309-7

Krupenye, C. (2020). The evolution of mentalizing in humans and other primates. In M. Gilead & K. Ochsner (Eds.), *The Neural Basis of Mentalizing: A Social-Cognitive and Affective Neuroscience Perspective*. Springer Press.

Krupenye, C., & Call, J. (2019). Theory of mind in animals: Current and future directions. *WIREs Cognitive Science*, *10*(6), e1503. https://doi.org/10.1002/wcs.1503

Krupenye, C., & Hare, B. (2018). Bonobos Prefer Individuals that Hinder Others over Those that Help. *Current Biology*, *28*(2), 280-286.e5. https://doi.org/10.1016/j.cub.2017.11.061

Krupenye, C., Kano, F., Hirata, S., Call, J., & Tomasello, M. (2016). Great apes anticipate that other individuals will act according to false beliefs. *Science*, *354*(6308), 110–114. https://doi.org/10.1126/science.aaf8110

Krupenye, C., Kano, F., Hirata, S., Call, J., & Tomasello, M. (2017). A test of the submentalizing hypothesis: Apes' performance in a false belief task inanimate control. *Communicative & Integrative Biology*, *10*(4), e1343771. https://doi.org/10.1080/19420889.2017.1343771

Krupenye, C., MacLean, E. L., & Hare, B. (2017). Does the bonobo have a (chimpanzee-like) theory of mind? In *Bonobos*. Oxford University Press. http://oxford.universitypressscholarship.com/view/10.1093/oso/9780198728511.001.0001/oso-9780198728511-chapter-6

Krupenye, C., Tan, J., & Hare, B. (2018). Bonobos voluntarily hand food to others but not toys or tools. *Proceedings of the Royal Society B: Biological Sciences*, *285*(1886), 20181536. https://doi.org/10.1098/rspb.2018.1536

Kummer, H., Anzenberger, G., & Hemelrijk, C. K. (1996). Hiding and perspective taking in long-tailed macaques (Macaca fascicularis). *Journal of Comparative Psychology*, *110*(1), 97–102. https://doi.org/10.1037/0735-7036.110.1.97

Kupferberg, A., Glasauer, S., & Burkart, J. M. (2013). Do robots have goals? How agent cues influence action understanding in non-human primates. *Behavioural Brain Research*, *246*, 47–54. https://doi.org/10.1016/j.bbr.2013.01.047

Kuroshima, H., Fujita, K., Adachi, I., Iwata, K., & Fuyuki, A. (2003). A Capuchin monkey (Cebus apella) recognizes when people do and do not know the location of food. *Animal Cognition*, *6*(4), 283–291. https://doi.org/10.1007/s10071-003-0184-9

Kuroshima, H., Fujita, K., Fuyuki, A., & Masuda, T. (2002). Understanding of the relationship between seeing and knowing by tufted capuchin monkeys (Cebus apella). *Animal Cognition*, *5*(1), 41–48. https://doi.org/10.1007/s10071-001-0123-6

Lake, B. M., Ullman, T. D., Tenenbaum, J. B., & Gershman, S. J. (2017). Building machines that learn and think like people. *Behavioral and Brain Sciences*, *40*. https://doi.org/10.1017/S0140525X16001837

Lamaury, A., Cochet, H., & Bourjade, M. (2019). Acquisition of joint attention by olive baboons gesturing toward humans. *Animal Cognition*, *22*(4), 567–575. https://doi.org/10.1007/s10071-017-1111-9

Leavens, D. A. (1998). Having a concept "see" does not imply attribution of knowledge: Some general considerations in measuring "theories of mind." *Behavioral and Brain Sciences*, *21*(1), 123–124. https://doi.org/10.1017/S0140525X98330708

Leavens, D. A., Bard, K. A., & Hopkins, W. D. (2019). The mismeasure of ape social cognition. *Animal Cognition*, *22*(4), 487–504. https://doi.org/10.1007/s10071-017-1119-1

Leavens, D. A., Hopkins, W. D., & Thomas, R. K. (2004). Referential Communication by Chimpanzees (Pan troglodytes). *Journal of Comparative Psychology*, *118*(1), 48–57. https://doi.org/10.1037/0735-7036.118.1.48

Lewis, L., Kano, F., Stevens, J., DuBois, J., Call, J., & Krupenye, C. (2021). Bonobos and chimpanzees preferentially attend to familiar members of the dominant sex. *Animal Behaviour*.

Liebal, K., Call, J., Tomasello, M., & Pika, S. (2004). To move or not to move: How apes adjust to the attentional state of others. *Interaction Studies*, *5*(2), 199–219. https://doi.org/10.1075/is.5.2.03lie

Liebal, K., & Kaminski, J. (2012). Gibbons (Hylobates pileatus, H. moloch, H. lar, Symphalangus syndactylus) follow human gaze, but do not take the visual perspective of others. *Animal Cognition*, *15*(6), 1211–1216. https://doi.org/10.1007/s10071-012-0543-5

Liszkowski, U., Carpenter, M., & Tomasello, M. (2008). Twelve-month-olds communicate helpfully and appropriately for knowledgeable and ignorant partners. *Cognition*, *108*(3), 732–739. https://doi.org/10.1016/j.cognition.2008.06.013

Liu, D., Wellman, H. M., Tardif, T., & Sabbagh, M. A. (2008). Theory of mind development in Chinese children: A meta-analysis of false-belief understanding across cultures and languages. *Developmental Psychology*, *44*(2), 523–531. https://doi.org/10.1037/0012-1649.44.2.523

Lohmann, H., & Tomasello, M. (2003). The Role of Language in the Development of False Belief Understanding: A Training Study. *Child Development*, *74*(4), 1130–1144. https://doi.org/10.1111/1467-8624.00597

Lorincz, E., Jellema, T., Barraclough, N., Xiao, D., & Perrett, D. (2005). *From Monkey Brain to Human Brain: A Fyssen Foundation Symposium*. MIT Press.

Luo, Y., & Baillargeon, R. (2007). DO 12.5-MONTH-OLD INFANTS CONSIDER WHAT OBJECTS OTHERS CAN SEE WHEN INTERPRETING THEIR ACTIONS? *Cognition*, *105*(3), 489–512. https://doi.org/10.1016/j.cognition.2006.10.007

Lurz, R. (2009). If chimpanzees are mindreaders, could behavioral science tell? Toward a solution of the logical problem. *Philosophical Psychology*, *22*(3), 305–328. https://doi.org/10.1080/09515080902970673

Lurz, R., Krachun, C., Mahovetz, L., Wilson, M. J. G., & Hopkins, W. (2018). Chimpanzees gesture to humans in mirrors: Using reflection to dissociate seeing from line of gaze. *Animal Behaviour*, *135*, 239–249. https://doi.org/10.1016/j.anbehav.2017.11.014

Lyons, D. E., & Santos, L. R. (2006). Ecology, Domain Specificity, and the Origins of Theory of Mind: Is Competition the Catalyst? *Philosophy Compass*, *1*(5), 481–492. https://doi.org/10.1111/j.1747-9991.2006.00032.x

MacLean, E. L., & Hare, B. (2012). Bonobos and chimpanzees infer the target of another's attention. *Animal Behaviour*, *83*(2), 345–353. https://doi.org/10.1016/j.anbehav.2011.10.026

MacLean, E. L., Hare, B., Nunn, C. L., Addessi, E., Amici, F., Anderson, R. C., Aureli, F., Baker, J. M., Bania, A. E., Barnard, A. M., Boogert, N. J., Brannon, E. M., Bray, E. E., Bray, J., Brent, L. J. N., Burkart, J. M., Call, J., Cantlon, J. F., Cheke, L. G., … Zhao, Y. (2014). The evolution of self-control. *Proceedings of the National Academy of Sciences*, *111*(20), E2140–E2148. https://doi.org/10.1073/pnas.1323533111

MacLean, E. L., Merritt, D. J., & Brannon, E. M. (2008). Social complexity predicts transitive reasoning in prosimian primates. *Animal Behaviour*, *76*(2), 479–486. https://doi.org/10.1016/j.anbehav.2008.01.025

MacLean, E. L., Sandel, A. A., Bray, J., Oldenkamp, R. E., Reddy, R. B., & Hare, B. A. (2013). Group Size Predicts Social but Not Nonsocial Cognition in Lemurs. *PLOS ONE*, *8*(6), e66359. https://doi.org/10.1371/journal.pone.0066359

Maille, A., Engelhart, L., Bourjade, M., & Blois-Heulin, C. (2012). To Beg, or Not to Beg? That Is the Question: Mangabeys Modify Their Production of Requesting Gestures in

Response to Human’s Attentional States. *PLOS ONE*, *7*(7), e41197. https://doi.org/10.1371/journal.pone.0041197

Marechal, L., Genty, E., & Roeder, J. J. (2010). Recognition of faces of known individuals in two lemur species (Eulemur fulvus and E. macaco). *Animal Behaviour*, *79*(5), 1157–1163. https://doi.org/10.1016/j.anbehav.2010.02.022

Marticorena, D. C. W., Ruiz, A. M., Mukerji, C., Goddu, A., & Santos, L. R. (2011). Monkeys represent others’ knowledge but not their beliefs. *Developmental Science*, *14*(6), 1406–1416. https://doi.org/10.1111/j.1467-7687.2011.01085.x

Martin, A. (2019). Belief Representation in Great Apes. *Trends in Cognitive Sciences*, *23*(12), 985–986. https://doi.org/10.1016/j.tics.2019.10.008

Martin, A., & Santos, L. R. (2014). The origins of belief representation: Monkeys fail to automatically represent others’ beliefs. *Cognition*, *130*(3), 300–308. https://doi.org/10.1016/j.cognition.2013.11.016

Martin, A., & Santos, L. R. (2016). What Cognitive Representations Support Primate Theory of Mind? *Trends in Cognitive Sciences*, *20*(5), 375–382. https://doi.org/10.1016/j.tics.2016.03.005

Melis, A. P., Call, J., & Tomasello, M. (2006). Chimpanzees (Pan troglodytes) conceal visual and auditory information from others. *Journal of Comparative Psychology*, *120*(2), 154–162. https://doi.org/10.1037/0735-7036.120.2.154

Melis, A. P., Call, J., & Tomasello, M. (2010). 36-month-olds conceal visual and auditory information from others. *Developmental Science*, *13*(3), 479–489. https://doi.org/10.1111/j.1467-7687.2009.00892.x

Melis, A. P., Hare, B., & Tomasello, M. (2006). Engineering cooperation in chimpanzees: Tolerance constraints on cooperation. *Animal Behaviour*, *72*(2), 275–286. https://doi.org/10.1016/j.anbehav.2005.09.018

Melis, A. P., & Tomasello, M. (2013). Chimpanzees' (Pan troglodytes) strategic helping in a collaborative task. *Biology Letters*, *9*(2), 20130009. https://doi.org/10.1098/rsbl.2013.0009

Melis, A. P., & Tomasello, M. (2019). Chimpanzees (Pan troglodytes) coordinate by communicating in a collaborative problem-solving task. *Proceedings of the Royal Society B: Biological Sciences*, *286*(1901), 20190408. https://doi.org/10.1098/rspb.2019.0408

Melis, A. P., Warneken, F., Jensen, K., Schneider, A.-C., Call, J., & Tomasello, M. (2011). Chimpanzees help conspecifics obtain food and non-food items. *Proceedings of the Royal Society B: Biological Sciences*, *278*(1710), 1405–1413. https://doi.org/10.1098/rspb.2010.1735

Meltzoff, A. N. (1995). Understanding the Intentions of Others: Re-Enactment of Intended Acts by 18-Month-Old Children. *Developmental Psychology*, *31*(5), 838–850. https://doi.org/10.1037/0012-1649.31.5.838

Meltzoff, A. N., & Brooks, R. (2008). Self-experience as a mechanism for learning about others: A training study in social cognition. *Developmental Psychology*, *44*(5), 1257–1265. https://doi.org/10.1037/a0012888

Met, A., Miklósi, Á., & Lakatos, G. (2014). Gaze-following behind barriers in domestic dogs. *Animal Cognition*, *17*(6), 1401–1405. https://doi.org/10.1007/s10071-014-0754-z

Meunier, H. (2017). Do monkeys have a theory of mind? How to answer the question? *Neuroscience & Biobehavioral Reviews*, *82*, 110–123. https://doi.org/10.1016/j.neubiorev.2016.11.007

Meunier, H., Prieur, J., & Vauclair, J. (2013). Olive baboons communicate intentionally by pointing. *Animal Cognition*, *16*(2), 155–163. https://doi.org/10.1007/s10071-012-0558-y

Micheletta, J., & Waller, B. (2012). Friendship affects gaze following in a tolerant species of macaque, Macaca nigra. *Animal Behaviour*, *83*, 459–467. https://doi.org/10.1016/j.anbehav.2011.11.018

Milligan, K., Astington, J. W., & Dack, L. A. (2007). Language and Theory of Mind: Meta-Analysis of the Relation Between Language Ability and False-belief Understanding. *Child Development*, *78*(2), 622–646. https://doi.org/10.1111/j.1467-8624.2007.01018.x

Milton, K. (1998). The social behavior of chimpanzees and bonobos. *Current Anthropology*, *39*(4), 411–412.

Moll, H., & Meltzoff, A. N. (2011). How Does It Look? Level 2 Perspective-Taking at 36 Months of Age: Level 2 Perspective-Taking. *Child Development*, *82*(2), 661–673. https://doi.org/10.1111/j.1467-8624.2010.01571.x

Moll, H., & Tomasello, M. (2004). 12- and 18-month-old infants follow gaze to spaces behind barriers. *Developmental Science*, *7*(1), F1–F9. https://doi.org/10.1111/j.1467-7687.2004.00315.x

Myowa-Yamakoshi, M., & Matsuzawa, T. (2000). Imitation of intentional manipulatory actions in chimpanzees (Pan troglodytes). *Journal of Comparative Psychology*, *114*(4), 381–391. https://doi.org/10.1037/0735-7036.114.4.381

Myowa-Yamakoshi, M., Scola, C., & Hirata, S. (2012). Humans and chimpanzees attend differently to goal-directed actions. *Nature Communications*, *3*(1), 693. https://doi.org/10.1038/ncomms1695

Novey, M. S. (1979). *The development of knowledge of others' ability to see* [PhD Dissertation]. May.

O'Connell, S., & Dunbar, R. I. M. (2003). A test for comprehension of false belief in chimpanzees. *Evolution and Cognition*, *9*(2), 131–140.

Okamoto, S., Tanaka, M., & Tomonaga, M. (2004). Looking back: The "representational mechanism" of joint attention in an infant chimpanzee (Pan troglodytes)1. *Japanese Psychological Research*, *46*(3), 236–245. https://doi.org/10.1111/j.1468-5584.2004.00255.x

Okamoto-Barth, S., Call, J., & Tomasello, M. (2007). Great Apes' Understanding of Other Individuals' Line of Sight. *Psychological Science*, *18*(5), 462–468. https://doi.org/10.1111/j.1467-9280.2007.01922.x

Olineck, K. M., & Poulin-Dubois, D. (2005). Infants' Ability to Distinguish Between Intentional and Accidental Actions and Its Relation to Internal State Language. *Infancy*, *8*(1), 91–100. https://doi.org/10.1207/s15327078in0801_6

Onishi, K. H., & Baillargeon, R. (2005). Do 15-Month-Old Infants Understand False Beliefs? *Science (New York, N.y.)*, *308*(5719), 255–258. https://doi.org/10.1126/science.1107621

Overduin - de Vries, A., Spruijt, B., & Sterck, E. (2013). Long-tailed macaques (Macaca fascicularis) understand what conspecifics can see in a competitive situation. *Animal Cognition*, *17*. https://doi.org/10.1007/s10071-013-0639-6

Palagi, E., & Dapporto, L. (2006). Beyond Odor Discrimination: Demonstrating Individual Recognition by Scent in Lemur Catta. *Chemical Senses*, *31*(5), 437–443. https://doi.org/10.1093/chemse/bjj048

Penn, D. C., Holyoak, K. J., & Povinelli, D. J. (2008). Darwin's mistake: Explaining the discontinuity between human and nonhuman minds. *Behavioral and Brain Sciences*, *31*(2), 109–130. https://doi.org/10.1017/S0140525X08003543

Penn, D. C., & Povinelli, D. J. (2007). On the lack of evidence that non-human animals possess anything remotely resembling a 'theory of mind.' *Philosophical Transactions of the Royal Society B: Biological Sciences*, *362*(1480), 731–744. https://doi.org/10.1098/rstb.2006.2023

Perner, J. (2012). MiniMeta: In search of minimal criteria for metacognition. In *Foundations of Metacognition*. Oxford University Press. http://oxford.universitypressscholarship.com/view/10.1093/acprof:oso/9780199646739.001.0001/acprof-9780199646739-chapter-006

Perner, J., Leekam, S. R., & Wimmer, H. (1987). Three-year-olds' difficulty with false belief: The case for a conceptual deficit. *British Journal of Developmental Psychology*, *5*(2), 125–137. https://doi.org/10.1111/j.2044-835X.1987.tb01048.x

Phillips, J., & Norby, A. (2019). Factive theory of mind. *Mind & Language*, *36*(1), 3–26. https://doi.org/10.1111/mila.12267

Phillips, W., Barnes, J. L., Mahajan, N., Yamaguchi, M., & Santos, L. R. (2009). 'Unwilling' versus 'unable': Capuchin monkeys' (Cebus apella) understanding of human intentional action. *Developmental Science*, *12*(6), 938–945. https://doi.org/10.1111/j.1467-7687.2009.00840.x

Pillow, B. H., & Pearson, R. M. (2012). Children's evaluation of the certainty of another person's inductive inferences and guesses. *Cognitive Development*, *27*(3), 299–313. https://doi.org/10.1016/j.cogdev.2012.05.002

Pokorny, J. J., & de Waal, F. B. M. (2009). Monkeys recognize the faces of group mates in photographs. *Proceedings of the National Academy of Sciences*, *106*(51), 21539–21543. https://doi.org/10.1073/pnas.0912174106

Pokorny, Jennifer J., & de Waal, F. B. M. (2009). Face recognition in capuchin monkeys (Cebus apella). *Journal of Comparative Psychology*, *123*(2), 151–160. https://doi.org/10.1037/a0014073

Pontzer, H., Durazo-Arvizu, R., Dugas, L. R., Plange-Rhule, J., Bovet, P., Forrester, T. E., Lambert, E. V., Cooper, R. S., Schoeller, D. A., & Luke, A. (2016). Constrained Total Energy Expenditure and Metabolic Adaptation to Physical Activity in Adult Humans. *Current Biology*, *26*(3), 410–417. https://doi.org/10.1016/j.cub.2015.12.046

Poss, S. R., Kuhar, C., Stoinski, T. S., & Hopkins, W. D. (2006). Differential Use of Attentional and Visual Communicative Signaling by Orangutans (Pongo pygmaeus) and Gorillas (Gorilla gorilla) in Response to the Attentional Status of a Human. *American Journal of Primatology*, *68*(10), 978–992. https://doi.org/10.1002/ajp.20304

Povinelli, D. J., & DeBlois, S. (1992). Young children's (Homo sapiens) understanding of knowledge formation in themselves and others. *Journal of Comparative Psychology*, *106*(3), 228–238. https://doi.org/10.1037/0735-7036.106.3.228

Povinelli, D. J., & Eddy, T. J. (1996). Chimpanzees: Joint Visual Attention. *Psychological Science*, *7*(3), 129–135. https://doi.org/10.1111/j.1467-9280.1996.tb00345.x

Povinelli, D. J., & Eddy, T. J. (1997). Specificity of gaze-following in young chimpanzees. *British Journal of Developmental Psychology*, *15*(2), 213–222. https://doi.org/10.1111/j.2044-835X.1997.tb00735.x

Povinelli, D. J., Eddy, T. J., Hobson, R. P., & Tomasello, M. (1996). What Young Chimpanzees Know about Seeing. *Monographs of the Society for Research in Child Development*, *61*(3), i. https://doi.org/10.2307/1166159

Povinelli, D. J., Nelson, K. E., & Boysen, S. T. (n.d.). *Inferences About Guessing and Knowing by Chimpanzees (Pan troglodytes)*. 15.

Povinelli, D. J., Nelson, K. E., & Boysen, S. T. (1990). Inferences about guessing and knowing by chimpanzees (Pan troglodytes). *Journal of Comparative Psychology*, *104*(3), 203–210. https://doi.org/10.1037/0735-7036.104.3.203

Povinelli, D. J., Parks, K. A., & Novak, M. A. (1991). Do rhesus monkeys (Macaca mulatta) attribute knowledge and ignorance to others? *Journal of Comparative Psychology*, *105*(4), 318–325. https://doi.org/10.1037/0735-7036.105.4.318

Povinelli, D. J., Perilloux, H. K., Reaux, J. E., & Bierschwale, D. T. (1998). *Young and juvenile chimpanzees' (Pan troglodytes) reactions to intentional versus accidental and inadvertent actions*. 15.

Povinelli, D. J., Rulf, A. B., & Bierschwale, D. T. (1994). Absence of knowledge attribution and self-recognition in young chimpanzees (Pan troglodytes). *Journal of Comparative Psychology*, *108*(1), 74–80. https://doi.org/10.1037/0735-7036.108.1.74

Povinelli, D. J., Theall, L. A., Reaux, J. E., & Dunphy-Lelii, S. (2003). Chimpanzees spontaneously alter the location of their gestures to match the attentional orientation of others. *Animal Behaviour*, *66*(1), 71–79. https://doi.org/10.1006/anbe.2003.2195

Powell, L. E., Isler, K., & Barton, R. A. (2017). Re-evaluating the link between brain size and behavioural ecology in primates. *Proceedings of the Royal Society B: Biological Sciences*, *284*(1865), 20171765. https://doi.org/10.1098/rspb.2017.1765

Powell, L. J., & Carey, S. (2017). Executive function depletion in children and its impact on theory of mind. *Cognition*, *164*, 150–162. https://doi.org/10.1016/j.cognition.2017.03.022

Premack, D., & Woodruff, G. (1978). Does the chimpanzee have a theory of mind? *Behavioral and Brain Sciences*, *1*(4), 515–526. https://doi.org/10.1017/S0140525X00076512

Pyers, J. E., & Senghas, A. (2009). Language Promotes False-Belief Understanding: Evidence From Learners of a New Sign Language. *Psychological Science*, *20*(7), 805–812. https://doi.org/10.1111/j.1467-9280.2009.02377.x

Pylyshyn, Z. (1978). When is attribution of beliefs justified? *The Behavioral and Brain Sciences*, *1*(4), 592–593.

Reader, S. M., Hager, Y., & Laland, K. N. (2011). The evolution of primate general and cultural intelligence. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *366*(1567), 1017–1027. https://doi.org/10.1098/rstb.2010.0342

Richerson, P. J., & Boyd, R. (2020). The human life history is adapted to exploit the adaptive advantages of culture. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *375*(1803), 20190498. https://doi.org/10.1098/rstb.2019.0498

Rochat, M. J., Serra, E., Fadiga, L., & Gallese, V. (2008). The Evolution of Social Cognition: Goal Familiarity Shapes Monkeys’ Action Understanding. *Current Biology*, *18*(3), 227–232. https://doi.org/10.1016/j.cub.2007.12.021

Rosati, A. G. (2018). 19. Chimpanzee Cognition and the Roots of the Human Mind. In *Chimpanzees and Human Evolution* (pp. 703–745). Harvard University Press. https://www.degruyter.com/document/doi/10.4159/9780674982642-019/html

Rosati, A. G., & Hare, B. (2009). Looking past the model species: Diversity in gaze-following skills across primates. *Current Opinion in Neurobiology*, *19*(1), 45–51. https://doi.org/10.1016/j.conb.2009.03.002

Ruiz, A., Gómez, J. C., Roeder, J. J., & Byrne, R. W. (2009). Gaze following and gaze priming in lemurs. *Animal Cognition*, *12*(3), 427–434. https://doi.org/10.1007/s10071-008-0202-z

Russell, Y. I., Call, J., & Dunbar, R. I. M. (2008). Image scoring in great apes. *Behavioural Processes*, *78*(1), 108–111. https://doi.org/10.1016/j.beproc.2007.10.009

Sánchez-Amaro, A., Tan, J., Kaufhold, S. P., & Rossano, F. (2020). Gibbons exploit information about what a competitor can see. *Animal Cognition*, *23*(2), 289–299. https://doi.org/10.1007/s10071-019-01333-7

Sandel, A. A., MacLean, E. L., & Hare, B. (2011). Evidence from four lemur species that ringtailed lemur social cognition converges with that of haplorhine primates. *Animal Behaviour*, *81*(5), 925–931. https://doi.org/10.1016/j.anbehav.2011.01.020

Santos, L. R., Nissen, A. G., & Ferrugia, J. A. (2006). Rhesus monkeys, Macaca mulatta, know what others can and cannot hear. *Animal Behaviour*, *71*(5), 1175–1181. https://doi.org/10.1016/j.anbehav.2005.10.007

Scaife, M., & Bruner, J. S. (1975). The capacity for joint visual attention in the infant. *Nature*, *253*(5489), 265–266. https://doi.org/10.1038/253265a0

Scerif, G., Gomez, J.-C., & Byrne, R. W. (2004). What do Diana monkeys know about the focus of attention of a conspecific? *Animal Behaviour*, *68*(6), 1239–1247. https://doi.org/10.1016/j.anbehav.2004.01.011

Schloegl, C., Kotrschal, K., & Bugnyar, T. (2007). Gaze following in common ravens, Corvus corax: Ontogeny and habituation. *Animal Behaviour*, *74*(4), 769–778. https://doi.org/10.1016/j.anbehav.2006.08.017

Schmelz, M., Call, J., & Tomasello, M. (2011). Chimpanzees know that others make inferences. *Proceedings of the National Academy of Sciences*, *108*(7), 3077–3079. https://doi.org/10.1073/pnas.1000469108

Schmelz, Martin, & Call, J. (2016). The psychology of primate cooperation and competition: A call for realigning research agendas. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *371*(1686), 20150067. https://doi.org/10.1098/rstb.2015.0067

Schmelz, Martin, Call, J., & Tomasello, M. (2011). Chimpanzees know that others make inferences. *Proceedings of the National Academy of Sciences*, *108*(7), 3077–3079. https://doi.org/10.1073/pnas.1000469108

Schmelz, Martin, Call, J., & Tomasello, M. (2013). Chimpanzees predict that a competitor's preference will match their own. *Biology Letters*, *9*(1), 20120829. https://doi.org/10.1098/rsbl.2012.0829

Schnoell, A. V., & Fichtel, C. (2012). Wild redfronted lemurs (Eulemur rufifrons) use social information to learn new foraging techniques. *Animal Cognition*, *15*(4), 505–516. https://doi.org/10.1007/s10071-012-0477-y

Senju, A., Southgate, V., Snape, C., Leonard, M., & Csibra, G. (2011). Do 18-Month-Olds Really Attribute Mental States to Others?: A Critical Test. *Psychological Science*, *22*(7), 878–880. https://doi.org/10.1177/0956797611411584

Shepherd, S. V., & Platt, M. L. (2007). Spontaneous social orienting and gaze following in ringtailed lemurs (Lemur catta). *Animal Cognition*, *11*(1), 13. https://doi.org/10.1007/s10071-007-0083-6

Shultz, S., Opie, C., & Atkinson, Q. D. (2011). Stepwise evolution of stable sociality in primates. *Nature*, *479*(7372), 219–222. https://doi.org/10.1038/nature10601

Silk, J. B., Beehner, J. C., Bergman, T. J., Crockford, C., Engh, A. L., Moscovice, L. R., Wittig, R. M., Seyfarth, R. M., & Cheney, D. L. (2010). Strong and Consistent Social Bonds Enhance the Longevity of Female Baboons. *Current Biology*, *20*(15), 1359–1361. https://doi.org/10.1016/j.cub.2010.05.067

Slocombe, K. E., & Zuberbuhler, K. (2007). Chimpanzees modify recruitment screams as a function of audience composition. *Proceedings of the National Academy of Sciences*, *104*(43), 17228–17233. https://doi.org/10.1073/pnas.0706741104

Snyder-Mackler, N., Burger, J. R., Gaydosh, L., Belsky, D. W., Noppert, G. A., Campos, F. A., Bartolomucci, A., Yang, Y. C., Aiello, A. E., O'Rand, A., Harris, K. M., Shively, C. A., Alberts, S. C., & Tung, J. (2020). Social determinants of health and survival in humans and other animals. *Science, 368*(6493). https://doi.org/10.1126/science.aax9553

Spadacenta, S., Dicke, P. W., & Thier, P. (2019). Reflexive gaze following in common marmoset monkeys. *Scientific Reports*, *9*(1), 15292. https://doi.org/10.1038/s41598-019-51783-9

Steiper, M. E., & Young, N. M. (2006). Primate molecular divergence dates. *Molecular Phylogenetics and Evolution*, *41*(2), 384–394. https://doi.org/10.1016/j.ympev.2006.05.021

Sterelny, K. (2019). The Origins of Multi-level Society. *Topoi*. https://doi.org/10.1007/s11245-019-09666-1

Subiaul, F., Vonk, J., Okamoto-Barth, S., & Barth, J. (2008). Do chimpanzees learn reputation by observation? Evidence from direct and indirect experience with generous and selfish strangers. *Animal Cognition*, *11*(4), 611–623. https://doi.org/10.1007/s10071-008-0151-6

Surian, L., & Franchin, L. (2020). On the domain specificity of the mechanisms underpinning spontaneous anticipatory looks in false-belief tasks. *Developmental Science*, *23*(6), e12955. https://doi.org/10.1111/desc.12955

Téglás, E., Gergely, A., Kupán, K., Miklósi, Á., & Topál, J. (2012). Dogs' Gaze Following Is Tuned to Human Communicative Signals. *Current Biology*, *22*(3), 209–212. https://doi.org/10.1016/j.cub.2011.12.018

Tempelmann, S., Kaminski, J., & Liebal, K. (2011). Focus on the essential: All great apes know when others are being attentive. *Animal Cognition*, *14*(3), 433–439. https://doi.org/10.1007/s10071-011-0378-5

Theall, L., & Povinelli, D. (1999). Do chimpanzees tailor their gestural signals to fit the attentional state of others? *Animal Cognition*, *2*, 207–214. https://doi.org/10.1007/s100710050041

Tomasello, M., & Haberl, K. (2003). Understanding attention: 12- and 18-month-olds know what is new for other persons. *Undefined*. /paper/Understanding-attention%3A-12-and-18-month-olds-know-Tomasello-Haberl/a3831c9014190b01f27907df20c5fc74ada9c1bc

Tomasello, Michael. (1999). The Human Adaptation for Culture. *Annual Review of Anthropology*, *28*(1), 509–529. https://doi.org/10.1146/annurev.anthro.28.1.509

Tomasello, Michael, & Call, J. (1997a). *Primate Cognition*. Oxford University Press.

Tomasello, Michael, & Call, J. (1997b). *Primate Cognition*. Oxford University Press.

Tomasello, Michael, & Call, J. (2008). Assessing the validity of ape-human comparisons: A reply to Boesch (2007). *Journal of Comparative Psychology*, *122*(4), 449–452. https://doi.org/10.1037/0735-7036.122.4.449

Tomasello, Michael, Call, J., & Hare, B. (1998). Five primate species follow the visual gaze of conspecifics. *Animal Behaviour*, *55*(4), 1063–1069. https://doi.org/10.1006/anbe.1997.0636

Tomasello, Michael, Call, J., & Hare, B. (2003). Chimpanzees understand psychological states – the question is which ones and to what extent. *Trends in Cognitive Sciences*, *7*(4), 153–156. https://doi.org/10.1016/S1364-6613(03)00035-4

Tomasello, Michael, Call, J., Nagell, K., Jaakkola, K., & Carpenter, M. (1994). The learning and use of gestural signals by young chimpanzees: A trans-generational study. *Primates*, *35*, 137–154. https://doi.org/10.1007/BF02382050

Tomasello, Michael, & Carpenter, M. (2005). Intention reading and imitative learning. *Perspectives on Imitation: From Neuroscience to Social Science, 2*, 133–148.

Tomasello, Michael, Carpenter, M., Call, J., Behne, T., & Moll, H. (2005). Understanding and sharing intentions: The origins of cultural cognition. *Behavioral and Brain Sciences*, *28*(5), 675–691. https://doi.org/10.1017/S0140525X05000129

Tomasello, Michael, Hare, B., & Agnetta, B. (1999). Chimpanzees, Pan troglodytes, follow gaze direction geometrically. *Animal Behaviour*, *58*(4), 769–777. https://doi.org/10.1006/anbe.1999.1192

Tomasello, Michael, Hare, B., Lehmann, H., & Call, J. (2007). Reliance on head versus eyes in the gaze following of great apes and human infants: The cooperative eye hypothesis. *Journal of Human Evolution*, *52*(3), 314–320. https://doi.org/10.1016/j.jhevol.2006.10.001

Uller, C. (2004). Disposition to recognize goals in infant chimpanzees. *Animal Cognition*, *7*(3), 154–161. https://doi.org/10.1007/s10071-003-0204-9

Ullman, T. D., Baker, C. L., Macindoe, O., Evans, O., Goodman, N. D., & Tenenbaum, J. B. (2009). *Help or Hinder: Bayesian Models of Social Goal Inference*. MIT. https://apps.dtic.mil/sti/citations/ADA537574

van de Waal, E., Claidière, N., & Whiten, A. (2015). Wild vervet monkeys copy alternative methods for opening an artificial fruit. *Animal Cognition*, *18*(3), 617–627. https://doi.org/10.1007/s10071-014-0830-4

Vick, S.-J., & Anderson, J. R. (2003). Use of human visual attention cues by olive baboons (Papio anubis) in a competitive task. *Journal of Comparative Psychology*, *117*(2), 209–216. https://doi.org/10.1037/0735-7036.117.2.209

Voelkl, B., & Huber, L. (2000). True imitation in marmosets. *Animal Behaviour*, *60*(2), 195–202. https://doi.org/10.1006/anbe.2000.1457

Völter, C. J., Mundry, R., Call, J., & Seed, A. M. (2019). Chimpanzees flexibly update working memory contents and show susceptibility to distraction in the self-ordered search task.

Proceedings of the Royal Society B: Biological Sciences, *286*(1907), 20190715. https://doi.org/10.1098/rspb.2019.0715

Völter, C. J., Tinklenberg, B., Call, J., & Seed, A. M. (2018). Comparative psychometrics: Establishing what differs is central to understanding what evolves. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *373*(1756), 20170283. https://doi.org/10.1098/rstb.2017.0283

Waal, E. van de, & Whiten, A. (2012). Spontaneous Emergence, Imitation and Spread of Alternative Foraging Techniques among Groups of Vervet Monkeys. *PLOS ONE*, *7*(10), e47008. https://doi.org/10.1371/journal.pone.0047008

Warneken, F., Hare, B., Melis, A. P., Hanus, D., & Tomasello, M. (2007). Spontaneous Altruism by Chimpanzees and Young Children. *PLOS Biology*, *5*(7), e184. https://doi.org/10.1371/journal.pbio.0050184

Warneken, F., & Tomasello, M. (2006). Altruistic Helping in Human Infants and Young Chimpanzees. *Science*, *311*(5765), 1301–1303. https://doi.org/10.1126/science.1121448

Wellman, H. M., Cross, D., & Watson, J. (2001). Meta-Analysis of Theory-of-Mind Development: The Truth about False Belief. *Child Development*, *72*(3), 655–684. https://doi.org/10.1111/1467-8624.00304

Whiten, Andew, & Byrne, R. (1988). Tactical deception in primates. *Behavioral and Brain Sciences*, *11*(2), 233–244. https://doi.org/10.1017/S0140525X00049682

Whiten, Andrew. (1994). *Grades of Mindreading. In: Children's Early Understanding of Mind*. Psychology Press.

Whiten, Andrew. (1996). When does smart behaviour reading become mindreading? In *Theories of Theories of Mind* (pp. 277–292). Cambridge University Press.

Whiten, Andrew. (2013). Humans are not alone in computing how others see the world. *Animal Behaviour*, *86*(2), 213–221. https://doi.org/10.1016/j.anbehav.2013.04.021

Whiten, Andrew, & Byrne, R. W. (1997). *Machiavellian Intelligence II: Extensions and Evaluations*. Cambridge University Press. https://doi.org/10.1017/CBO9780511525636

Wilkinson, A., Mandl, I., Bugnyar, T., & Huber, L. (2010). Gaze following in the red-footed tortoise (Geochelone carbonaria). *Animal Cognition*, *13*(5), 765–769. https://doi.org/10.1007/s10071-010-0320-2

Wimmer, H., & Perner, J. (1983). *Beliefsabout beliefs: Representationand constraircing function of wrong bekfs in young children'sunderstanding of deception*. *13*(1), 26. https://doi.org/10.1016/0010-0277(83)90004-5

Wobber, V., Wrangham, R., & Hare, B. (2010). Bonobos Exhibit Delayed Development of Social Behavior and Cognition Relative to Chimpanzees. *Current Biology*, *20*(3), 226–230. https://doi.org/10.1016/j.cub.2009.11.070

Wood, J. N., Glynn, D. D., Phillips, B. C., & Hauser, M. D. (2007). The Perception of Rational, Goal-Directed Action in Nonhuman Primates. *Science*, *317*(5843), 1402–1405. https://doi.org/10.1126/science.1144663

Woodward, A. L. (1998). Infants selectively encode the goal object of an actor's reach. *Cognition*, *69*(1), 1–34. https://doi.org/10.1016/S0010-0277(98)00058-4

Wrangham, R. (2009). *Catching Fire: How Cooking Made Us Human*. Basic Books.

Yamamoto, S., Humle, T., & Tanaka, M. (2009). Chimpanzees Help Each Other upon Request. *PLOS ONE*, *4*(10), e7416. https://doi.org/10.1371/journal.pone.0007416

Yamamoto, S., Humle, T., & Tanaka, M. (2012). Chimpanzees' flexible targeted helping based on an understanding of conspecifics' goals. *Proceedings of the National Academy of Sciences, 109*(9), 3588–3592. https://doi.org/10.1073/pnas.1108517109