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Abstract

Theory of mind (ToM; a.k.a., mind-reading, mentalizing, mental-state attribution, and perspective-taking) is the ability to ascribe mental states, such as desires and beliefs, to others, and it is central to the unique forms of communication, cooperation, and culture that define our species. As a result, for forty years, researchers have endeavored to determine whether ToM is itself unique to humans. Investigations in other species (e.g., apes, monkeys, corvids) are essential to understand the mechanistic underpinnings and evolutionary origins of this capacity across taxa, including humans. We review the literature on ToM in nonhuman animals, suggesting that some species share core social cognitive mechanisms with humans. We focus principally on innovations of the last decade and pressing directions for future work. Underexplored types of social cognition have been targeted, including ascription of mental states, like desires and beliefs, that require simultaneously

representing one's own and another's conflicting motives or views of the world. Ongoing efforts probe the motivational facets of ToM, how flexibly animals can recruit social cognitive skills across cooperative and competitive settings, and appropriate motivational contexts for comparative inquiry. Finally, novel methodological and empirical approaches have brought new species (e.g., lemurs, dogs) into the lab, implemented critical controls to elucidate underlying mechanisms, and contributed powerful new techniques (e.g., looking-time, eye-tracking) that open the door to unexplored approaches for studying animal minds. These innovations in cognition, motivation, and method promise fruitful progress in the years to come, in understanding the nature and origin of ToM in humans and other species.

Graphical/Visual Abstract and Caption



Caption: Forty years of research has sought to determine whether nonhuman animals, like this bonobo, have a theory of mind.

Introduction

Theory of mind is the ability to ascribe mental states, such as desires and beliefs, to others, and it is central to human social life (Premack & Woodruff, 1978). Also known as mind-reading or mental state attribution, this capacity to infer what others are thinking allows us to interpret, predict, and even manipulate others' behavior. We regularly make use of theory of mind when attempting to communicate or to comprehend others' communication (what did she *intend* to convey?), when competing or cooperating (will my opponent or teammate *see* me coming?), deceiving or helping (what does he *want*?). Right now, for example, while writing this, we are attempting to infer your perspective. We're imagining what your *goals* are in reading this paper, what background *knowledge* you might bring to the table, and how we can communicate in ways that will be both intelligible and stimulating. We are building theories about the unobservable content of your mind, predicated on a theory that other beings have minds in the first place. This capacity for mind-reading is central to much of the social and cognitive substrate that makes us human, including forms of communication, cooperation, and culture that are believed to set us apart from other animals. And consequently, for the last forty years, researchers have sought to determine whether theory of mind itself may be unique to our species.

Why study theory of mind in non-human animals?

There are a number of reasons to study theory of mind in non-human animals, and indeed an empirical focus on theory of mind—in humans and non-humans—has roots in animal work. In a seminal paper, Premack and Woodruff (1978) coined the term “theory of mind” in order to ask: “Does the chimpanzee have a theory of mind?” Today, human theory of mind is a thriving area of research in social, cognitive, developmental, and even clinical psychology and increasingly in neuroscience and anthropology as well (Baillargeon, Scott, & He, 2010; Baron-Cohen, Leslie, & Frith, 1985; Barrett et al., 2013; Hare, 2017; Saxe & Baron-Cohen, 2006; Tomasello, Melis, Tennie, Wyman, & Herrmann, 2012; Wellman, Cross, & Watson, 2001), but the study of animal theory of mind has

not stood still and a growing focus on humans has only elevated the importance of comparisons with animals (Call & Tomasello, 2008; Whiten, 2013). Animal cognition work stands to contribute in two principal ways to our understanding of the minds of humans and other species—by providing unique insights into cognitive mechanisms and evolutionary origins.

The cognitive architecture of theory of mind is hotly debated. Although we often think of it as a single capacity, theory of mind is likely comprised of a suite of interacting mechanisms and the nature of those subcomponents and their relationships remains unclear. Many have suggested, for example, that theory of mind results from special human cognitive products, like language and culture, and that its development is at least partly driven by our unique culture and socialization practices (C. M. Heyes & Frith, 2014; Liu, Wellman, Tardif, & Sabbagh, 2008; Lohmann & Tomasello, 2003; Milligan, Astington, & Dack, 2007; Pyers & Senghas, 2009). Thus, demonstrating theory of mind capacities in any non-human species would indicate that those capacities can arise and operate in the absence of human language and culture. Such findings would suggest that linguistic or cultural input simply enhances theory of mind, perhaps through explicit teaching of mental state concepts or by expanding the descriptive and recursive nature of the representations one can have of others' minds. We also do not know the extent to which theory of mind depends on or is simply enhanced by auxiliary mechanisms like inhibitory control and memory (Carlson, Moses, & Breton, 2002; Powell & Carey, 2017). Finding theory of mind in species with more limited inhibitory control or memory than humans would provide some insight toward understanding the minimum requirements for theory of mind to emerge.

Moreover, humans' closest primate relatives can play a particularly crucial role in identifying the cognitive architecture of human theory of mind through elucidation of its evolutionary precursors. This process has important implications for understanding the evolutionary origins of theory of mind, of course, but also its mechanistic underpinnings (Krupenye, MacLean, & Hare, 2017; Krupenye, Rosati, & Hare, 2015). Reconstructing evolutionary history allows us to understand how evolution built human social cognition and provides important insight into its constituent

mechanisms and how they interact in humans. For example, developmental trajectories may mirror evolutionary trajectories, with the evolutionarily most ancient mechanisms providing the foundation, in development, for the emergence of later-developing human-unique capacities. By studying humans' closest extant relatives, the great apes (family *Hominidae*; our absolute closest being chimpanzees [*Pan troglodytes*] and bonobos [*Pan paniscus*], followed by gorillas [*Gorilla sp.*], and then orangutans [*Pongo sp.*]), we can discriminate mechanisms that are unique to humans from those that were already present in our common ancestor (i.e., those that are shared with at least chimpanzees and bonobos). Apes are not monkeys but they are part of a broader phylogenetic group called *Catarrhini* that also includes the monkeys of Africa and Asia (Old World Monkeys; family *Cercopithecidae*). By looking beyond apes to Old World monkeys, we can determine which aspects of ape theory of mind evolved earliest and are also shared with monkeys, and which evolved later and are only present in apes. This information allows us to reconstruct the cognitive phenotype of our common ancestors at different points in our evolutionary history, clarifying which mechanisms are most basal and which build on one another. It also allows us to identify the building blocks that were already present 6-9 million years ago at the start of humans' unique evolutionary trajectory and to speculate about the events that must have subsequently occurred for our unique mechanisms to evolve. Demonstrating theory of mind in our closest ape relatives, for example, would suggest that uniquely human language and cultural capacities were built on evolutionarily ancient social cognition—rather than language or culture providing the foundation for theory of mind.

Broader phylogenetic comparisons can tell us whether the mechanisms involved in theory of mind also evolved convergently (i.e., independently) in distantly related species (e.g., in corvids, like crows, ravens, and jays) (Emery & Clayton, 2004). If social cognitive mechanisms are adaptations to a species' social or physical ecology, these comparisons can shed light on the selective pressures that drove their evolution as well (MacLean et al., 2012). For example, the social intelligence hypothesis proposes that social cognition evolved in response to the demands of social living (e.g., competing with groupmates for reproductive opportunities) (Byrne & Whiten, 1988; Dunbar & Shultz, 2007;

Humphrey, 1976; Jolly, 1966). According to this hypothesis, phylogenetic comparisons should reveal that species that inhabit the most socially complex groups have evolved more sophisticated social cognitive abilities than those that face fewer social challenges. Other hypotheses postulate that features of the physical environment, like feeding ecology, place different cognitive demands on animals and predict that more sophisticated abilities will have evolved in species that rely on fruits rather than leaves or that must exploit otherwise inaccessible resources through tool-use and extractive foraging (Milton, 1981, 1988; Reader & Laland, 2002; Rosati, 2017). Finally, comparisons of key closely related species, such as between domesticates and their wild counterparts, can also clarify how known evolutionary pressures, like artificial selection (i.e., selective breeding) against aggression during domestication, shape cognition (Hare, 2017; Hare, Brown, Williamson, & Tomasello, 2002; Hare, Wobber, & Wrangham, 2012; Krupenye, MacLean, et al., 2017). By manipulating or controlling for socialization—for example, intensive versus minimal interaction with humans—these studies can additionally disentangle environmental and genetic effects on cognitive and behavioral development. Thus, studies of animal theory of mind are critical to understand both the mechanistic underpinnings and the evolutionary origins of these abilities in humans.

State of the art 10 years back

In 2008, Call and Tomasello (2008) revisited the question that launched theory of mind research three decades earlier: “Does the chimpanzee have a theory of mind?” (Premack & Woodruff, 1978). Only 10 years before, there had been considerable consensus from the experimental literature that theory of mind may be unique to humans—despite anecdotal evidence that wild animals engaged in behaviors like deception that *could* be underlain by theory of mind (Anderson, Montant, & Schmitt, 1996; Byrne & Whiten, 1988; D. Cheney & R. Seyfarth, 1990; de Waal, 1982; C. Heyes, 1998; Kummer, Anzenberger, & Hemelrijk, 1996; Povinelli & Eddy, 1996b; Povinelli, Nelson, & Boysen, 1990; Povinelli, Parks, & Novak, 1991; Povinelli, Rulf, & Bierschwale, 1994; Tomasello & Call, 1997; Whiten & Byrne, 1988). By 2008, Call and Tomasello (2008) concluded

that things had changed: several tasks provided converging evidence that apes were sensitive to the goals and intentions that underlie others' actions. For example, they were more patient with an individual who intended to feed them but was unable to do so than with one who was unwilling to share food, they discriminated and responded appropriately to intentional versus accidental actions, they helped others achieve their goals, and they completed others' failed actions (Buttelmann, Carpenter, Call, & Tomasello, 2007; Buttelmann, Schütte, Carpenter, Call, & Tomasello, 2012; Call, Hare, Carpenter, & Tomasello, 2004; Call & Tomasello, 1998; Krupenye, Tan, & Hare, 2018; Myowa-Yamakoshi & Matsuzawa, 2000; Tomasello & Carpenter, 2005; Warneken, Hare, Melis, Hanus, & Tomasello, 2007; Warneken & Tomasello, 2006; Yamamoto, Humle, & Tanaka, 2012). There was also a variety of evidence suggesting that apes were aware of what others could see, and perhaps hear, and what others knew on the basis of seeing. For example, apes followed others' gaze around barriers and checked back with the actor if they could not find the target of her attention (Brauer, Call, & Tomasello, 2005; Call, Hare, & Tomasello, 1998; Okamoto, Tanaka, & Tomonaga, 2004; Okamoto-Barth, Call, & Tomasello, 2007; Povinelli & Eddy, 1996a; Tomasello, Call, & Hare, 1998; Tomasello, Hare, & Agnetta, 1999; Tomasello, Hare, & Fogleman, 2001; Tomasello, Hare, Lehmann, & Call, 2007). They relied on visual gestural communication more when a recipient was oriented toward them than away and would even move to the front of the recipient before beginning to gesture (Gómez, 1996; Hostetter, Cantero, & Hopkins, 2001; Kaminski, Call, & Tomasello, 2004; Leavens, Hostetter, Wesley, & Hopkins, 2004; Liebal, Call, Tomasello, & Pika, 2004; Povinelli & Eddy, 1996b; Povinelli, Theall, Reaux, & Dunphy-Lelii, 2003; Tomasello, Call, Nagell, Olguin, & Carpenter, 1994). And, in competitive tasks, chimpanzees concealed their approach and preferentially targeted food that a competitor could not see or was ignorant about (Brauer, Call, & Tomasello, 2007; Hare, Call, Agnetta, & Tomasello, 2000; Hare, Call, & Tomasello, 2001, 2006; Kaminski, Call, & Tomasello, 2008; Karg, Schmelz, Call, & Tomasello, 2015a; Melis, Call, & Tomasello, 2006). These studies suggested that apes may have a non-egocentric view of the world—that they could recognize and exploit the ways in which their perceptual access may differ from others. However, a few studies

failed to find evidence that apes could go beyond understanding of others' knowledge or ignorance to represent their beliefs. In several experiments, a competitor or cooperator watched an object be hidden in one location but was absent while it was moved. Although apes could witness the entire baiting and track their partner's attention, they did not take advantage of the fact that their competitor or cooperator would falsely believe that the object was still in the location where she had last seen it (Call & Tomasello, 1999; Hare et al., 2001; Kaminski et al., 2008; Krachun, Carpenter, Call, & Tomasello, 2009, 2010). Taken together, this work suggested that apes were able to track the goals, perceptions, and knowledge that motivate others' actions but that they could not represent what others believed (Call & Tomasello, 2008; Hare, 2011). Related work suggested that monkeys (rhesus macaques, *Macaca mulatta*; capuchin monkeys, *Sapajus apella/Cebus apella*) were also sensitive to others' goals and intentions and that both monkeys (rhesus macaques) and corvids (common ravens, *Corvus corax*; California scrub-jays, *Aphelocoma californica*; Eurasian jays, *Garrulus glandarius*; jackdaws, *Coloeus monedula*; Clark's nutcracker, *Nucifraga columbiana*) were sensitive to others' visual and auditory perspectives (Anderson, Kuroshima, Takimoto, & Fujita, 2013; Bugnyar, 2011; Bugnyar & Heinrich, 2005; Bugnyar & Kotrschal, 2002; Bugnyar, Stowe, & Heinrich, 2004; Clary & Kelly, 2011; Dally, Emery, & Clayton, 2004, 2005, 2006; Drayton & Santos, 2014a; Emery & Clayton, 2001; Flombaum & Santos, 2005; Hare, Addessi, Call, Tomasello, & Visalberghi, 2003; Legg & Clayton, 2014; Legg, Ostojić, & Clayton, 2016; Phillips, Barnes, Mahajan, Yamaguchi, & Santos, 2009; Rochat, Serra, Fadiga, & Gallese, 2008; Santos, Nissen, & Ferrugia, 2006; Shaw & Clayton, 2013; Tornick, Rushia, & Gibson, 2016; von Bayern & Emery, 2009).

Skeptics suggested—and hold to this day—that no particular study has provided unequivocal evidence of animal theory of mind, since in most cases subjects had access to some behavioral information that they could use to predict others' actions (C. Heyes, 1998, 2015; Penn & Povinelli, 2007; Povinelli & Vonk, 2003) (but see Halina, 2015 for an argument against this so-called "logical problem"). As one example, during the course of an animal's life, she may have learned that agents tend to pursue desirable objects that are in front of them, within their "line of gaze." Consequently,

in experiments where such information is available, she could expect agents to pursue objects they can see based on physical relationships between those agents and objects, without representing that the agents can actually *see* the objects. But, for many, the convergence of findings across a great many paradigms—coupled with experimental manipulations to control for individual explanations (see Hare, 2011 Table 1)—suggested that a common mind-reading mechanism may provide a more parsimonious explanation than the diverse suite of behavior rules that would be necessary to explain successful performance across tasks (Call & Tomasello, 2008).

Focus

In the remainder of the present article, we review advances of the last decade and discuss what we see as the most pressing avenues for future work. These current and future directions are organized around three interlinked themes. In the Cognition section, we address the types of mental state attribution being investigated in theory of mind tasks and, to some extent, the representations underlying them. In the Motivation section, we address the motivational substrate involved in experimental tests for theory of mind. And, finally, in the Methods section, we detail novel methodologies and empirical approaches that are moving the field forward. In the sections that follow, we will address new tests and controls aimed at distinguishing alternative explanations of observed behavior. However, the present paper endeavors principally to highlight advances and future directions in theory of mind research, rather than to confront alternative explanations (for papers with this latter goal, see Hare, 2011; Martin & Santos, 2016). Accordingly, the question of interpretation will arise periodically throughout the paper and we will, for example, review new efforts to refute particular alternatives. However, we will also often discuss “sensitivity” to particular mental states without making strong claims about the underlying mechanisms that permit animals to respond appropriately to them. In many cases, as we will discuss, elucidating these mechanisms requires further empirical and philosophical scrutiny.

COGNITION

Until recently, research on animal theory of mind has focused largely on two classes of abilities. First, work on animals' understanding of conative or motivational states has concentrated on the ability to identify others' goals and intentions. In the last decade, researchers have begun to push the boundaries of animals' understanding by investigating whether they grasp the transience and subjectivity of these motivational states. Specifically, they have tested whether animals can attribute context-induced preferences (e.g., understanding that an actor will prefer food A over food B because the actor has already become satiated on food B) and whether they know that others' desires and preferences may differ from, and even conflict with, their own.

Second, work on understanding of cognitive or epistemic states has investigated whether animals are aware of *what* others can perceive or have perceived (e.g., what others can or cannot see, or what they know or remain ignorant about)—what is called level I perspective-taking. More recently, research has made ground in clarifying whether any animals recognize that others are acting not just based on awareness or lack of awareness of reality but instead based on beliefs about the world (including beliefs that are false). Although still at a nascent stage, this work is also increasingly opening directions for investigating level II perspective-taking (understanding *how* something appears from another's perspective). These parallel lines of inquiry—into attribution of subjective desires and of false beliefs—are particularly crucial because both types of mentalizing require, by definition, awareness of a self-other distinction and, specifically, the capacity to recognize and represent the ways in which others' motives and views differ from one's own.

Desires

Understanding that others' minds and mental states differ from one's own is central to theory of mind. In human development, an early milestone of this sort is the emerging recognition that desires are subjective. By 9 months, human infants appear to comprehend that preferences are

specific to individuals—infants do not generalize one agent’s preference to a second novel agent (Buresh & Woodward, 2007; Henderson & Woodward, 2012)—and around 18 months they know that individuals can even have desires and preferences that conflict with the child’s own (Repacholi & Gopnik, 1997; but see Ruffman, Aitken, Wilson, Puri, & Taumoepeau, 2018). Substantial work on animals’ understanding of others’ motivational states suggests that some species can infer the goals and intentions that underlie others’ actions, but, until recently, it has been unclear whether they treat preferences and desires as subjective and, specifically, whether they are aware that others may hold desires that conflict with the participant’s own (Buttelmann, Call, & Tomasello, 2009; Kano & Call, 2014b; Rochat et al., 2008).

Ostojić, Shaw, Cheke, and Clayton (2013) developed an ingenious method for investigating desire-state attribution in Eurasian jays by capitalizing on their natural food-sharing behavior (Legg, Ostojić, & Clayton, 2015; Ostojić, Cheke, Shaw, Legg, & Clayton, 2016) (Figure 1). During the mating season, males provision females, leading the researchers to wonder whether the males were taking into account what the females wanted. In their first experiment, the researchers established that desires can be manipulated through specific satiety—that jays could be sated on one food, reducing their desire for that food, while still being hungry for other foods. Males or females were pre-fed one of two types of larvae and were then allowed to eat both types. To assess the impact of pre-feeding on jays’ relative preferences for food A versus food B, their choices in each condition were compared with baseline preferences (from a baseline condition in which they were only pre-fed their maintenance diet) and then compared between test conditions (pre-fed food A versus pre-fed food B). Jays who were pre-fed food A showed a greater shift from baseline preferences toward a relative preference for food B than did jays who were pre-fed food B. That is, when jays became specifically sated on one food, they decreased their desire for that food while their desire for the other remained constant. In the desire-understanding sharing experiment, males watched as females were pre-fed one of the two types of larvae (i.e., her desire for one food was reduced by pre-feeding while her desire for the non-pre-fed food remained constant), while males themselves

were pre-fed maintenance diet (i.e., males' desires were not manipulated; Figure 1A). Then males could choose to share either type of larvae with the female (Figure 1B and 1C). Subjects shifted their choice of food flexibly depending on what the female had been pre-fed—increasing their choice of foods that she still desired. In a control condition in which males could not witness their partner pre-feeding, sharing behavior differed significantly from the test condition, indicating that, at the time of test, jays were not simply responding to behavioral cues from the female about what she wanted. Having observed her pre-feeding was necessary to appropriately respond to her desires.

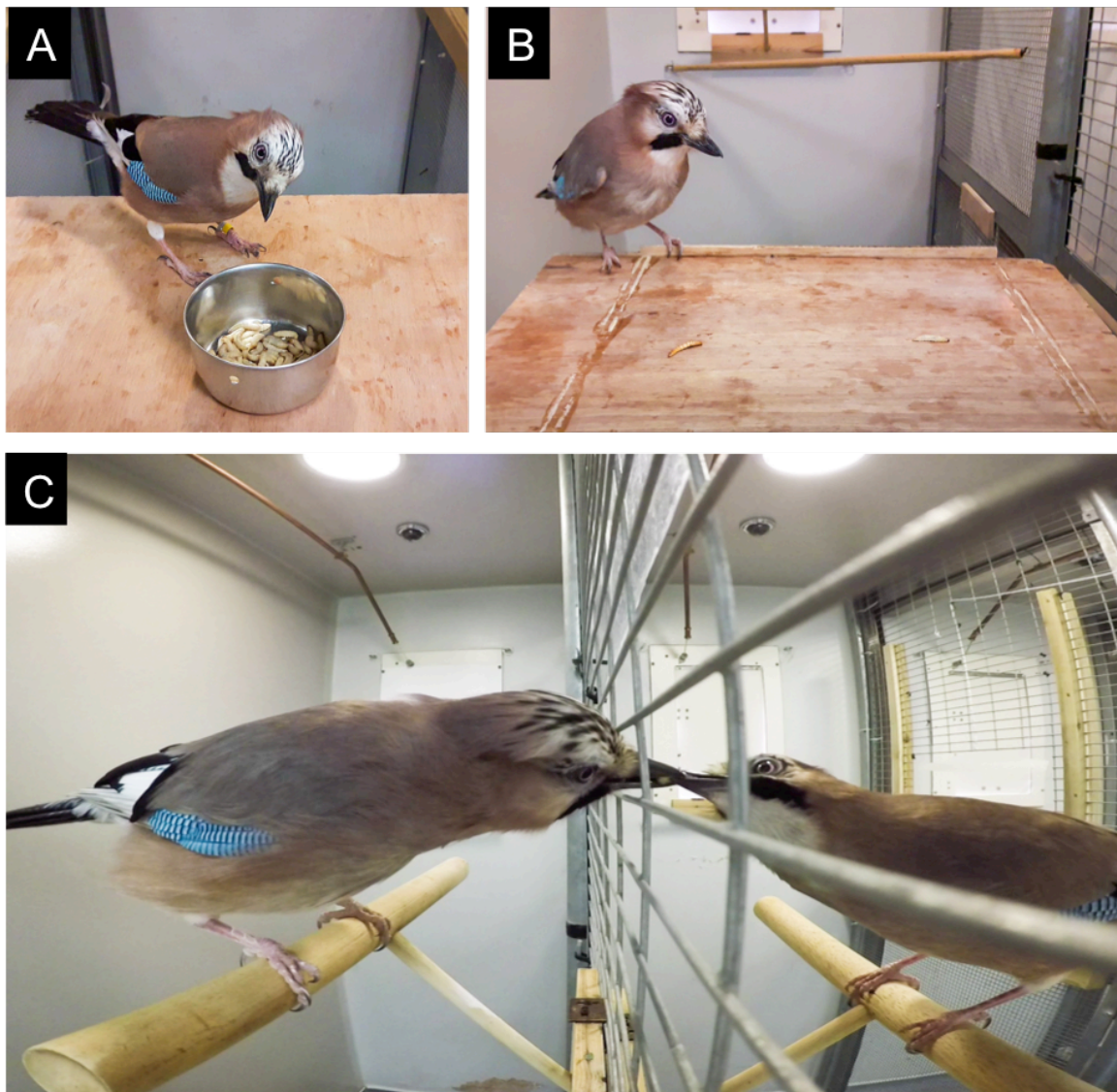


Figure 1. Desire attribution experiments with Eurasian jays. (a) A female was satiated on one type of food, decreasing her desire for that food relative to others, while her male partner watched. (b)

Males could then choose between the sated (undesired) food and a desired alternative. (c) Males shifted their choice of foods to share with the female depending on what she still wanted. Copyright: Ljerka Ostojić and Lovre Čulina.

In these studies, males' desires differed from females' in that males were sated on neither food (i.e., females desired a single food while males desired both). However, an important question is whether jays can also respond appropriately to desires that directly conflict with their own. To tackle this question, Ostojić et al. (2014) pre-fed both males and females the same or different foods so that they would have matched or mismatched desire states. When their states were matched, males delivered the desired food to their partners. When their states were mismatched, males showed an intermediate response, suggesting that their sharing behavior was biased by their own desire but that they still took their partner's desire into account.

Another key question is whether jays' sensitivity to desires is specific to the cooperative food-sharing context or whether it might extend flexibly to other social settings. To address this question, Ostojić et al. (2017) investigated whether Eurasian jays and California scrub-jays would take an observer's desires into account in a caching context in which they could potentially cache undesired food to avoid it being pilfered by the observer. Cachers watched as observers were pre-fed one of two types of food and, indeed, showed increased tendencies to cache the food that the observer did not desire. However, this caching strategy persisted in another condition in which cachers could not witness the observer's pre-feeding. These experiments indicate that jays are sensitive to others' desires in diverse contexts, but that they may deploy different mechanisms in each setting. The observer's behavior at the time of caching was sufficient to shift the cacher's strategy, whereas, in the food-sharing context, the partner's behavior at the time of sharing was not sufficient; jays needed to witness the pre-feeding in order to show sensitivity to their partner's desire. This body of work suggests that some nonhuman species are sensitive to internal states that differ from their own and that an understanding of subjective desires may have evolved

convergently in humans and jays. Whether this ability is shared with primates or other species remains a key question for future work.

Beliefs

False beliefs are epistemic states that conflict with reality (e.g., believing that there are cookies in the cabinet, when in fact your sibling has already eaten them). Understanding others' false beliefs has long been seen as the defining signature of a "full-blown" theory of mind (Baron-Cohen et al., 1985; Dennett, 1978; Pylyshyn, 1978; Wellman et al., 2001). This is the case because attributing false beliefs requires simultaneously representing two conflicting views of the world—one's own, which aligns with reality, and that of another, which does not. Previous work suggested that apes, monkeys, and corvids were sensitive to others' knowledge and ignorance but not their beliefs. Attributing false beliefs is similar to attributing ignorance in that both require a non-egocentric view of the world in which an animal distinguishes between the information it has about the world and that which is possessed by another agent. However, they differ, critically, in that one can attribute ignorance by representing a single view of the world (reality) and recognizing that another agent simply has incomplete access to it (e.g., that the agent has not seen an object be hidden under a box and therefore has no awareness that there is or isn't an object under the box). In contrast, to attribute false beliefs, one must represent two distinct views of the world—one's own (which corresponds to reality) and the mutually incompatible view of another (e.g., you believe that an object is under a box, where you have last seen it, but I know that it is no longer there). As such, in its richest forms, false belief understanding relies not only on attributions of whether or not an agent has perceived an object (level I perspective-taking), but also of *how* the situation appears from the agent's perspective—including how this appearance may differ from one's own perspective (level II perspective-taking) (Flavel, Everett, Croft, & Flavel, 1981). It is this meta-representational capacity that is thought to be at the heart of human communication, cooperation, and culture.

A handful of previous studies failed to find evidence of false belief understanding in apes in interactive social contexts involving food (Call & Tomasello, 1999; Hare et al., 2001; Kaminski et al., 2008; Krachun et al., 2009, 2010), possibly because they overtaxed apes' inhibitory control and memory capacities (see "Methods: Novel Techniques" section for further discussion). Indeed, children also fail a variety of false belief tasks until age 4—perhaps owing in part to overwhelming cognitive demands, since even infants can pass tasks specifically designed to minimize these demands (Baillargeon et al., 2010; Scott & Baillargeon, 2017; Wellman et al., 2001).

In traditional false belief tasks, a participant watches as one actor sees an object hidden in one of two locations and then leaves the scene. While away, the object is moved or removed, and, when the actor returns, the participant is asked where the actor will search for the object. If participants understand that the actor has a false belief, they should indicate that he will search for the object in the location where he last saw it hidden. To implement this traditional design under minimal task demands, developmental psychologists identified nonverbal measures of action prediction (Clements & Perner, 1994; Onishi & Baillargeon, 2005; Southgate, Senju, & Csibra, 2007). For example, anticipatory looking methods exploit participants' tendency to look to locations where they expect an event to imminently occur (Cannon & Woodward, 2012; Kano & Call, 2014b; Kano & Hirata, 2015; Lorincz et al., 2005). Participants watch videos of traditional false belief events, while their gaze direction is non-invasively recorded with an infrared eye-tracker positioned beneath the monitor. In the final scenes of the video, as an actor ambiguously approaches two locations to search for a hidden object, human infants look to the location where the actor falsely believes the object is hidden—anticipating the actor's search (Schneider, Bayliss, Becker, & Dux, 2012; Senju, Southgate, Snape, Leonard, & Csibra, 2011; Senju, Southgate, White, & Frith, 2009; Southgate et al., 2007; Surian & Geraci, 2012).

Capitalizing on these innovations, Krupenye, Kano, Hirata, Call, and Tomasello (2016) developed a pair of eye-tracking false belief experiments for chimpanzees, bonobos, and orangutans (Figure 2). To motivate apes to attend to an actor's false belief, the researchers contextualized

traditional false belief scenarios within social dramas that were specifically designed to maximize apes' interest. For example, in one study, a human actor engaged in an agonistic conflict with a costumed gorilla (Figure 3). The actor then attempted to search for the gorilla, who had originally hidden in one of two locations while the actor was watching but later fled the scene while the actor was away. Across two studies, apes attended closely to the social events, and then looked in anticipation of the actor searching where he falsely believed the gorilla (or other goal object) to be—even though apes themselves knew that it was no longer there. This study provided the first evidence that apes may be sensitive not just to others' knowledge or ignorance but also to their beliefs (Table 1).



Figure 2. Eye-tracking setup. An infrared eye-tracker non-invasively records an orangutan's gaze as she attends to pictures and videos presented on a monitor, just outside of her enclosure. A nearby laptop controls stimuli presentation. Subjects voluntarily approach the setup to view the stimuli and sip a slow stream of juice. Copyright: Christopher Krupenye and Leipzig Zoo.

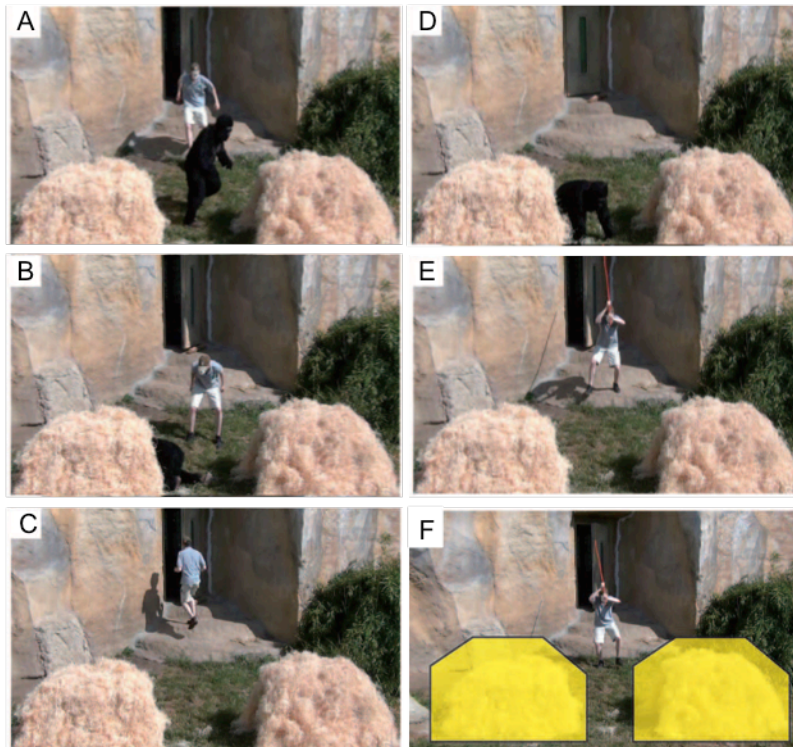


Figure 3. False belief tests with great apes. Apes' gaze is recorded as they witness an actor chase a costumed gorilla into a hiding place on the right (A), and watch as the gorilla moves to a second location on the left (B). The actor then leaves through a door (C), and, while away, the gorilla flees the scene (D). The actor returns, falsely believing that the gorilla is still on the left. As he approaches centrally toward the two locations (E), apes' looks in advance of his search are automatically coded based on pre-determined areas-of-interest (F). Apes look in anticipation of the actor searching for the gorilla on the left, where the actor falsely believes the gorilla to be.

Paired conditions within each of the studies controlled for low-level explanations—apes could not succeed by looking to the first or last location of the goal object or the last location the actor attended (Southgate et al., 2007) (Table 1). Apes closely tracked all events, making it clear that they had not simply overlooked the object's movement (C. Heyes, 2014a). Moreover, they could not have solved the task by attributing ignorance to the actor rather than a false belief. Apes did not expect the actor to err or exhibit uncertainty (Baillargeon et al., 2010); they specifically anticipated that he would search for his goal where he falsely believed it to be. Applying an interpretation

previously offered for human adults and infants (C. Heyes, 2014a, 2014b), C. Heyes (2017) suggested that apes may have been submentalizing: predicting behavior via domain-general psychological processes, including several low-level cueing effects. C. Heyes (2017) recommended that studies test for submentalizing with inanimate controls—stimuli matched for low-level perceptual cues but devoid of social or agentic features. If participants show comparable levels of attention, submentalizing predicts that domain-general processes will elicit common patterns of anticipatory looking, even in inanimate controls. Krupenye, Kano, Hirata, Call, and Tomasello (2017) implemented Heyes’s proposed control, and found no evidence that submentalizing could explain the findings from their false belief test (Kano, Krupenye, Hirata, Call, & Tomasello, 2017). These results suggest that apes’ ability to predict the behavior of an agent with a false belief is, at the very least, based on a rich understanding of social cues. It remains an open question, however, whether apes were fully representing the actor’s beliefs (the mentalist account), tracking what Butterfill and Apperly (2013) call belief-like states (the minimalist account; Apperly & Butterfill, 2009), or relying on a sophisticated rule learned during their lives that agents tend to search for things where they last saw them (the behavior rule account; Perner & Ruffman, 2005) (see Table 1 for more detail).

Given apes’ previous failures in various interactive false belief tasks (Call & Tomasello, 1999; Hare et al., 2001; Kaminski et al., 2008; Krachun et al., 2009, 2010), another important question is whether or how their sensitivity to others’ beliefs contributes to decision-making. Buttelmann, Buttelmann, Carpenter, Call, and Tomasello (2017) tested apes in an active helping paradigm in which a human actor placed an object in one of two boxes. The object was then moved to the other box while the actor was present (true belief condition) or absent (false belief condition) and, finally, both boxes were locked. In both conditions, the actor then returned and attempted to open the box that originally contained the object (which was now empty) and pushed both boxes forward, allowing the subject to unlock one. In the false belief condition, apes instead unlocked the other box, which now contained the object. The mentalist account would suggest that they recognized that the actor was still pursuing the object but had sought it in its original location because he had not

witnessed its transfer. In the true belief condition, they unlocked the two boxes at chance level. They knew that the actor knew about the object's new location, so unlocked the box containing the object significantly less than in the false belief condition, but their chance performance may reflect some uncertainty about whether the actor could have really wanted to open an empty box. These findings suggest that apes' sensitivity to beliefs can indeed translate into action.

Is sensitivity to beliefs restricted to apes? Martcorena, Ruiz, Mukerji, Goddu, and Santos (2011) tested free-ranging rhesus macaques in a violation-of-expectation task (Onishi & Baillargeon, 2005). Monkeys watched an actor, with a true or false belief about an object's location, search for that object in the correct or incorrect hiding place. Monkeys looked longer when the actor with a true belief searched in the incorrect location than in the correct location, suggesting that they expected the knowledgeable actor to find the object. In contrast, they looked equally long when the actor with the false belief searched in the correct and incorrect locations, suggesting that they did not have clear expectations about what that actor would do. A second looking time study also found no evidence that macaques were sensitive to others' beliefs (Martin & Santos, 2014, 2016). These results are consistent with those from a pioneering anticipatory looking experiment on a single macaque (Lorincz et al., 2005), although that experiment employed different methods than those used by Krupenye et al. (2016). Taken together, these studies raise the possibility that the mechanisms underlying apes' sensitivity to others' beliefs may have evolved uniquely in the ape lineage. However, to further test this hypothesis, it will be important to investigate monkeys' sensitivity in the sorts of paradigms in which apes have excelled.

Future Directions

Despite these advances, a number of outstanding questions remain. To date, evidence for sensitivity to subjective desires is limited to jays and sensitivity to beliefs is restricted to apes. Future work should investigate the extent to which these abilities are shared with other species, through

homology or convergence, and whether shared capacities reflect common or only superficially similar cognitive mechanisms.

In jays, it would also be interesting to know which cues of specific satiety provide sufficient information to permit sensitivity to desires. Moreover, results from different contexts suggested that, in caching but not food-sharing, jays may be able to rely on a partner's behavior alone. It thus remains unclear whether jays employ entirely separate mechanisms in these different contexts or whether their social cognitive toolkit is comprised of interlinked behavior-reading and mind-reading mechanisms that are flexibly deployed, as necessary, across contexts. Finally, since these birds have, in different paradigms, shown sensitivity to desires as well as visual perspective (Legg & Clayton, 2014; Legg et al., 2016; Ostojić et al., 2017; Ostojić et al., 2014; Ostojić et al., 2013), a key question is whether they can integrate these two types of social information to maximize their behavioral strategies. Do jays adjust their behavior flexibly on the basis of a robust and unified understanding of others' interacting mental states or are they relying on domain-specific strategies that trump one another in particular contexts?

The question of whether apes can represent others' beliefs in the same way as humans is also unresolved. Future work should focus on the development of tasks for which the mentalist, minimalist, and behavior rule accounts offer differing predictions. Change-of-location tasks (where an individual has a false belief because a goal object has changed locations since the individual last saw it), like those used by Krupenye et al. (2016), are the most commonly employed false belief manipulations. However, all three accounts predict success in such tasks (Table 1). Thus, it will be critical to explore other paradigms, like those involving false beliefs about identity or false perceptions (Scott & Baillargeon, 2009; Scott, Richman, & Baillargeon, 2015; Song & Baillargeon, 2008), which offer the potential to discriminate these hypotheses and may even necessitate level II perspective-taking.

Another important direction involves further investigating how false belief inferences translate into behavioral strategies. That is, in which active contexts beyond the helping interactions

examined by Buttelmann et al. (2017) will apes show evidence of sensitivity to beliefs? Paramount in this effort will be developing naturalistic paradigms that minimize task demands. For example, apes' fixation on food is likely both distracting and taxing on their inhibitory control abilities. Thus, it may not be insignificant that food was central to all false belief tasks that apes previously failed (Call & Tomasello, 1999; Hare et al., 2001; Kaminski et al., 2008; Krachun et al., 2009, 2010) but was absent from all those that they passed (Buttelmann et al., 2017; Krupenye et al., 2016).

Advances in animals' sensitivity to others' knowledge and beliefs have also opened up questions about how they represent ignorance. Martin and Santos (2016) have suggested that truly understanding others' ignorance may require the kind of representational architecture involved in understanding others' beliefs—since ignorance, like a false belief, is a mental state that is in some ways decoupled from reality. In many tasks, animals respond differently to actors who are knowledgeable versus ignorant. However, it remains unclear whether they do so by ascribing knowledge to one individual and ignorance to the other, or by only making ascriptions to the knowledgeable individual (Martin & Santos, 2016). Thus, an important question for future work is what animals really know about others' ignorance and whether they make specific predictions about how ignorant individuals will behave.

Finally, the extent to which animals can combine mental state inferences with other inferential abilities and with information about physical entities remains little understood. For example, Eckert, Rakoczy, Call, Herrmann, and Hanus (2018) tested whether chimpanzees could integrate information about agents with statistical reasoning inferences. Chimpanzees could choose from which of two populations to receive a sample of food—one with a majority of preferred food and one with a majority of non-preferred food—each from a different experimenter. In some cases, experimenters had biases to deliver one food over the other, independent of proportions within the population. Chimpanzees flexibly integrated social information with statistical inferences: they chose based on proportional information when they lacked information about the experimenter's biases or when the experimenter did not have visual access to the food while sampling, but chose based on

experimenter biases when experimenters did have visual access. Future work should continue to examine how flexibly animals can integrate inferences about agents with other inferential or reasoning abilities and with information about the physical constraints of the situation.

MOTIVATION

Motivation is another key aspect of social cognition and it is central to the development of effective social cognitive tasks. Many of the best experiments are those that elegantly mimic natural circumstances—that challenge animals with the sorts of problems that selection built their cognition to solve (e.g., D. L. Cheney & R. M. Seyfarth, 1990; Cheney & Seyfarth, 2007). Such tasks can be considered to have a high degree of ecological validity (Hare, 2001). The strength of ecologically valid tasks derives from the generalizability of their results to natural contexts but also, importantly, from their ability to motivate subjects to participate—and to put their cognitive skills to use.

Although more artificial tasks can probe the flexibility of cognition, these tasks risk failing to detect cognition in the first place if they cannot elicit sufficient motivation from participants. One of the chief advances of the last decade, and an important continued direction, is an effort to determine the breadth of contexts in which animals are motivated to utilize theory of mind. This work clarifies how flexibly animals can employ their social cognitive skill, and also the range of social and ecological challenges that may be responsible for its evolution.

Many of the earliest studies on primate theory of mind involved object-choice tasks: subjects could choose to search for food under one of several containers and, although the subjects had not witnessed the baiting, they could rely on cooperative-communicative cues from knowledgeable and ignorant human experimenters who pointed to different cups (Call & Santos, 2012; Krupenye, 2017). Researchers reasoned that, if animals could infer that the experimenter who witnessed the baiting knew where the food was hidden while the other did not, they should follow the communicative cues of the knowledgeable experimenter to find the hidden food. Primates tended to fail these sorts of tasks (Itakura, Agnetta, Hare, & Tomasello, 1999; Povinelli & Eddy,

1996b; Povinelli et al., 1990; Povinelli et al., 1991; Povinelli et al., 1994), which contributed to the prevailing assessment at the time that theory of mind might be unique to humans (C. Heyes, 1998; Tomasello & Call, 1997). However, Tomasello, Call, and Hare (2003) later suggested that primates' failure in these tasks may have reflected a lack of ecological validity rather than a lack of theory of mind. It may simply be that primates do not use communicative cues like pointing cooperatively, and thus they are unable to understand such cues in cooperative contexts.

Hare (2001) proposed that focusing instead on competitive contexts could yield more promise, since primates likely rely on their social cognitive abilities for competition and, consequently, should be highly motivated to use these skills in competitive contexts. And, indeed, it was in competitive contexts that many of the first theory of mind skills were demonstrated in primates and corvids (Bugnyar & Kotrschal, 2002; Emery & Clayton, 2001; Flombaum & Santos, 2005; Hare et al., 2000; Hare et al., 2001). The success of competitive paradigms canalized research in that direction and even led some to offer that primate social cognition may be specific to the competitive domain (Lyons & Santos, 2006).

A key development in theory of mind research has been a recent effort to understand whether animals also use their social cognitive abilities outside of competitive contexts. Schmelz and Call (2016) have called, in particular, for increasing work on theory of mind in cooperative contexts—where a variety of social strategies have been documented (de Waal, 1982; Melis, Hare, & Tomasello, 2006; Tan & Hare, 2013; Warneken & Tomasello, 2006; Watts & Mitani, 2001).

As discussed above, work with Eurasian jays suggests that they are sensitive to others' desires in both competitive and cooperative contexts (Ostojić et al., 2017; Ostojić et al., 2014; Ostojić et al., 2013). Chimpanzees have been shown to provide help based on an understanding of others' goals, even as part of a collaborative task requiring sensitivity to the different roles they and a partner must play to reach a common goal (Melis & Tomasello, 2013; Warneken et al., 2007; Warneken & Tomasello, 2006; Yamamoto, Humle, & Tanaka, 2009; Yamamoto et al., 2012). Recent evidence also suggests that apes, rhesus macaques, dogs (*Canis lupus familiaris*), and ravens are

sensitive to others' perspectives in cooperative contexts as well as neutral ones (Bugnyar, 2011; Bugnyar & Heinrich, 2005; Buttelmann et al., 2017; Catala, Mang, Wallis, & Huber, 2017; Drayton & Santos, 2017, 2018; Grueneisen, Duguid, Saur, & Tomasello, 2017; Kaminski, Brauer, Call, & Tomasello, 2009; Karg et al., 2015a; Krupenye et al., 2016; MacLean & Hare, 2012; MacLean, Krupenye, & Hare, 2014; Maginnity & Grace, 2014; Marticorena et al., 2011). In the wild, chimpanzees even appear to selectively inform ignorant groupmates of nearby snakes more than knowledgeable ones (Crockford, Wittig, Mundry, & Zuberbuhler, 2012; Crockford, Wittig, & Zuberbuhler, 2017). These studies suggest that many species are able to flexibly use their social cognitive abilities across competitive and cooperative settings.

Future Directions

Future work should continue to explore theory of mind in cooperative contexts. Perhaps most critically, Tomasello, Carpenter, Call, Behne, and Moll (2005) have proposed that shared intentionality, the capacity to structure cooperative activities around shared goals, is the defining difference between human and nonhuman cognition at the heart of our cultural minds. Thus, it will be imperative to further clarify the extent to which the motivational and cognitive underpinnings of this ability are unique to humans (Melis & Tomasello, 2013).

Motivation must also be considered for investigating understudied species, particularly from a comparative perspective. To elucidate the differences between species, it is important to employ a dual approach. For example, despite being humans' other closest relative, bonobos have received vastly less empirical attention—particularly with regard to theory of mind research—than have chimpanzees. Understanding the nuanced differences between bonobos and chimpanzees will require testing bonobos in a combination of validated tasks that have provided positive evidence of chimpanzee theory of mind as well as novel tasks that are specifically designed to maximize motivation and ecological validity for bonobos (Krupenye, MacLean, et al., 2017). Existing tasks are appealing—and important—because they have been validated with one or more species and they

permit direct empirical comparisons with these species; however, they have often been designed with a particular species in mind and may thus disadvantage other taxa for which the task context is less motivating or intuitive. Chimpanzee tasks have largely focused on competitive contexts, which may be more stressful and less motivating for bonobos (Wobber, Hare, et al., 2010), and, therefore, such tasks can only reveal the niceties of ape theory of mind in concert with those designed specifically for bonobos (Krupenye, MacLean, et al., 2017; Krupenye et al., 2018).

Finally, we advocate for the development of tasks in which animals are motivated by rewards other than food. For example, social events have major consequences for group-living animals, such as primates and corvids, and consequently these species have become attuned to third-party interactions (Anderson et al., 2013; Bergman, Beehner, Cheney, & Seyfarth, 2003; Herrmann, Keupp, Hare, Vaish, & Tomasello, 2013; Krupenye & Hare, 2018; Massen, Pasukonis, Schmidt, & Bugnyar, 2014; Paz-y-Miño, Bond, Kamil, & Balda, 2004; Russell, Call, & Dunbar, 2008; Subiaul, Vonk, Okamoto-Barth, & Barth, 2008; Wittig, Crockford, Langergraber, & Zuberbuhler, 2014). Thus, for many taxa, dramatic third-party social events, such as agonistic or mating interactions, may offer a highly motivating context in which to embed particular kinds of theory of mind tasks. In this way, social information itself can serve as an ecologically valid motivation, rather than potentially distracting food rewards. This has already proven effective in recently successful false belief tests with apes in which information about an actor's false belief was contextualized within engaging third-party conflicts (Krupenye et al., 2016) as well as in tests of third-party knowledge itself (D. L. Cheney & R. M. Seyfarth, 1990; Cheney & Seyfarth, 2007). Third-party social contexts likely will continue to be fruitful for the development of other tasks of a related nature, and recent evidence suggesting that some species may flexibly attribute agency beyond social partners (and predators and prey) to animated agents (Krupenye & Hare, 2018) means that both controlled live-action and animated stimuli may be suitable for future investigations.

METHODS

Advances in methodological and empirical approaches have been paramount to the discoveries of the past decade. In particular, during this period there has been inclusion of novel species, novel controls, novel techniques, and novel experimental settings.

Novel Species

Most social cognition research has focused on primates and corvids but testing a broader range of species is essential to understand the phylogenetic distribution of social cognition. As discussed earlier, this phylogenetic approach contributes to our understanding of both the mechanisms and evolution of theory of mind. The last decade has seen expansion of social cognitive research to include several key taxa, including lemurs and dogs.

Within primates, strepsirrhines—including lemurs, galagos, and lorises—are our most distant relatives. They represent the sister clade to haplorhines, which includes all monkeys and apes. Ring-tailed lemurs (*Lemur catta*) are among the most social species of lemur and phylogenetic comparisons among several lemur species have revealed that they are also the most sensitive to others' perspectives (Maclean et al., 2013; Sandel, MacLean, & Hare, 2011) (but see Ruiz, Gomez, Roeder, & Byrne, 2008). As predicted by the social intelligence hypothesis, these findings raise the possibility that ring-tailed lemur social cognition has evolved convergently with monkeys and apes as a result of their more complex social environments (Jolly, 1966). However, their social cognition appears to be more limited than that of monkeys and apes. While lemurs preferentially steal food from competitors who cannot see them, unlike monkeys, they do not appear to take into account whether their competitor can hear them (Bray, Krupenye, & Hare, 2014; Santos et al., 2006). This minimal sensitivity suggests that lemurs may respond to overt cues of visual orientation but lack the richer integrated understanding of perspective exhibited by monkeys and apes. Importantly, since perspective-taking abilities do not appear to be shared across all primates, this body of work provides the strongest evidence that the theory of mind mechanisms documented in corvids, dogs,

and monkeys and apes (which are at least superficially similar) have evolved convergently, multiple times.

Dogs are another key species for social cognitive research. They provide a valuable tool for understanding cognitive evolution, especially when compared with their wild counterparts, wolves (*Canis lupus*), because changes in their traits are largely the result of a known domestication process involving artificial selection against aggression (Hare et al., 2002; Hare et al., 2005; Hare & Tomasello, 2005). Recent work suggests that dogs possess at least some basic perspective-taking abilities (Bräuer, Call, & Tomasello, 2004; Call, Brauer, Kaminski, & Tomasello, 2003; Catala et al., 2017; Kaminski et al., 2009; Kaminski, Pitsch, & Tomasello, 2013; MacLean, Krupenye, et al., 2014; Maginnity & Grace, 2014; Marshall-Pescini, Ceretta, & Prato-Previde, 2014; Udell, Dorey, & Wynne, 2011; Virányi, Topál, Gacsi, Miklósi, & Csányi, 2004; Virányi, Topál, Miklósi, & Csányi, 2006). For example, they steal food when a human experimenter cannot see them, when searching for hidden food they preferentially follow points of a knowledgeable experimenter over an ignorant one, and when given an ambiguous fetch cue they selectively retrieve a toy that the experimenter can see over one that she cannot see. However, it remains unclear whether these abilities are also shared with wolves (and whether human socialization plays any role in their emergence or detectability). Future work must clarify the extent to which dog social cognition is analogous (or homologous) with primates and corvids, and whether shared traits are the result of domestication or deeper evolutionary events in carnivores, mammals, or amniotes (i.e., mammals, birds, and reptiles) more broadly.

Novel Controls

The last decade has also seen some important innovations in experimental controls (Table 2). Behavior-reading proponents have long argued that existing tasks cannot distinguish behavior-reading from mind-reading because subjects have access to a number of behavioral cues that they can use to predict a partner's behavior (C. Heyes, 2015). Although researchers have attempted to

control for many such cues (see Hare, 2011 Table 1), a key advance of the last few years has been the development of paradigms in which subjects must make different inferences about an actor's perspective despite the actor exhibiting identical behavior in key phases of all conditions (e.g., Buttelmann, Carpenter, & Tomasello, 2009; Luo, 2011; Luo & Baillargeon, 2007; Tomasello & Haberl, 2003). For example, MacLean and Hare (2012) presented chimpanzees and bonobos with situations in which a human experimenter either had or had not seen an object visible to the subject. The experimenter then oriented toward the object, expressed surprise, and vocalized emotively. Subjects were significantly more likely to search for an alternative target of the experimenter's attention when he had previously seen the object than when it was novel to him (see also Drayton & Santos, 2017 for similar work with rhesus macaques). That is, primates tracked the experimenter's attention and responded differently, and appropriately, to the same behavior from the experimenter at the time of test, depending on whether the experimenter had previously attended to the object or not.

Another common alternative explanation for theory of mind findings is that subjects may attend to an actor's 'line of gaze' and predict the actor's behavior according to the relevant geometric relationships—without actually representing those relationships as *seeing* (Povinelli & Vonk, 2004). Previous work, for example, showed that chimpanzees gesture more when a human with food has a 'direct line of gaze' to them (i.e., when he is facing them) than when he does not (Gómez, 1996; Hostetter et al., 2001; Kaminski et al., 2004; Leavens et al., 2004; Liebal et al., 2004; Povinelli & Eddy, 1996b; Povinelli et al., 2003; Tomasello et al., 1994). To dissociate 'line of gaze' from seeing, Lurz, Krachun, Mahovetz, Wilson, and Hopkins (2018) adjusted the task so that in some conditions the experimenter faced away from the subject (i.e., there was no 'line of gaze') but could still see her through a mirror. As predicted by the mentalistic hypothesis, they found that chimpanzees gestured more in all conditions in which the experimenter could actually see them than in those conditions in which she could not, independent of whether the experimenter actually had a

'line of gaze' to the subjects. This finding suggests that chimpanzees' inferences are not based on simple geometric calculations about 'line of gaze.'

Another critical control has been the implementation of tasks in which subjects do not see the competitor at all and thus are not offered any visual cues to base their choices on. For example, Schmelz, Call, and Tomasello (2011) challenged pairs of chimpanzees with a competitive game in which they took turns searching for hidden food. The subject watched as one piece of food was hidden under a board, producing a visible slant, and a second piece of food was hidden in a secret hole in the table. His competitor could not see any of the baiting and was also not visible to the subject. When subjects could choose first (as well as in nonsocial controls in which no competitor was present), chimpanzees preferentially selected the food under the slanted board. However, when they chose second and had to consider which option their competitor had likely already obtained, chimpanzees were significantly more likely to select the secret food option. Chimpanzees likely recognized that their partner would remain ignorant to the location of the secret food but would correctly infer that the slanted board was slanted because food was hidden beneath it. They may have also expected their competitor to act in the same way they would have acted if they were in their competitor's circumstances (Schmelz, Call, & Tomasello, 2013). Critically, subjects made their attributions without any cues about their partner's perspective.

Bugnyar, Reber, and Buckner (2016) performed a related experiment with ravens in which subjects could cache food while a peephole potentially permitting observation by a competitor was either open or closed. Ravens cached food significantly more when the peephole was closed than when it was open, even though a competitor could be heard behind the peephole in all conditions. Thus, ravens adjusted their behavior based only on an inference that a competitor possessed or lacked visual access to their caching efforts. These findings suggest that simple associative cues related to orientation and gaze behavior cannot explain animals' success in theory of mind tasks.

The strongest test for mind-reading was proposed twenty years ago by C. Heyes (1998) and reaffirmed recently (C. Heyes, 2015). The goggles task was designed to investigate whether

organisms can attribute mental states by projecting onto others a novel perceptual state that subjects had only recently experienced for the first time (C. Heyes, 1998; Povinelli & Vonk, 2003, 2004). For example, subjects could wear one of two identical pairs of goggles that either permitted or precluded vision. If subjects then observed an experimenter wearing the same goggles and treated her as capable or incapable of seeing, depending on whether the subjects had experienced the goggles as see-through or opaque, this would be evidence that they had used their own self-experience to infer the experimenter's mental state. Karg, Schmelz, Call, and Tomasello (2015b) implemented this design in a competitive context in which chimpanzees could attempt to steal from a human experimenter by reaching into either of two compartments. Except for different colored rims, the lids of the compartments appeared to be identical from the subject's perspective, but, from the perspective of the experimenter, one was actually see-through and the other opaque. In the training phase, the subjects first experienced the perceptual affordances of the lids (i.e., when raised, subjects could see a peanut through one but not the other). In the test phase, when facing a competitor, subjects then preferred to steal from the compartment with the opaque lid (successfully preventing the competitor from seeing their theft), but showed no preference in a nonsocial control. These findings are consistent with the possibility that chimpanzees used their own self-experience to correctly attribute perceptual access to their competitor (but see C. Heyes, 2014a for discussion of the relationship between occlusive materials, distal presentation, and behavior-reading versus mindreading; Senju et al., 2011). Taken together, this innovative body of experiments provides increasingly firm evidence that at least some primates and corvids can model what others see and know.

Novel Techniques

The introduction of novel techniques to measure gaze duration and direction has also had a transformative impact on theory of mind research (Kano, Krupenye, Hirata, & Call, 2017) (Figure 2). Comparative psychologists have adapted methods originated by developmental psychologists to

study the minds of preverbal infants (Baillargeon, Scott, & Bian, 2016; Cannon & Woodward, 2012; Gergely, Knadasdy, Csibra, & Biro, 1995; Kovacs, Teglas, & Endress, 2010; Onishi & Baillargeon, 2005; Southgate et al., 2007; Woodward, 1998). Many traditional methods for studying human theory of mind involve asking participants whether they can predict what an actor will do next (on the basis of a particular mental state) (Baron-Cohen et al., 1985; Wellman et al., 2001; Wimmer & Perner, 1983). For nonverbal populations, the solution for assessing predictions has been to develop elegant but elaborate paradigms. For example, chimpanzee chess is a competitive game in which subjects take turns searching for hidden food under several cups and, when the subject chooses second, she must consider which cup her competitor has likely already chosen (based, for instance, on where she knows her competitor saw food hidden) (Kaminski et al., 2008; Karg, Schmelz, Call, & Tomasello, 2016; Schmelz et al., 2011, 2013). Despite their conceptual simplicity, verbal tasks as well as those like chimpanzee chess impose notable demands on ancillary mechanisms like memory and inhibitory control—making it unclear whether negative results stem from lack of social cognition or heightened task demands. Gaze-based methods, like anticipatory looking and violation-of-expectation (described in the section on beliefs), facilitate the study of social cognition under minimally demanding conditions by implicitly measuring participants' predictions. They have upended the field of developmental psychology (Baillargeon et al., 2016; Baillargeon et al., 2010), and are increasingly shifting the empirical landscape in comparative psychology as well. These methods have already provided evidence that apes and monkeys can predict others' actions on the basis of their goals and knowledge and that apes may even be able to do so on the basis of others' beliefs (Drayton & Santos, 2014b, 2018; Kano & Call, 2014b; Krupenye et al., 2016; Marticorena et al., 2011; Martin & Santos, 2014; Myowa-Yamakoshi, Scola, & Hirata, 2012; Rochat et al., 2008). Eye-tracking methods have also identified species differences in propensity for eye-contact, gaze-following, and social attention, and have probed components of long-term memory (Hattori, Kano, & Tomonaga, 2010; Kano & Call, 2014a; Kano & Hirata, 2015; Kano, Hirata, & Call, 2015; Kano, Moore, et al., 2018; Kano, Shepherd, Hirata, & Call, 2018; Kano & Tomonaga, 2010). Despite these important advances, gaze-

based methods hold immense latent potential that we expect will continue to unlock new opportunities and approaches for the study of animal theory of mind.

At this moment, these methods are particularly important additionally because they are necessary to verify and build on foundational discoveries in the study of human and animal cognition. Anticipatory looking and violation-of-expectation phenomena have produced robust findings in a variety of domains, including social cognition, with diverse populations. For example, human adults show largely replicable and consistent performance on a variety of published gaze-based false belief tasks (Kulke & Rakoczy, 2018; Kulke, von Duhn, Schneider, & Rakoczy, 2018; Low & Watts, 2013; Schuwerk, Priewasser, Sodian, & Perner, 2018; Senju et al., 2009), and our own unpublished task. Similarly, great apes exhibited consistent success in our first set of similar tasks, across two studies each involving two conditions (Krupenye et al., 2016), and they have continued to perform successfully in related unpublished follow-ups (see also Buttelmann et al., 2017). Monkeys have also performed consistently across the tasks in which they have been tested (Drayton & Santos, 2017, 2018; Marticorena et al., 2011; Martin & Santos, 2014). In human children, however, although a great many gaze-based false belief tasks have provided positive evidence for infant theory of mind (e.g., Baillargeon et al., 2010; Barrett et al., 2013; Scott & Baillargeon, 2017), recent efforts to replicate some of these tasks have produced a mix of replications, partial replications, and nonreplications (Kulke & Rakoczy, 2018; Sabbagh & Paulus, 2018). In many cases, replication attempts have departed, to varying degrees, from the stimuli, study populations, and procedures specified in the original methodologies, making it difficult to identify the sources of variation in results and the robustness of individual paradigms in general (Baillargeon, Buttelmann, & Southgate, 2018; Poulin-Dubois et al., 2018). Given the central importance of these findings to theories of cognition and development and the potential of these methods for novel discoveries, a key task moving forward will be determining the reliability of false belief findings in human infants and identifying factors that impact their emergence and detectability across paradigms. Across all populations, as we develop novel approaches and build on existing findings, it will be important to

use diverse tasks to evaluate the convergence of evidence for theoretically-important discoveries.

We also advocate the continued exchange of methodologies across human adult, infant, and animal psychology.

Novel Settings

A good deal of early experimental work on animal social cognition—namely, third-party knowledge or social knowledge—was conducted with wild populations (D. L. Cheney & R. M. Seyfarth, 1990; Cheney & Seyfarth, 2007). In contrast, most experimental work on theory of mind has been completed in captivity. The trade-off is that captive settings permit much more power over experimental conditions, allowing researchers to strictly control for alternative explanations and to collect data more easily, whereas field settings permit investigation of cognition in contexts in which animals reliably use these abilities naturally. For more than a decade, Santos and colleagues have developed fruitful theory of mind tasks for the free-ranging rhesus macaques of Cayo Santiago, in Puerto Rico (Drayton & Santos, 2014b, 2017, 2018; Flombaum & Santos, 2005; Marticorena et al., 2011; Martin & Santos, 2014; Santos et al., 2006), and more recently Crockford and colleagues have implemented theory of mind experiments with chimpanzees in the Budongo forest of Uganda (Crockford et al., 2012; Crockford et al., 2017). Both lines are yielding important insights. Further efforts to investigate theory of mind in the wild will help clarify its function, including both the proximate and ultimate benefits accrued from its use in natural contexts (Ashton, Ridley, Edwards, & Thornton, 2018).

Future Directions

We advocate the pursuit of several important empirical approaches and methodological directions—relating to and extending advances in species, controls, techniques, and settings but organized around the four levels of analysis of behavior that were proposed by Tinbergen (1963). Only by investigating proximate (mechanism and ontogeny) and ultimate (phylogeny and function)

causes can we fully understand the nature and origin of behavior. Clarification of the mechanisms underlying animal theory of mind requires continued efforts to develop innovative empirical approaches with stronger controls and which exploit novel methodological opportunities, like those offered by gaze-based paradigms. It will also be important to better understand the cognitive architecture of theory of mind. This involves delineating its constituent social (e.g., intention-attribution, belief sensitivity) and nonsocial (e.g., inhibitory control, memory, self-awareness, metacognition, and future-oriented cognition) cognitive mechanisms, their representational underpinnings, and their relationship to one another. Large cognitive batteries will help clarify the extent to which individual differences in cognitive mechanisms can be identified and related to one another, and whether these skills and relationships vary across taxa. Experiments can also more directly assess the contribution of particular mechanisms to theory of mind by testing, for example, whether taxing a potential constituent mechanism like inhibitory control reduces performance on theory of mind tasks (e.g., Powell & Carey, 2017).

Cognitive tests and batteries administered at different time-points in an animal's life will also be critical as these will clarify the ontogeny of social cognition. Cognitive development remains little explored in nonhumans but is also of high importance. Heterochronic shifts in developmental patterns may contribute substantially to species differences in adult cognition (Hare et al., 2012; Krupenye, MacLean, et al., 2017; Wobber, Wrangham, & Hare, 2010). Understanding how theory of mind is built during development is also critical for clarifying its underlying mechanisms and their relationship to one another. Recently, some effort has been made to investigate the ontogenetic origins of several types of cognition in nonhuman animals (Krupenye & Hare, 2018; Rosati & Hare, 2012; Wobber, Herrmann, Hare, Wrangham, & Tomasello, 2014; Wobber, Wrangham, et al., 2010), but the developmental origins of theory of mind remain largely unexplored in other species (Tomasello et al., 2001).

Turning to ultimate causes and in particular phylogeny, it is critical to continue to improve the coverage of species tested in social cognitive tasks, in order to identify cases of continuity as well

as convergence. These efforts will require controlled experiments to determine whether superficially similar abilities are actually underpinned by common neural and psychological mechanisms. Broad phylogenetic analyses, as well as targeted comparisons between key sister taxa (e.g., dogs and wolves), will be important for understanding how social cognition evolved across taxa (Hare et al., 2012; MacLean, Hare, et al., 2014; MacLean et al., 2012). These comparisons should target a range of species that face varying degrees and varieties of social and ecological challenges, including minimally social species, to determine the phylogenetic origins of social cognition and whether it can arise only in the presence of selective pressures from the social environment.

Inferences about the function of theory of mind are implicit in task designs, since tasks are often engineered around contexts in which cognition is believed to confer benefits in the wild (e.g., deception and social competition). We would additionally benefit from more targeted investigations of both the proximate (immediate: e.g., sneaky copulations, escaping aggression) and ultimate (fitness: e.g., enhanced reproductive success, offspring survival) benefits of theory of mind within-species in captive and wild settings. These efforts will elucidate the evolutionary processes that drove social cognitive evolution across species (Humphrey, 1976). Together, these four empirical approaches will permit a holistic understanding of the nature and origin of theory of mind in humans and other taxa.

Conclusion

The study of theory of mind has grown dramatically in the last four decades, and so has the importance of research with non-human animals. This work provides unique insights into cognitive mechanisms—including the role of language, culture, and executive function in theory of mind—and into evolution—including the evolutionary history of theory of mind and the selective pressures that drove its evolution across species. Research has already made huge strides in identifying theory of mind capacities in nonhuman animals from corvids to primates to dogs. Recent advances in studying

cognitive mechanisms have further blurred the lines between humans and non-humans, raising the possibility that some of the richest theory of mind abilities, such as understanding of subjective desires and false beliefs, may not be the exclusive province of our species. Distant relatives of humans, Eurasian jays, show sensitivity to others' desires, even when they conflict with the subject's own. Our closest relatives, the great apes, show sensitivity to perspectives that differ from their own, responding appropriately to others' false beliefs. Continued investigation will be essential to clarify the extent to which the cognitive mechanisms possessed by humans are truly shared across taxa, and whether these common mechanisms reflect shared ancestry or evolutionary convergence.

Work exploring the motivations involved in theory of mind has revealed that at least some species appear capable of using their social cognitive skills flexibly across cooperative, competitive, and neutral contexts. Consideration of motivations will be crucial for future species comparisons, for investigation of the precursors of shared intentionality in nonhumans, and for the development of social cognitive tasks not centered around food. Finally, new methods and empirical approaches—including novel species, novel controls, novel techniques, and novel settings—have pushed the boundaries of our understanding of theory of mind in animals. Research on lemurs and dogs sheds light on the evolutionary origins of theory of mind; new controls constrain the possible explanations for animals' success in theory of mind tasks, strongly suggesting that apes and corvids can at least represent what others can see; burgeoning techniques like eye-tracking and looking time analyses provide a powerful new window into animals' minds; and exploration of theory of mind in the wild provides insights into its natural ecology and function. These advances, in concert with Tinbergen's four levels of analysis, will ensure sustained progress in our effort to understand the nature and origin of theory of mind in humans and other species.

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Research Resources

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Table 1. Interpretation of apes' successful performance in false belief tests. We outline hypotheses, their explanations, and how they have or have not been controlled for. In the conclusion column, 'X' denotes hypotheses that have been controlled for whereas '?' denotes hypotheses that remain potential explanations for apes' successful performance.

Hypothesis	Explanation	Control	Conclusion
Perceptual	Subjects looked to the first or last location the goal object inhabited (Southgate et al., 2007)	In the FB1 condition of Krupenye et al. (2016), the target location of the actor's false belief was the last location the object inhabited whereas in the FB2 condition it was the first. Thus, neither rule can explain correct performance across conditions	X
Perceptual	Subjects looked to the last location the actor attended (Southgate et al., 2007)	In the FB1 condition of Experiment 2 of Krupenye et al. (2016), after the actor watched the object being moved to its final location, the actor's attention was directed to the incorrect location, before the actor left the scene	X
Attention	Subjects did not notice the removal of the goal object after the actor's departure from the scene (C. Heyes, 2014a)	Eye-tracking analyses showed that apes closely tracked all key events, including removal of the object (Krupenye et al., 2016)	X
Submentalizing	Subjects were submentalizing-- i.e., anticipating on the basis of domain-general cueing effects (C. Heyes, 2017)	In an inanimate control suggested by C. Heyes (2017), involving stimuli matched for perceptual features but with minimized agentic characteristics, apes attended closely but made markedly fewer looks to the target and distractor locations than in the original test and did not show a significant pattern of looking to the target location (Kano, Krupenye, Hirata, Call, et al., 2017; Krupenye, Kano, et al., 2017)	X
Ignorance	Subjects attributed ignorance	Apes did not expect the actor to	X

	to the actor rather than a false belief (Baillargeon et al., 2010)	err or to exhibit uncertainty; they specifically anticipated that the actor would search for the object where he falsely believed it to be	
Behavior Rule	During the course of their lives, subjects had learned that "agents tend to search for things where they last saw them" (Perner & Ruffman, 2005)	Stimuli involved a constellation of novel features to minimize the possibility that learned behavior rules could be applied. However, all change-of-location tasks, in which an actor has a false belief that an object is located where he last saw it, are open to this interpretation	?
Minimalist Account	Subjects attributed to the actor a belief-like state, noting that the actor "encountered" the goal object in a particular location and "registered" it there, without fully representing that the actor believed that the object was in that location (Apperly & Butterfill, 2009; Butterfill & Apperly, 2013)	The minimalist account predicts success in change-of-location false belief tasks because, in those tasks, the location where an actor falsely believes an object to be located is also the last location where the actor "registered" that object. However, minimal theory of mind does not permit its bearers to attribute false beliefs about identity and thus predicts failure in change-of-identity tasks. This prediction remains untested.	?
Mentalist Account	Subjects attributed to the actor a belief that the object was located in the location where the actor last saw it, even though subjects knew that it was no longer there	The mentalist account predicts success in both change-of-location and change-of-identity false belief tasks. The latter part of this prediction remains untested.	?

Table 2. Recent novel controls for lower level explanations of animal theory of mind tasks.

Hypothesis	Control	Reference
Animals are responding to behavioral cues that differ between conditions	At the time of test, experimenters provide identical cues between conditions	(Drayton & Santos, 2017; MacLean & Hare, 2012)

<p>Animals predict behavior by identifying which features of the environment are within an actor's geometric 'line of gaze'</p>	<p>Mirrors are used to dissociate an experimenter's 'line of gaze' from what she can see (i.e., in some conditions, an experimenter can see something via a mirror, even though she does not have a direct 'line of gaze')</p>	<p>(Lurz et al., 2018)</p>
	<p>Subjects never see the actor/competitor and therefore do not have access to his 'line of gaze'</p>	<p>(Bugnyar et al., 2016; Schmelz et al., 2011, 2013)</p>
<p>Animals can read behavior but not minds</p>	<p>Subjects receive perceptual experience of novel barriers (i.e., one is opaque and the other see-through, even though both look the same). Subjects then face a task in which they can succeed by attributing the same perceptual access to an actor</p>	<p>(Karg et al., 2015b)</p>
<p>Other important controls throughout the years</p>		<p>(Table 1 of Hare, 2011)</p>