The primate origins of human social cognition

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Abstract

The ability to understand the mental states of other individuals is central to human social behavior, yet some theory of mind capacities are shared with other species. Comparisons of theory of mind skills across humans and other primates can provide a critical test of the cognitive prerequisites necessary for different theory of mind skills to emerge. A fundamental difference between humans and non-humans is language: while language may scaffold some developing theory of mind skills in humans, other species do not have similar capacities for or immersion in language. Comparative work can therefore provide a new line of evidence to test the role of language in the emergence of complex social cognition. Here we first provide an overview of the evidence for shared aspects of theory of mind in other primates, and then examine the evidence for apparently human-unique aspects of theory of mind that may be linked to language. We finally contrast different evolutionary processes, such as competition and cooperation, that may have been important for primate social cognition versus human-specific forms of theory of mind. We argue that this evolutionary perspective can help adjudicate between different proposals on the link between human-specific forms of social cognition and language.

Keywords: primates, social cognition, cognitive evolution, cooperation, competition

Introduction

Theory of mind is a set of social cognitive processes that allow individuals to understand the mental states of others: what others perceive, think, and believe. These abilities are crucial for humans to function our social world, and enable a suite of novel human behaviors that interpret and even modify the mental states of others, such as intentional communication, teaching and deception (Baron-Cohen, Leslie, & Frith, 1985; Byrne & Whiten, 1990; Tomasello & Carpenter, 2007; Ziv & Frye, 2004). Theory of mind is therefore thought to be a key, evolutionarily-novel aspect of the human mind (Baron-Cohen, 1999; Hare, 2017; Herrmann, Call, Hernández-Lloreda, Hare, & Tomasello, 2007; Saxe, 2006; Tomasello, 2014; Whiten & Byrne, 1991). Yet even though theory of mind is central to many perspectives on human uniqueness, there is variation in how 'human unique' different components of theory of mind are: some of these abilities are shared with other species to at least some degree (Hare, Call, & Tomasello, 2001; Kaminski, Call, & Tomasello, 2008; Marticorena, Ruiz, Mukerji, Goddu, & Santos, 2011; Martin & Santos, 2014). Understanding why some, but not all, theory of mind abilities emerge in other species can elucidate the nature of the developmental 'building blocks' that enable theory of mind abilities in humans.

One critical difference between the social landscape of humans and non-human primates is language: while human infants and children can utilize language to potentially scaffold developing their theory of mind skills, non-human primates cannot. Accordingly, comparative studies of cognition in animals that lack language can provide a new line of evidence to tease apart the complex causal relationship between theory of mind and language seen in humans. For example, one possibility is that language causally enables the development of theory of mind abilities (Carruthers, 1998; De Villiers, 2007; De Villiers, 2005; Harris, 2005; Karmiloff-Smith, 1994; Nelson, 2005). Yet another possibility is that the causal relationship goes in the other direction: theory of mind abilities critically scaffold language abilities (Baldwin, 1993; Tomasello, 2009). Indeed, in some views it is impossible to understand typical human communicative interactions without assuming shared knowledge of relevant intentions and beliefs (Baldwin & Moses, 1994; Clark & Marshall, 1981; Grice, 1957), suggesting that theory of mind is the more foundational ability. Finally, the causal relationship between theory of mind and language could be bidirectional, and dependent on the specific skill in question (e.g. Charman et al., 2000; De Villiers, 2007; Lohmann & Tomasello, 2003; Tomasello & Rakoczy, 2003). For example, early emerging forms of theory of mind, such as joint attention and goal attribution, may scaffold language development, whereas language may then scaffold later-emerging theory of mind skills, such as false belief attribution.

Research on the development of language and social cognition in humans have provided variable support for these different potential causal relationships. In line with the proposal that language scaffolds theory of mind, several measures of language exposure correlate with theory of mind development. For example, mothers' use of mental state terminology correlates with their children's theory of mind development (Ruffman, Slade, & Crowe, 2002); bilingual children achieve theory of mind understanding more quickly than monolingual children (Goetz, 2003); children who receive language training increase their scores on theory of mind tasks (Hale & Tager-Flusberg, 2003); autistic individuals show language deficits early in development, as well as impairments in theory of mind understanding (Happé, 1995; Tager-Flusberg, Paul, & Lord, 2005); and deaf individuals who lack exposure to language are slower to achieve these conceptual developments than deaf native signers (Pyers & Senghas, 2009; Woolfe, Want, & Siegal, 2002). Yet other work supports the view that theory of mind in fact enables language. In particular, joint attention—attending to the same object as another individual, with both individuals knowing that they are attending to the same object (Tomasello, 1995)–is an early-emerging theory of mind ability that has been causally linked to language development. In line with this, responding to adults' bids for attention has been associated with vocabulary development (Morales et al., 2000a; Morales et al., 2000b; Tomasello & Farrar, 1986), a number of studies have found that theory of mind ability correlates with pragmatic language skills such as irony understanding and contingent conversation (Matthews, Biney, & Abbot-Smith, 2018), and children with autistic spectrum disorder display fewer joint attentional behaviors alongside delayed language development (Dawson et al., 2004; Tager-Flusberg et al., 2005; Wilkinson, 1998).

Here we argue that comparative work can provide a new line of evidence to help delineate between these proposals. Animals neither have human-like language, nor do they have cognitive structures that enable them to later acquire language like preverbal infants do. Consequently, a comparative approach can provide novel insights into how these cognitive skills are related (Gómez, 2005; Rosati, Wobber, Hughes, & Santos, 2014). If language is strictly necessary for the development of a given theory of mind ability, nonhuman animals should not demonstrate this theory of mind ability. However, if the reverse causal relationship is true, such that a given theory of mind ability is necessary for language, some animals may show such a theory of mind skill, even though they do not then go on to acquire language. A key aspect of this logic is that language may sometimes play a facultative role in human social development, without necessarily being an obligatory precondition for a given theory of mind skill to emerge. In addition, a comparative approach is crucial to understand the evolutionary context that facilitated the emergence of complex cognitive abilities, including those that appear to be unique to humans (Harvey & Purvis, 1991; MacLean et al., 2012; Rosati, 2017). By comparing patterns of cognition across different species that vary in their socioecological characteristics, it is possible to make inferences regarding what context promote the emergence of those skills and their evolutionary *function* more broadly. This comparative approach is an important tool for evolutionary biologists to understand the emergence of different traits, including cognition (Darwin, 1859; Harvey & Pagel, 1991; MacLean et al. 2012; Tinbergen, 1963)

In this review, we first provide an overview of the theory of mind abilities that appear to be shared with other species, comprising abilities such as social attention, goal attribution, perspective taking, and knowledge attribution. Then, we turn our attention to some aspects of theory of mind that currently appear to be largely unique to humans, including false belief understanding, complex forms of perspective taking, and shared intentionality—with an eye to links between these skills and language. Finally, we will contrast the different potential evolutionary processes that may have resulted in primate social cognition versus human-specific forms of theory of mind abilities. We use this evidence to argue that comparative approaches focused on animal cognition can help differentiate between different proposals on the link between human-specific forms of social cognition and language.

Evolutionarily-shared components of theory of mind

Human theory of mind consists of several components that differ in their complexity, and often emerge in a common sequence over human development (Wellman, Fang, Liu, Zhu, & Liu, 2006; Wellman & Liu, 2004). These components include understanding others' subjective desires, taking their visual perspective, understanding whether they are knowledgeable or ignorant, and attributing false beliefs about the world. Given that no other species has language, theory of mind abilities in other primates must be causally independent from both language and the cognitive structures that evolved to support language development in humans (e.g. cognitive processes that are present in pre-verbal infants). Here, we will examine theory of mind abilities where there is currently strong evidence that other animals also share these abilities. We focus primarily on work on primate social cognition, given that primates are the closest relatives of humans and therefore a crucial evolutionary model for understanding human cognition (Byrne, 2000; Herrmann et al., 2007; MacLean et al., 2012; Rosati, 2017; Tomasello, 2014). However, it is important to note that several of these abilities may be even more widely shared with other mammals and birds as well (Byrne, Bates, & Moss, 2009; Emery & Clayton, 2009; Hare & Tomasello, 2005; Kaminski & Marshall-Pescini, 2014).

Social attention

Social attention, or looking in the direction that another individual is looking, is a foundational social ability in humans. For example, longitudinal work has indicated that gaze-following responses in the first year of life predict later-developing theory of mind abilities, as well as language and communication abilities such as depth of vocabulary and gesture use, suggesting that this basic ability to look where others look scaffolds more complex social capacities in human development (Brooks & Meltzoff, 2005; Charman et al., 2000; Morales et al., 2000a; Morales et al., 2000b). Yet current work also indicates that representatives of all major primate taxonomic groups follow the gaze of others in some situations (Rosati & Hare, 2009; Rosati, Santos, & Hare, 2010). Indeed, gaze-following is a social ability that has been widely studied across many different primate species, including humans' closest relatives the great apes (Bräuer, Call, & Tomasello, 2005; Tomasello, Hare, & Agnetta, 1999; Tomonaga et al., 2004); many Old World catarrhine monkey species like macaques (Emery, Lorincz, Perrett, Oram, & Baker, 1997; Goossens, Dekleva, Reader, Sterck, & Bolhuis, 2008; Itakura, 1996; Joly et al., 2017;

Rosati, Arre, Platt, & Santos, 2016; Tan, Tao, & Su, 2014; Teufel, Gutmann, Pirow, & Fischer, 2010; Tomasello, Call, & Hare, 1998; Tomasello, Hare, & Fogleman, 2001), platyrrhine New World monkeys species like capuchins (Amici, Aureli, Visalberghi, & Call, 2009; Burkart & Heschl, 2006; Neiworth, Burman, Basile, & Lickteig, 2002), and even some lemur species—strepsirrhine primates that are the most distantly related primates relative to humans (Itakura, 1996; Ruiz, Gómez, Roeder, & Byrne, 2009; Sandel, MacLean, & Hare, 2011; Shepherd & Platt, 2008). As such, the basic ability to attend to what others are attending to appears to be widely shared across primates, including strepsirrhines that may have diverged from the lineage leading to humans more than 70 million years ago (Steiper & Young, 2006).

Yet while a basic ability to co-orient seems widespread, the cognitive mechanisms used to gaze follow differs across species (Bettle & Rosati, 2016; Rosati & Hare, 2009; Shepherd, 2010). At one end of the spectrum, gaze-following behaviors can result from more reflexive psychological processes that are invoked in response to observed behavioral cues such as head and eye direction, without further reasoning about the social context (Deaner & Platt, 2003; Friesen & Kingstone, 1998; Shepherd, 2010). Many nonhumans may gaze-follow only in this simplistic way. Yet gaze-following can also involve sensitivity to what the other individual can see, including some form of mentalistic reasoning. One way to test this in nonhumans comes are experiments requiring 'geometric' gaze-following, where the animal needs to reorient their body in order to see what an actor sees, not just reflexively match the actor's head direction (Bettle & Rosati, 2019; Okamoto-Barth, Call, & Tomasello, 2007; Tomasello et al., 1999). For example, the actor may look at a target location that is outside of the individual's original line-of-sight because it is blocked by a barrier (see Figure 1). Young children will move to look behind a barrier that a demonstrator is looking behind (Moll & Tomasello, 2004), a key piece of evidence that they do apply this sort of mentalistic reasoning to gaze-following situations. Similarly, all four great ape species (Bräuer et al., 2005; MacLean & Hare, 2012; Okamoto-Barth et al., 2007; Tomasello et al., 1999), macaques (Bettle & Rosati, 2019), and some New World monkey species (Amici et al., 2009; Burkart & Heschl, 2006) also reorient around barriers to some degree. This indicates that gaze-following in many primates reflects a flexible response that accounts for the actor's line-of-sight.

Another component of social attention, building on the ability to track where others are looking, is to actually direct other's attention to specific aspects of the environment. This capacity requires attending to the current attention of others, but also requires the motivation and understanding of how to successfully direct other's attention. Indeed, many primate species will direct the attention of other individuals in some situations, in a manner that suggests they are attuned to the receiver's attentional state. In particular, great apes preferentially use gestures when the receiver is facing towards them (Kaminski, Call, & Tomasello, 2004), will move into areas where the receiver can better see their gestures (Liebal, Call, Tomasello, & Pika, 2004; Povinelli, Theall, Reaux, & Dunphy-Lelii, 2003), and will even produce 'attention-getting' sounds before producing gestures when their partner is not attending (Hostetter, Cantero, & Hopkins, 2001). Further, chimpanzees will tactically switch their communicative behaviors between auditory and visual modalities, according to the receiver's state (Leavens, Hostetter, Wesley, & Hopkins, 2004). While great apes exhibit the largest gestural repertories and most flexible gesture use of gesture in their natural behavioral interactions (Call & Tomasello, 2007; Pika & Liebal, 2012), some other primate species also can sometimes tailor their gestures to when someone is attending to them in experimental contexts. This includes gibbons (Liebal, Pika, & Tomasello, 2004), some Old World monkey species (olive baboons; Meunier, Prieur, & Vauclair, 2013, rhesus macaques; Canteloup, Bovet, & Meunier, 2015) and New World monkeys (tufted capuchins; Defolie, Malassis, Serre, &

Meunier, 2015, Hattori, Kuroshima, & Fujita, 2010, squirell monkeys; Anderson, Kuroshima, Hattori, & Fujita, 2010). Overall, this suggests that many primates can also account for the reciever's attentional state during communication.

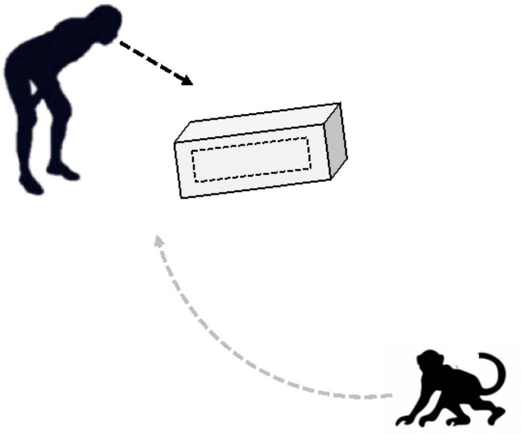

Figure 1: Testing geometric gaze-following in primates (adapted from Bettle & Rosati, 2019). The monkey watches as a human demonstrator looks towards behind a free-standing box. In the barrier condition, the monkey cannot see the target location, whereas in the no-barrier condition there is a window cut into the box allowing the monkey to see the target location from their starting position. In order to observe the target of the demonstrator's gaze in the barrier condition, the monkey therefore has to reorient by approaching behind the apparatus.

Goal understanding

The ability to interpret others' actions in terms of underlying goals and intentions is also central to how humans interpret others' behavior. A key point is that 'intentions' are not directly observable, but organize other's behavior into a coherent sequence of actions. In particular, we perceive others' actions not merely as raw physical movements ("she moves her right hand towards the apple"), but rather as sequences of intentional actions ("she *wants* the apple"). This kind of inference about other's intentions further allows us to make novel predictions about how others will act under new circumstances (for example, if the apple is moved to a new location). In humans, this ability emerges early in development, within the first year of life (Behne, Carpenter, Call & Tomasello, 2005; Gergely, Nádasdy, Csibra, & Bíró, 1993; Sommerville, Woodward, & Needham, 2005; Tomasello, Carpenter, Call, Behne, & Moll, 2005). This early skill has been linked to language development across infancy and early childhood, as it is easier to establish the correct referent to a new word—and hence understand which object the person is talking about—if one is sensitive to the speaker's intent (Berman, Chambers, & Graham, 2010; Csibra, 2010; De Villiers, 2007; Tomasello, 1995). The ability to attribute goals to others may also be important to later-emerging theory of mind abilities such as shared intentions, where two individuals mutually share a joint goal (Tomasello & Rakoczy, 2003). Consequently, understanding whether other primates interpret others' actions in terms of underlying goals is key to elucidating the basic components necessary for language as well as later-emerging theory of mind abilities.

Currently, there is strong evidence that at least some species also interpret other's behaviors in terms of underlying goals, differentiating between situations where actors make superficially similar actions but have different underlying intentions (Call, Hare, Carpenter, & Tomasello, 2004; Canteloup & Meunier, 2017; Herrmann & Tomasello, 2006; Kano & Call, 2014b; Phillips, Barnes, Mahajan, Yamaguchi, & Santos, 2009; Uller, 2004; Yamamoto, Humle, & Tanaka, 2012). First, some primates are sensitive to whether the behavior of others is intentional or accidental, showing that they are accounting for the other individual's goal: both chimpanzees and orangutans are more likely to choose a box that a demonstrator has intentionally marked to indicate that it contains food, compared to a box that the demonstrator accidentally marked (Call & Tomasello, 1998). Second, species including chimpanzees, capuchins and Tonkean macaques respond differently to a human who is *unwilling* to give them food (e.g., teasing them), compared to one who is *unable* to give food because they are clumsy: they are more willing to wait patiently, and show less frustration behaviors, when the humans is intending (but failing) to give them the food (Call et al., 2004; Canteloup & Meunier, 2017; Phillips et al., 2009). Finally, some primates also show evidence of goal attribution in tasks that measure cognition using looking time measures that parallel techniques used with young infants. For example, macaques (Rochat, Serra, Fadiga, & Gallese, 2008) and chimpanzees (Uller, 2004) expect individuals to take an efficient route to reach their goal: individuals who previously saw a demonstrator reaching for a particular object behind a barrier look longer at an ‘unexpected’ subsequent event where the demonstrator still uses this (now inefficient) movement to reach the object once the barrier is removed. Similarly, bonobos, chimpanzees, and orangutans will look in anticipation towards objects that they expect an actor will reach for based on the demonstrator’s preferences (Kano & Call, 2014b). Overall, this suggests that several anthropoid primates (New World monkeys, Old World monkey, and apes) conceive of other’s behaviors in terms of underlying intentions.

Other evidence that primates are sensitive to underlying goals stems from how they use their goal understanding to inform other behaviors. For example, in great apes, patterns of social learning depend on the demonstrator’s underlying goals. Like human infants, chimpanzees preferentially imitate intentional actions compared to accidental ones (Tomasello, Carpenter, & Hobson, 2005), and selectively imitate actions that have been freely chosen rather than those that have been forced by circumstance (Buttelmann, Carpenter, Call, & Tomasello, 2007), building on findings that human children engage in ‘rational imitation’ (Gergely, Bekkering, & Király, 2002). Furthermore, apes appear to favor using ‘goal emulation’ as a social learning strategy over pure imitation of actions (Tomasello, 1994). That is, chimpanzees selectively attend to the actions that are relevant to an underlying goal, and will selectively copy behaviors that serve that goal as opposed to blindly copying all observed behaviors (Horner & Whiten, 2005). Finally, chimpanzees can infer other’s goals in order to help them achieve those goals: they will help both conspecifics and humans by giving them an out-of-reach object that they want (Melis, Call, & Tomasello, 2011;

Warneken, Hare, Melis, Hanus, & Tomasello, 2007; Warneken & Tomasello, 2006; Yamamoto et al., 2012). There is similar evidence for instrumental helping behavior in other species, including bonobos and capuchins (Barnes, Hill, Langer, Martinez, & Santos, 2008; Krupenye, Tan, & Hare, 2018). As such, this suggests that the ability to infer other's goals, as well as the motivation to help others achieve their goals, can emerge in the absence of language.

Visual and auditory perspective-taking

Perspective-taking is the ability to see the world from another person's perspective and make inferences about what another individual experiences (Flavell, 1977). Establishing what another person can see or hear enables inferences about what information they have access to, and hence what they know and even believe (Sodian, Thoermer, & Metz, 2007). Accordingly, this ability is a crucial foundation for other abilities like knowledge- and belief-attribution, and also emerges fairly early in development: infants begin to be able to judge what other individuals can and cannot see around 14-24 months (Flavell, Everett, Croft, & Flavell, 1981; Moll & Tomasello, 2004, 2006; Sodian et al., 2007). One proposal is that perspective-taking is scaffolded by language, because language exposure enables children to be presented with descriptions of the same object from different perspectives, as well as to situations where people experience the same situation but construe it in different ways (Clark, 1997).

Yet the ability to judge what others can and cannot see is not unique to humans. There is clear evidence that chimpanzees and at least some other primate species can also infer other's perspective. Some of the strongest evidence for this comes from food competition paradigms, where an individual competes for access to food rewards with a competitor (Call & Tomasello, 2008). For example, when chimpanzees are faced with a choice between approaching two different pieces of food—one piece that only they can see, and another that a dominant conspecific can also see—they will preferentially approach the ‘safe’ piece of food that only they have visual access to (Bräuer, Call, & Tomasello, 2007; Hare, Call, Agnetta, & Tomasello, 2000). This indicates that the subjects are accounting for what food the dominant individual can see from their visual perspective, and accordingly are choosing to try and attain the food that this individual cannot see. They show a similar response when interacting with a human who has been established as a competitor, and will even attempt to conceal their approach behind a barrier when possible (Hare, Call, & Tomasello, 2006; Melis, Call, & Tomasello, 2006). In these kinds of setups, rhesus monkeys (Flombaum & Santos, 2005; Lyons & Santos, 2006) and ring-tailed lemurs (MacLean et al., 2013; Sandel et al., 2011) will also preferentially try to steal food that a human competitor cannot see (see Figure 2). Therefore, the ability to deduce what others see from their unique perspective can emerge in the absence of language.

Importantly, perspective-taking does not only comprise *visual* perceptions. Humans can represent other’s perceptions across other sensory modalities, such as audition, and evidence for similar skills in other animals provides further evidence that they have a deeper understanding of visual and auditory information as opposed to have learned behavioral associations in a few limited contexts. In fact, both rhesus macaques and chimpanzees account for whether a potential competitor cannot just see but also hear their approach to attain food, and in some cases will flexibly combine both types of perceptual information. For example, chimpanzees will preferentially use a silent route to attain food when competing with a human demonstrator, compared to a noisy route (Melis, Call, et al., 2006). Rhesus macaques will similarly steal food from a ‘quiet’ container compared to a noisy one that would alert the competitor to their approach—but show no preference when their competitor is facing them and is therefore is already altered to their present (Santos, Nissen, & Ferrugia, 2006).

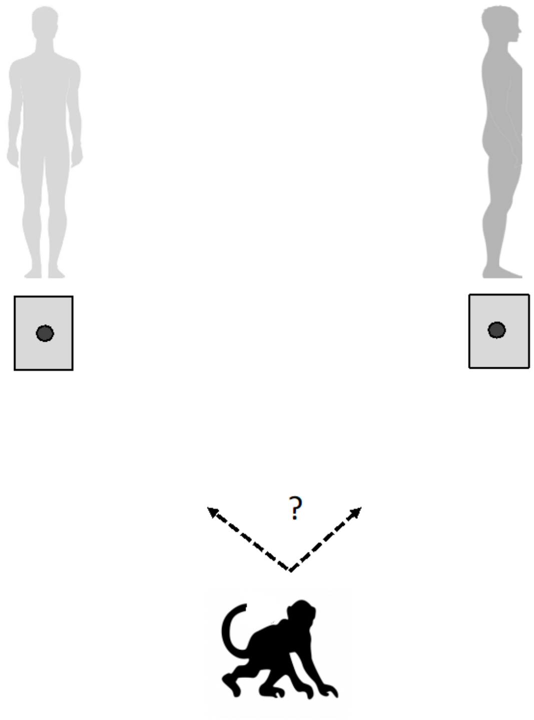

Figure 2: Testing visual perspective-taking in primates (adapted from Flombaum & Santos 2005). The monkey has the opportunity to 'steal' a contested grape from one of two human competitors. One of these competitors can see the grape in front of them as well as the monkey's approach, whereas the other cannot (for example, because their eyes are covered or they are turned away).

However, it is important to note that unlike the situation with gaze following and goal attribution abilities—where many diverse species appear to exhibit the skill in question—there is robust evidence for perspective taking in more limited primate species—several other primate species do not seem to readily attribute perspectives to others, at least in the competitive contexts that have been successfully used with chimpanzees and macaques. For example, capuchins (Hare, Addessi, Call, Tomasello, & Visalberghi, 2003), common marmosets (Burkart & Heschl, 2007), and Tonkean macaques (Canteloup, Piraux, Poulin, & Meunier, 2016; Costes-Thiré, Levé, Uhlrich, De Marco, & Thierry, 2015) have been tested in food competition paradigms similar to those described above, but may depend more on behavioral cues from their competitor, rather than pure inferences about what the competitor can see in the absence of overt behavioral signals. Several other lemur species also fail to use information about other's visual perspective in the same situation where ring-tailed lemurs use this information to outcompete a human (MacLean et al., 2013; Sandel et al., 2011). Similarly, even species that do readily attribute perceptions in some contexts may not flexibly do so in others. For example, ring-tailed lemurs use information about a competitor's visual perspective, but not their auditory perspective (Bray, Krupenye, & Hare, 2014). Similarly, chimpanzees can use some information about other's auditory perspective in some contexts but not others: they do not account for whether a competitor could deduce the location of a hidden food item by the sound that was made when it was placed there in a situation where an experimenter, rather than the chimpanzee themselves, made the sound (Bräuer, Call, & Tomasello, 2008). This implies that while some primates are capable of accounting for whether or not another individual can hear their own actions, they might not spontaneously remember and account for what others can hear in a more general sense. Accordingly, while the ability to infer what another individual can and cannot hear appears to emerge in the absence of language, one possibility is that language might enable better 'scorekeeping', or memory for who has heard what, regardless of who or what produced the noise, facilitating a more complex set of cognitive inferences about other's perspectives.

Knowledge attribution

The ability to attribute knowledge and ignorance to others allows individuals to make predictions about how people will act, based upon facts that they know (or do not know) about the world. This ability is present by 3-4 years of age (Clements & Perner, 1994; Sullivan & Winner, 1991; Wellman & Bartsch, 1988), and may emerge even earlier, at 12-13 months (Bohn, Zimmermann, Call, & Tomasello, 2018; Liszkowski, Carpenter, & Tomasello, 2008; Surian, Caldi, & Sperber, 2007; Tomasello & Haberl, 2003). In humans, the ability to track what other individuals are knowledgeable and ignorant appears related to language. In particular, children are sensitive to cues concerning speaker's knowledge or ignorance, and are more likely to learn a new word for a given referent if the speaker appears knowledgeable about that referent (Sabbagh & Baldwin, 2001). In addition, cross-linguistic differences in exposure to language about knowing or thinking appears to alter the developmental trajectory of theory of mind abilities. Chinese children are frequently exposed to mental state language about 'knowing' (Tardif & Wellman, 2000), while Western children are more likely to hear mental state language about 'thinking' (Bartsch & Wellman, 1995). Accordingly, Chinese children develop the ability to ascribe knowledge and ignorance earlier than do Western children, a cross-cultural difference that has been attributed in part to how language facilitates social cognitive development.

Similar to visual perspective-taking, some of the most definitive evidence for knowledge attribution in nonhumans comes from competition paradigms where animals compete with a conspecific or human for access to food. In one influential early example of this setup (Hare et al., 2001), a subordinate and dominant chimpanzee competed for food hidden behind opaque barriers such that no food was directly visible to the dominant– in contrast to work on visual perspective-taking. While the dominant did not always see the food being hidden, the subordinate always saw the baiting procedure as well as the dominant's visual access to these events. Thus, if the subordinate could track what the dominant had seen in the past, and understand how seeing leads to knowledge, they could infer what food the dominant knew about. In fact, subordinates preferentially approached food that the dominant did not see baited. In work elaborating on this setup (Kaminski et al., 2008), chimpanzees played a 'back-and-forth' competitive game in which two chimpanzees made sequential choices about food hidden in three cups. Chimpanzees again had an asymmetric knowledge of the distribution of two food items—the subject saw two items hidden, whereas their competitor had only witnessed one of the items being hidden—and furthermore could not see each other's choices directly. In fact, subjects tactically chose the cup that they (but not their competitor) saw baited with food specifically when they made the second choice, indicating that they inferred that their competitor knew about the other piece of food and would have chosen it already. Thus, chimpanzees can attribute knowledge or ignorance to their competitor, and use this understanding to inform their behavioral strategies (see also Bohn, Call & Tomasello, 2016).

There is some evidence for similar abilities in other species. For example, Marticorena, Ruiz, Mukerji, Goddu & Santos (2011) used a looking time paradigm models on prior work with human infants (Onishi & Baillargeon, 2005) to assess if rhesus monkeys would attribute knowledge to a human demonstrator. Monkeys observed the human watching a lemon moved on a track into one of two boxes in front of her. Once the lemon was hidden inside a box, the demonstrator would then either reach into the box where she saw the lemon hidden, or into the other (empty) box. If the subjects expected the demonstrator to act in accordance with her knowledge, they should be surprised when she reached into the wrong box. Indeed, monkeys looked longer when the human reached into the empty box compared to the box where the lemon had gone, indicating that monkeys can attribute knowledge to others based on what others saw in the past, and further predict that others will act in accordance with the knowledge (see also; Drayton & Santos, 2018; Martin & Santos, 2014). This understanding of what others know can feed into other aspects of animals' social interactions. For example, some primates will modulate their gaze following responses to account for what their social partner has seen in the past and thus knows now. MacLean and Hare (2012) found that chimpanzees and bonobos searched longer for an alternative target of a demonstrator's gaze when the actor had previously seen the object in his direct line-of-sight. This suggests that apes can track whether other individuals are knowledgeable about the presence of other objects, and then use this understanding to track which objects other individuals are likely to be attending to right now. Similar results have been found for rhesus macaques, who also look longer for an alternative target when the demonstrate has previously seen the object in her line of sight (Drayton & Santos, 2017). Overall, this pattern of results suggests that nonhuman primate species who understand what others can see, such as chimpanzees and rhesus macaques, can also make inferences about how these perceptions lead to knowledge.

Human-unique components of theory of mind

Current evidence indicates that humans share some components of theory of mind with other primates, including understanding of goals and intentions, basic forms of perspective-taking and attribution of knowledge and ignorance. In some cases, these skills are even shared with several, distantly-related primates spanning nonhuman great apes, Old World monkeys, New World monkeys, and even lemurs—suggesting that these skills may be fairly widespread. This pattern of results provides strong support for the proposal that some theory of mind abilities can emerge in the absence of language. Yet human theory of mind nevertheless appears to go beyond that of other species in a number of ways, and these more human-specific abilities might be dependent upon language or upon the cognitive structures that facilitate language. Here, we will detail ways in which current evidence suggests some aspects of theory of mind reasoning are unique to humans.

Level-2 perspective-taking

As detailed earlier, many primates are sensitive to what others can see or hear—but another aspect of perspective-taking concerns understanding not just *whether* an object is perceivable, but also *how* that object appears different from another's' perspective. This ability is sometimes termed level-2 perspective taking (Flavell et al., 1981; Flavell, Shipstead, & Croft, 1978). There is evidence that level-2 perspective taking may emerge as early as 3 years of age (Moll & Meltzoff, 2011), although some studies have argued that it emerges later, at around 4 years (Flavell et al., 1981; Masangkay et al., 1974). One way this ability has been tested in children is to place a picture of a tortoise between the child and another person, and then ask the child whether it is lying on its back or standing from the other person's perspective (Masangkay et al., 1974). Level-2 perspective taking therefore requires the ability hold two different viewpoints at the same time, decoupling one's own perspective of the world from another's perspective (Moll & Kadipasaoglu, 2013). One possibility is that while simple forms of perspective-taking that focus on the presence (or absence) of objects can occur in the absence of language, the high representational demands for this form of perspective-taking does require language, more similar to false belief reasoning (De Villiers, 2007). Indeed, level-2 perspective taking may be especially challenging because it requires the subject to 'hold in their mind' a mental representation of what the other individual experiences.

Along these lines, some of the same nonhuman species that can account for what others can or cannot see in a visual field seem to struggle when they must make more subtle distinctions concerning how objects appear different from another perspective. For example, Karg et al. (2016)

adapted the basic food competition paradigm described previously to test if chimpanzees could account for how objects appeared to others. Pairs of chimpanzees competed over two breadsticks, and the trick was that while the subject could see that both breadsticks were of the same size, from the competitor's perspective one food stick appeared to be larger. This is because the sticks were attached to a board facing the subject: one stick reached further over the edge, such that it appeared bigger from the competitor's perspective (see Figure 3). Thus, if the chimpanzees were sensitive to the competitor's visual perspective, they should choose the stick that appears smaller when facing a competitor who made the first choice. Unlike children, however, the chimpanzees behaved similarly regardless of whether another individual was present or not. As such, this suggests that chimpanzees do not consider what an object looks like from another's perspective in a situation where human children do.

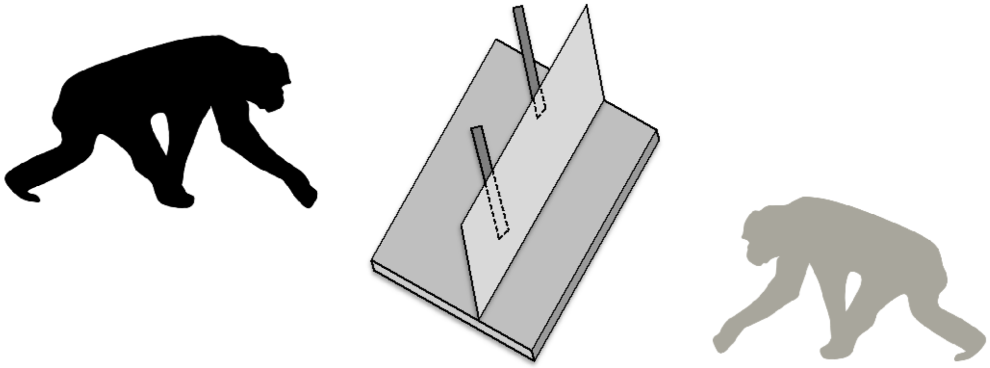

Figure 3: Testing level-2 visual perspective-taking in primates (adapted from Karg et al 2016). Here, two chimpanzees have a different perspective on the same objects (two breadsticks). While the subject chimpanzee (on the left) can see that both breadsticks are the same size, from the competitor's perspective one breadstick looks larger due to the placement of an occluder. The competitor gets to make a choice while the subject cannot observe, and then the subject can make a choice. If they can take their partner's perspective, they should infer that the partner will first select the breadstick that appeared larger to them.

Other work shows that chimpanzees can use their own self-experience to predict what a competitor sees in unusual contexts. For example, chimpanzees can infer that if they can see through a particular container lid that (at first glance) appears opaque, then a potential competitor can also see through this lid (Karg, Schmelz, Call, & Tomasello, 2015). Similarly, chimpanzees with prior experience of mirrors understand that mirrors allow people to gain visual access to objects and events that are behind them, even if their head and eyes are pointed away from these objects (Lurz, Krachun, Mahovetz, Wilson, & Hopkins, 2018). However, it is unclear whether these responses are truly driven by taking the perspective of the demonstrator to infer what she could see. For example, chimpanzees may have learned a new physical feature of the objects in question (e.g. which lid could be seen through, and how mirrors change line of sight), and then imparted this experience upon the demonstrator without truly taking their visual perspective.

Yet some other primate species do show some understanding of subjective points of view, the ability to hold two alternative representations of an object in mind simultaneously. In particular, great apes can differentiate between objects that appear small or larger due to the effects of distorting lenses, or other objects occluding the true size of the objects, when they make choices about food rewards for themselves (Karg, Schmelz, Call, & Tomasello, 2014; Krachun, Call, & Tomasello, 2009; Krachun, Lurz, Russell, & Hopkins, 2016). Brown capuchins and Tonkean macaques have also demonstrated the ability to discriminate appearance form reality in similar experiments using visual illusions produced by mirrors or distorting lenses (Hirel, Thiriau, Roho, & Meunier, 2020). This indicates that the challenge posed by level-2 perspective-taking is not necessarily due to holding two (contradictory) representations in mind at once, but rather might stem from the challenge specifically of holding *another individual's* perception in mind when it conflicts with one's own. For example, one possibility is that the memory of personally experiencing the object in each different state (such as seeing a piece of food prior to the application of a distorting lens, and after the application of this lens) is necessary to ensure understanding in nonhuman primates, so they may struggle in level-2 perspective tasks because they do not have a memory of personally experiencing their partner's perspective (Karg, Schmelz, Call, & Tomasello, 2016). This ability may critically rely upon language to support the high representational demands of considering multiple different individual's perspectives simultaneously. Language is frequently invoked for these kinds of representational abilities (Carruthers 2002; Karmiloff-Smith 1992; Spelke 2003), for example with regard to supporting false belief attributions described below. This suggests a crucial difference between different forms of perspective-taking: whereas basic present/absent distinctions may be shared with other primates, other forms of perspective-taking that hinge on understanding how things appear may hinge on human-unique mechanisms.

False belief understanding

The ability to model the false beliefs of other individuals has long been regarded as a benchmark test for mature theory of mind (Call & Tomasello, 1999; Dennett, 1978; Gopnik, 1993; Wimmer & Perner, 1983). Modeling others' false beliefs requires the ability to simultaneously represent two conflicting views of the world: the other individual's false belief, as well as the individual's own (true) belief. In this manner, false belief understanding provides especially strong evidence that the individual recognizes the distinction between their mind, the minds of others, and the true state of the world. From around the age of 4-5, children can pass explicit false belief tasks, where they must make direct inferences, via explicit verbal report or making a behavioral choice, regarding the belief states of another agent (Baron-Cohen, Leslie, & Frith,1985; Gopnik &

Astington, 1988; Wellman, Cross, & Watson, 2001; Wellman & Liu, 2004; Wimmer & Perner, 1983). Language is often strongly associated with false belief understanding in these contexts. For example, there is a positive relationship between children's language development and performance in such explicit false belief tasks (Astington & Jenkins, 1999; De Villiers, 2005; Hughes & Dunn, 1998; Milligan, Astington, & Dack, 2007; Peterson & Siegal, 1999; Ruffman et al., 2002). One proposal is that language contains syntactical structures that facilitate representation of false beliefs—such as complement syntax, or the manner in which propositions can be embedded under mental state verbs within a sentence (De Villiers, 2007; De Villiers, 2005). More generally, children who are immersed in language are frequently presented with different mental perspectives and mental-state terminology, which may facilitate the conceptual developments that underpin false belief understanding (Harris, De Rosnay & Pons, 2005; Peterson & Wellman, 2009; Tomasello, 2018; Wellman & Liu, 2004).

Yet it is also possible that observed relationships between language ability and performance on false belief tasks is due to the fact many explicit false belief tasks involve verbal responses, or because false-belief understanding is reliant upon general processes such as executive function that might be facilitated by language (Bloom & German, 2000; Fodor, 1992; Frye, Zelazo, & Palfai, 1995; Hughes & Ensor, 2007; Jacques & Zelazo, 2005). In line with this, even young infants may be successful on 'implicit' false belief tests that utilize different response measures, such as looking time or anticipatory looking patterns to assess infants' cognitive processes (Knudsen & Liszkowski, 2012; Onishi & Baillargeon, 2005; Rakoczy, 2012; Scott & Baillargeon, 2009; Song, Onishi, Baillargeon, & Fisher, 2008; Southgate, Senju, & Csibra, 2007; Surian et al., 2007; although note that some studies have not replicated these effects: Grosse Wiesmann et al. 2018; Kulke et al. 2018; Phillips et al. 2015; Poulin-Dubois & Yott, 2018). Why might infants succeed on ‘implicit’ false belief tasks prior to success on ‘explicit’ tasks? This may be because implicit tasks do not involve verbal instructions or responding, but it also could be because these setups generally have reduced executive demands, such as simpler sequences of events to track over time. Comparative research can parse between these alternatives: if language is causal to the development of false belief understanding, then no primate species will show false belief understanding. On the other hand, if domain-general deficits, such as executive function, can explain infants’ failures in explicit false belief tasks (rather than lack of language), then primate species may also pass some false belief tasks involving lower domain-general demands.

One major line of work testing whether nonhuman can attribute false beliefs has used competitive paradigms, similar to other work showing that several species can use other’s visual perspective or knowledge attribution to win in contest competitions discussed previously (Hare et al., 2001; Kaminski et al., 2008; Krachun, Call, & Tomasello, 2010; Krachun, Carpenter, Call, & Tomasello, 2009). In these versions testing false belief attribution, the competitor does not simply lack visual access or knowledge of a food reward—they actually have a mistaken belief about the location of food, such as because its location has been surreptitiously switched. For example, while chimpanzees do account for a competitor’s knowledge (e.g., ‘true beliefs’) about the location of food in a back-and-forth competitive game (Kaminski et al 2008), they do not take advantage of a competitor’s false beliefs about the location of a food item in the same context, such as when the food’s location has been surreptitiously switched (see Figure 4). In contrast, six-year-old children do account for other’s false beliefs in this same situation.

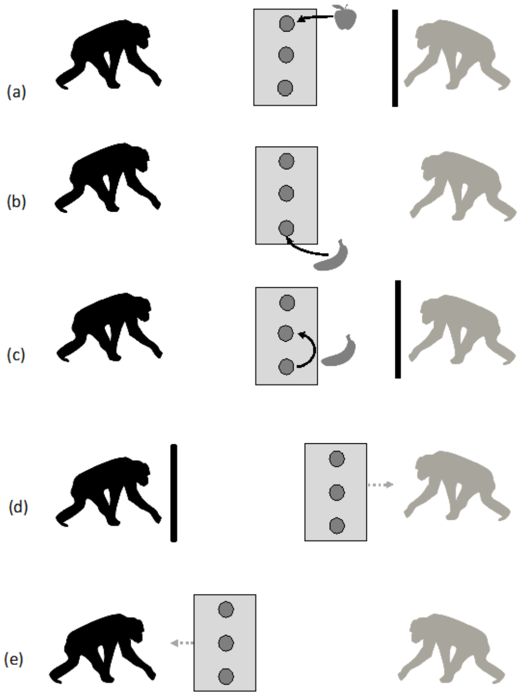

Figure 4: Testing false belief understanding in primates (adapted from Kaminski et al. 2008). Two chimpanzees play a back-and-forth game to acquire food hidden in containers. (a) The subject chimpanzee (on the left) watches as a low value food item (apple) is hidden; the competitor's view is occluded. (b) Both chimpanzees watch as a high value food item (banana) is hidden. (c) The subject chimpanzee alone watches as the banana is moved: the competitor now has a false belief about the banana's location. In control conditions, the banana is put back in the same original location. (d) The competitor makes a choice while the subject's view is occluded. (e) The subject chimpanzee makes a choice. If they understand when their competitor has a false belief, they should choose the banana when its location was switched, but choose the apple when it was not.

Extensions of this work suggest that this kind of failure to account for other's false belief in explicit tasks is fairly widespread, both across different paradigms and across species. For example, chimpanzees and bonobos also do not account for other's false beliefs in other change-of-location tasks across various kinds of setups, suggesting that this failure to account for other's false beliefs does not stem from a particular aspect of the experimental setup used (Call & Tomasello, 1999; Krachun et al., 2009). Chimpanzees also do not account for other's false beliefs in a change-of-contents task (Krachun et al., 2010), based upon similar work with human infants

(Perner, Leekam, & Wimmer, 1987). Here, a demonstrator has a false belief about the contents of a box (such as whether it contains a piece of banana or grape), and apes could use this knowledge to predict where she will put it. Overall, this line of work suggests that while great apes will utilize an understanding of others' knowledge and perspective to outcompete them for food, they do not appear to utilize their explicit false beliefs in similar contexts (but see Buttlemann et al 2017 for some potential evidence that apes can attribute false beliefs in an explicit paradigm; but note that this task may be assessing knowledge attribution). Outside of great apes, there is little evidence that other primates can understand false beliefs. For example, while rhesus macaques expect a demonstrator to reach towards a box where she knows there is food, they appear to make no prediction about what she will do when she has a false belief about the food's location (Marticorena et al., 2011; Martin & Santos, 2014, 2016).

In contrast to these findings from explicit tasks, some recent studies have found that great apes may be more successful at implicit tasks that assess false-belief attribution using anticipatory looking measures modeled on the tasks demonstrating some level of false belief comprehension in much younger infants (Krupenye, Kano, Hirata, Call, & Tomasello, 2016; Kano, Krupenye, Hirata and Call, 2019). For example, Krupenye et al (2016) utilised eye tracking to implement an anticipatory looking paradigm modelled a prior study with infants (Southgate et al., 2007) that was designed to reduce executive function demands and involved a 'social drama' designed to capture and sustain the apes' interest. In one scenario, for example, a human engaged in physical conflict with an ape chacacter (another actor in a gorilla suit), who then hides in a haystack. While the human briefly leaves to obtain a weapon, the gorilla secretly moves from their original hiding place. When the human re-entered the scene, before the human takes any direct action, apes exhibit anticipatry looks towards the original hiding place, presumably anticipating that the actor would look for the gorilla there. This suggests that apes understand that the actor has a false belief about the location of their rival.

A critical question is therefore whether this kind of implicit measure is indeed tapping into false belief attribution, or rather involves another, more simple skill that may foster mature false belief undertsanding (Rakoczy, 2017; Tomasello, 2018). Indeed, the relationship between these kinds of implicit measures and more canonical ‘explicit’ false belief measures is also a topic of major debate in human development (Apperly & Butterfill, 2009; Baillargeon, Scott, & He, 2010; Grosse Wiesmann, Friederici, Singer, & Steinbeis, 2017; Perner & Ruffman, 2005; Poulin-Dubois et al., 2018; Rakoczy, 2017; Ruffman & Perner, 2005; Tomasello, 2018). In any case, current evidence suggests that the cognitive skills supporting behavior in implicit false belief tasks can emerge in pre-verbal infants and non-human animals, whereas explicit use of other’s false beliefs to make a behavior choice may be more dependent on language and is likely absent in nonhumans.

Shared intentionality

False beliefs attribution and level-2 perspective taking both involve reasoning about other’s mental states when they *conflict* with one’s own perceptions or beliefs. Yet nonhumans may also struggle to reason about mental states that are *shared* with oneself. One influential recent proposal is that a key distinction between human and nonhuman theory of mind actually hinges on novel cooperative forms of social cognition that involve shared mental states, such as having a joint goal and mutually knowing that this goal is shared (Tomasello, 2014; Tomasello & Carpenter, 2007; Tomasello et al., 2005; Tomasello & Rakoczy, 2003). This proposal has implications for our understanding of language evolution and development, since language is often thought to rely upon a ‘common cognitive ground’ to enable interpersonal communication (Sperber & Wilson, 1986;

Tomasello, 2010; Tomasello et al., 2005), or upon the ability of the signaler and receiver to recognize each other's shared goal to communicate (Grice, 1957). Thus, understanding whether primates exhibit shared intentions is a crucial question for both the evolution of social cognition and the evolution of language.

A critical early component of shared intentionality is joint attention, where two or more individuals mutually share attention towards something in the world—and, crucially, both individuals are *aware* that they are attending to the same item (Tomasello, 1995; Tomasello & Carpenter, 2007). Joint attentional skills, such as following others' gestures or gaze to share a common focus of reference, is seen at 6-9 months and may predict later vocabulary (Carpenter, Nagell, Tomasello, Butterworth, & Moore, 1998; Morales et al. 2000b, Tomasello, 1995). Sharing attention in this way is thought to create a common 'frame-of-reference' that enables the development of social cognitive abilities. Yet while species such as chimpanzees are sensitive to the attentional state of others in terms for following their gaze, there is no strong evidence that these behaviors are truly 'joint' such that both individuals are aware that they are attending to the same item (Carpenter & Call, 2013). First, other primates' gaze-following are generally directed towards a particular goal item, such as food, and appear to be motivated by egocentric concerns such as attaining this goal item (e.g. Carpenter & Tomasello, 1995; Leavens & Racine, 2009; Tanner & Byrne, 2010). Along similar lines, while great ape communication might involve a 'common cognitive ground' in that individuals can account for what the receiver has experienced when producing a food-related gesture or a predator alarm call (Bohn, Call & Tomasello, 2016, Crockford, Wittig, Mundry & Zuberbühler, 2012), there is little evidence that they utilize this sensitivity merely to share attention the way infants can. While children will sometimes follow other's direction of attention to get what they want, children will also engage in joint attentional interactions simply to share attention with others in the context of a mutual interaction with no other instrumental goal. For example, children are satisfied when an adult responds to the bid for attention simply by attending to the object and then back to them (Liszkowski, Carpenter, Henning, Striano, & Tomasello, 2004), suggesting that they are motivated to simply share in this interaction with another person. Similarly, when playing a social game with no concrete reward, children will attempt to reengage their partner if they abruptly stop playing, whereas chimpanzees do not (Warneken et al., 2006).

Shared intentions also can take the form of a joint goal to work together to obtain mutual outcomes. While primates are often very sophisticated in their abilities to cooperate with others (Fletcher, Warneken, & Tomasello, 2012; Grueneisen, Duguid, Saur, & Tomasello, 2017; Melis, Hare, & Tomasello, 2006a; Melis & Tomasello, 2019; Yamamoto et al. 2012), it does not seem that these interactions are motivated by joint goals in the same way that superficially similar human interactions are. For example, chimpanzees' collaborative activities hinge on their own self-benefit: unless the instrumental benefit of working together is actually greater than what could achieve by working alone, they prefer to act alone. In contrast, 3-year-old children prefer the social interaction even if it does not provide greater material rewards (Bullinger, Melis, & Tomasello, 2011; Rekers, Haun, & Tomasello, 2011). Similarly, young children who work together to receive mutual outcomes seem to view their interactions in terms of joint commitments, such that the goal (and thus the cooperative act itself) is not completed unless both partners reap their designated rewards. As such, 3-year-old children who are inadvertently 'lucky' and get their portion before their partner does—or receive more than their partner even though both contributed equal work—will continue to cooperate or share rewards with their partner in order to complete the joint goal (Hamann, Warneken, Greenberg, & Tomasello, 2011). In contrast, chimpanzees seem to understand the need for a partner to satisfy their own individualistic goal (Melis et al., 2006), but stop acting once they receive their rewards— even if their partner has not received their share (Greenberg, Hamann, Warneken, & Tomasello, 2010; Hamann et al., 2011).

Attributing cooperative intentions

These differences in how children and nonhuman primates conceive of joint actions is one aspect of a potentially more far-reaching difference between human and nonhuman theory of mind: the ability of conceive of *cooperative* mental states in others. Importantly, all of the early evidence for sophisticated theory of mind abilities in non-human primates came from situations where subjects had to compete with another individual, for example to get access to food (Flombaum & Santos, 2005; Hare et al., 2000, 2001; Kaminski et al., 2008; Santos et al., 2006). Indeed, historically the successes of work using these competitive paradigms stood in contrast to earlier evidence involving cooperative interactions, for example where animals had to infer that humans wanted to share rewards or information with others (Povinelli, Eddy, Hobson, & Tomasello, 1996; Tomasello, Call, & Hare, 2003a, 2003b). This set of results let to several proposals arguing that nonhuman primates are either unable or unmotivated to utilize their social cognitive abilities in cooperative situations (Hare, 2001; Hare & Tomasello, 2004; Lyons & Santos, 2006; Tomasello & Carpenter, 2007). This could represent a critical difference between the cognitive abilities of humans and other primates, because humans are skilled at utilizing theory of mind to enable successful cooperative interactions (Bratman, 1992; Buttelmann, Carpenter, & Tomasello, 2009; Grueneisen et al., 2017; Tomasello, 2014). In particular, humans are also able to recognize others' communicative intentions, a potentially crucial component in language evolution (Grice, 1957; Sperber & Wilson, 1968; Scott-Phillips et al. 2015; Tomasello 2010).

Can nonhuman primates understand cooperative intentions? There is some evidence that apes can sometimes understand others' cooperative communication, particularly when they can use their large gestural repertoires (Byrne, Cartmill, Genty, Graham, Hobaiter & Tanner, 2017; Hobaiter & Byrne, 2011; Hobaiter & Byrne, 2014; Leavens & Hopkins, 1998; Tomasello, George, Kruger, Jeffrey & Evans, 1985). For example, chimpanzees will persist in their communicative intents if they do not observe a response from their audience (Leavens, Russell & Hopkins, 2005; Liebal, Call, Tomasello & Pika, 2004; Roberts, Vick & Buchanan-Smith, 2013), and appear to adjust their communication according to the audience's knowledge (Crockford et al., 2012). But studies that test primates in situations that are closely matched apart from the social context—whether the task is competitive or cooperative—suggest that competitive motives are more robustly understood than are cooperative ones. For example, one such study presented chimpanzees with a choice task where food was hidden underneath one of two possible containers (Hare & Tomasello, 2004). In the cooperative condition, a demonstrator pointed to the cup containing the food—that is, they helpfully attempted to provide information to assist the chimpanzees. In the competitive condition, in contrast, the demonstrator produced a similar action—reaching out their arm towards one container—but here they were effortfully trying (but failing) to obtain that container for themselves. Despite the similarities of these communicative gestures, chimpanzees only successfully inferred the location of the food in the competitive condition (see also Herrmann & Tomasello, 2006; Bohn et al. 2016; Bohn, Call & Tomasello, 2019; Dezecache et al. 2019). Outside of great apes, there is little evidence that other primates are sensitive to others' cooperative communicative intent or even produce such intentional communicative cues (Fischer & Price, 2017). Overall, this suggests that cooperative communicative behaviors may be less common, or less flexible, in nonhumans. Given that the ability to recognize communicative intent is foundational to human language (Grice, 1957; Scott-Phillips et al. 2015; Moore 2018), increased sensitivity to communicative intent in humans may have been a critical evolutionary shift facilitating the emergence of language.

Other work has examined how readily animals use information about other's intentions (cooperative or otherwise) to make social decisions. This line of work suggests that while others' intentions are important for shaping behavior in more competitive contexts, they are less important in cooperative contexts. For example, chimpanzees are more likely to punish individuals who intentionally stole food from them, compared to identical rewards outcomes where the other chimpanzee received food but did not intentionally steal it (Jensen, Call, & Tomasello, 2007b; Riedl, Jensen, Call, & Tomasello, 2012). However, chimpanzees are equally likely to accept or reject offers in an ultimatum game regardless if the offer signals more cooperative intentions (e.g. choosing the highest of possible offers) or less cooperative intentions (choosing the lowest; Jensen, Call, & Tomasello, 2007; Kaiser, Jensen, Call, & Tomasello, 2012; although see Schmelz, Grueneisen, Kabalak, Jost, & Tomasello, 2017 for evidence that chimpanzees do reward partners who previously assisted them in the past). In contrast, this kind of intention-attribution plays a crucial role in how humans interpret such offers (Falk, Fehr, & Fischbacher, 2003).

Yet it is important to note that some primates can be quite successful at mutualistic cooperation, where both partners gain benefits from working together (Melis & Warneken, 2016; Tomasello et al., 2012; Warneken, 2018). For example, pairs of chimpanzees and bonobos will jointly pull two ends of a rope to bring a board of food rewards within reach (Hare, Melis, Woods, Hastings, & Wrangham, 2007; Melis et al., 2006a; Melis, Hare, & Tomasello, 2006b). In such contexts, apes exhibit patterns of social decision-making that suggest that they are sensitive to some forms of cooperative intentions, at least when such intentions have repercussions for their own payoff. For example, chimpanzees will select a more effective collaborative partner over a less effective one (Melis, Hare, & Tomasello, 2006); account for what a cooperator can see (Grueneisen et al., 2017); and help by giving others tools they need to complete the joint action (Bullinger et al., 2014). Chimpanzees can also utilize communicative gestures of another chimpanzee to facilitate mutualistic benefits (Melis and Tomasello, 2019), although note that other experimental tasks have failed to find evidence that chimpanzees utilize cooperative communication to solve cooperative problems (Bullinger, Melis, & Tomasello, 2014; Warneken, Chen & Tomasello, 2006). There is also some evidence that capuchins attend to their partner in mutualistic tasks, for exampling by pulling more often when their partner is present, and looking at their partners (De Waal & Davis, 2003; Mendres & de Waal, 2000; although see Visalberghi, Quarantotti, & Tranchida, 2000 for evidence that capuchins do not account for the role of their partner). Other primate species can successfully cooperate in similar tasks where they must simultaneously pull a handle or rope, although the degree to which they actually understand their partner's role remains unclear (orangutans; Chalmeau, Lardeux, Brandibas, & Gallo, 1997, Japanese macaques; Kaigaishi, Nakamichi, & Yamada, 2019, Barbary macaques; Molesti & Majolo, 2016, Werdenich & Huber, 2002). Thus,_with the possible exception of chimpanzees, at present there is relatively little evidence that primates robustly use theory of mind to enable cooperation.

The evolutionary history of human-unique social cognition

Current comparative evidence shows that while some components of theory of mind are shared with other primate species, humans also seem to possess some theory of mind abilities that are derived in our species. In particular, humans appear uniquely skilled at theory of mind processes that have high representational demands—such as attributing false beliefs or reasoning about how objects appear from other's subjective perspective. In addition, humans routinely engage in collaborative interactions where participants share mental states, as in shared intentionality, whereas other species may not possess such cognitive mechanisms or be more constrained in their deployment. This kind of phylogenetic analysis is crucial for understanding what social abilities are shared between humans and at least some other species, and thus cannot strictly require language. Yet comparative research is also crucial for addressing evolutionary questions about the *function* or purpose of these abilities: why did these theory of mind abilities emerge in the first place? This kind of ultimate perspective human social cognition helps illuminate what these proximate mechanisms were 'built' to do. In the next section, we address theoretical perspectives concerning the evolutionary processes that shaped shared versus human-unique social cognitive abilities.

Cognition for competition versus cooperation

One of the dominant explanations for the evolution of social intelligence across primates concerns the crucial role of complex social life (Humphrey, 1976; Jolly 1966; Dunbar, 1998) and many versions of this idea focus on the critical importance of social intelligence for being able to outcompete, outwit, or deceive group-mates (Byrne & Corp, 2004; Byrne & Whiten, 1990, 1991; Byrne & Whiten, 1990; De Waal & Waal, 2007; Hare & Tomasello, 2004; Lyons & Santos, 2006; Moll & Tomasello, 2007; Whiten & Byrne, 1988). In this view, social cognitive evolution is driven by a 'mental chess game' where each individual seeks to outwit the other in competitive interactions, to attain resources such as food or mates via skillful political maneuvering (De Waal & Waal, 2007). There are several lines of evidence in support of this view. Some work focuses on naturalistic observations of primate behavior, such as incidents of ‘tactical deception’, which appear to be likely instances of primates actually using their theory of mind skills in real social interactions (Kummer, 1982; Whiten & Byrne, 1988). Other work has tried to link these kinds of behaviors to neurobiological substrates by examining the relationship between brain size and competitive deceptive interactions in natural behavioral repertoires, and found a positive association (Byrne & Corp, 2004). A final line of evidence in support of this claim comes from experimental contexts showing that primates appear to show the most robust social cognitive abilities specifically in competitive contexts (Hare & Tomasello, 2004). Indeed, many of the species that demonstrate particularly sophisticated theory of mind abilities in experiments—such as chimpanzees, rhesus macaques, and ring-tailed lemurs—are characterized by relatively high levels of competition or aggression in their natural social groups (Flombaum & Santos, 2005; Hare et al., 2000, 2001; Hare & Tomasello, 2004; Kaminski et al., 2008; Santos et al., 2006).

Yet humans as a species are marked by our exceptional forms of cooperation (Bowles & Gintis, 2003; Henrich, 2015; Richerson & Boyd, 2008; Tomasello, 2014). Humans cooperate flexibly across different contexts, with strangers, and in vast networks—aspects of cooperation that are not routinely seen in other primate species (Bowles & Gintis, 2003; Henrich, 2015; Moll & Tomasello, 2007; Tomasello, 2014). Even highly competitive behaviors that seem fairly specific to humans, such as inter-group warfare, involve high levels of within-group cooperation in order to outcompete a different group (Bowles, 2006, 2009). Humans are further characterized by a high degree of interpersonal tolerance, allowing individuals to calmly sit near others and work together on cooperative endeavors, which is often absent is other primate species (Burkart, Hrdy, & Van Schaik, 2009; Hare, 2017) where a lack of interpersonal tolerance can constrain cooperation (Cronin, 2012; Hare et al., 2007; Melis et al., 2006b).

Crucially, this kind of flexible cooperation is facilitated when individuals recognize shared goals as an opportunity to work together, and effectively coordinate online (Bratman, 1992; Brownell & Carriger, 1990; Eckerman & Whitehead, 1999; Tomasello & Carpenter, 2007; Warneken et al., 2006). In line with the special nature of human cooperation, human cooperation therefore appears to depend on new psychological abilities—those very psychological abilities that appear especially well-developed or unique to humans (see Figure 5). First, the ability to model what others experience from their perspective (level-2 perspective-taking) is especially useful for 'mutual attunement' (Paal & Bereczkei, 2007), or adjusting one's behavior online in response to the other individual to effectively reach a shared goal. That is, it is easier to act in concert with another person if you can accurately model what they can see and hear from their perspective (Dumontheil, Küster, Apperly, & Blakemore, 2010). In addition, rich perspective-taking abilities permit individuals to consider joint actions in a non-egocentric way (for example, to take a bird's eye view), which can allow cooperative partners to effectively switch between complementary actions (Carpenter, Tomasello, & Striano, 2005; Warneken, 2018). In this way, effective cooperation may hinge on individuals to reason about how objects and events appear to others, not just whether others are aware of their existence at all—a crucial difference from competitive interactions.

Second, explicit false belief reasoning may also play a crucial role in human cooperation. False belief attribution in animals is often considered in light of its utility for outcompeting an opponent, such as to get access to valuable resources if an individual is aware of other's false beliefs about the location of this item (Byrne & Corp, 2004; Byrne & Whiten, 1990). Yet a rich understanding of other's beliefs, involving clear judgements of others' mental states that feed in to subsequent behavioral decisions, may be of even greater use in cooperative interactions. First, understanding others' beliefs is crucial for managing one's reputation, and avoiding problems where another individual might believe they were not sufficiently compensated for their actions (Hamann et al., 2011; Tomasello & Hamann, 2012; Warneken, Lohse, Melis, & Tomasello, 2011)—key issues for cooperation (Milinski, Semmann, & Krambeck, 2002; Rand & Nowak, 2013; Warneken, 2018). False belief reasoning is also crucial to avoid miscommunication in joint action. If two people plan to meet at a coffee shop, but one mistakenly believes that their partner means a different coffee shop, they can nevertheless successfully coordinate if this false belief is detected. In line with this, children as young as six will use recursive false belief attributions (e.g. 'I know that you don't know that I know') to ensure that they will coordinate their behavior act in the same location (Grueneisen et al., 2017). More broadly, many potential cooperative encounters can be considered to be 'mixed strategy' games where each individual has a number of different potential strategies, some of which may be cooperative and some selfish (Skyrms, 2004). Therefore, the critical challenge is to determine when another individual will cooperate, as the worst outcome is to be 'left high and dry' by trying to cooperate with a selfish partner. Hence, the ability to read the intentions of others, which is recursively informed by their own beliefs ('I intend to cooperate because I believe the other player will cooperate') is critical. Along these lines, theory of mind abilities and their associated brain regions appear crucial to making inferences about the other's strategies in these kinds of cooperative games (Yoshida, Seymour, Friston, & Dolan, 2010).

Finally, shared intentionality (and attributing cooperative or helpful intentions more broadly) is intrinsically tied to cooperation. Shared intentions involve the formation of a shared goal to which all parties are committed, and mutually know that they are committed (Bratman, 1992; Tomasello & Carpenter, 2007). Without this kind of shared intention, individuals might pre-emptively stop cooperating once they have reached their individual goal (e.g. an individual might fail to take turns, once they have received their reward in a game). In line with this, when an adult suddenly stops playing a collaborative game, toddlers will attempt to reengage him, while chimpanzees do not (Warneken et al., 2006). Thus, children are inherently invested in the collaborative aspect of the game, while chimpanzees construe these events in a more individualistic manner. Furthermore, actively sharing psychological states during cooperation can facilitate effective coordination. That is, signaling cooperative intent (for instance via eye contact; Call, 2009; Wyman, Rakoczy, & Tomasello, 2013; Siposova, Tomasello, & Carpenter, 2018) rather than relying upon your partner to infer it can avoid miscoordination. These kinds of skills are beneficial in cooperative social environments, but would appear to be pointless (or even counterproductive) in more competitive situations. For example, signaling to share attention may facilitate joint action with others who share similar motives—but has no advantage if no one responds, or if other exploit this information to act selfishly.

It is important to note that in humans, the way that these theory of mind abilities enable cooperation is functionally interwoven with language. As alluded to above, many forms of cooperation are facilitated by communicating about how, where, and when individuals will act. That is, language can be used to pre-emptively plan cooperative acts, and therefore allows individuals to coordinate complex behavioral solutions to problems far beyond the scope of cooperation seen in nonhumans (Bickerton, 2009; Mercer & Littleton, 2007). Accordingly, a number of studies have linked children's language ability to engage in cooperation (Fawcett & Garton, 2005; Teasley, 1995; Vriens-van Hoogdalem, de Haan, & Boom, 2016). Language also plays a crucial role in the exchange of cultural information (Pinker, 2003), including the establishment of social norms. Such norms are a crucial ingredient of human cooperation as they often provide informal rules about how to act and distribute resources when interacting with others (Warneken, 2018).

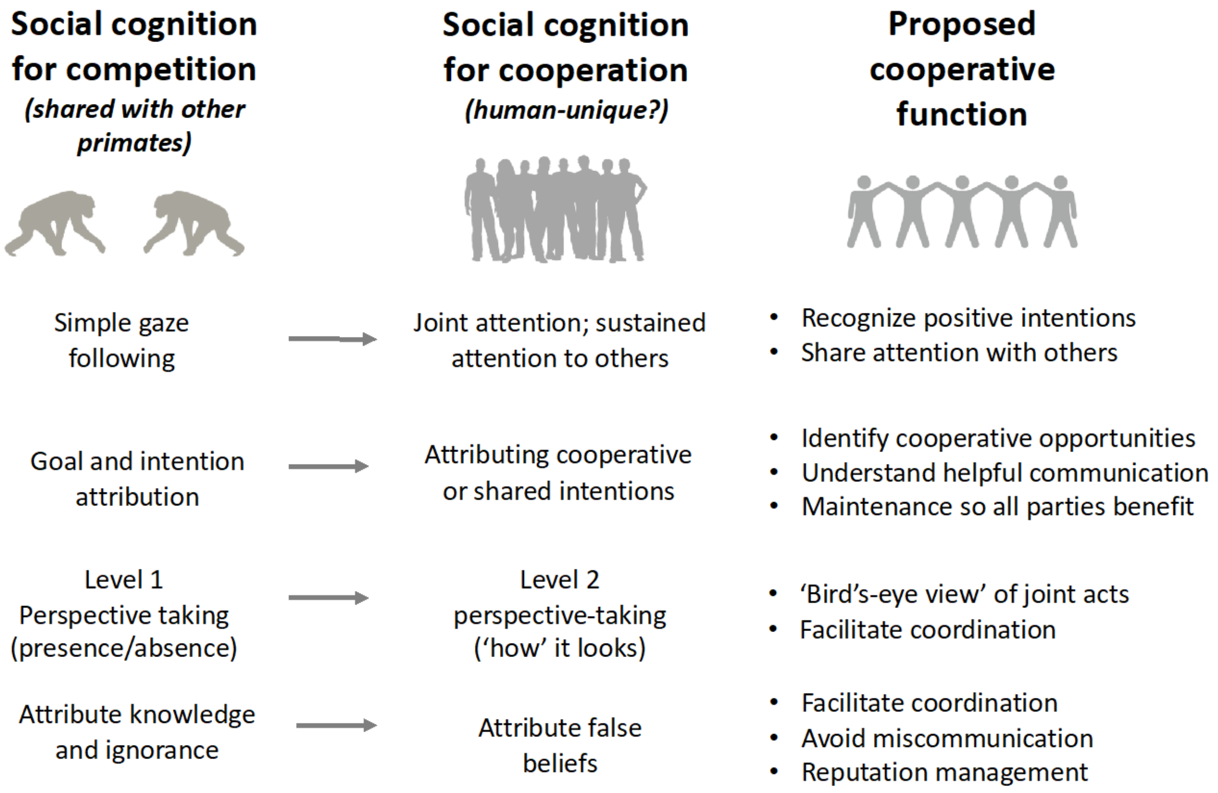

Figure 5: Evolutionary transitions from non-human to human theory of mind. Human unique-components of theory of mind are proposed to extend or elaborate on components of social cognition shared with other primate species. Whereas nonhuman primate social cognition may serve a primarily competitive function, novel components of human social cognition are proposed to scaffold cooperative behaviors.

Testing evolutionary links between social cognition and cooperation

Human-unique forms of social cognition appear to enable new forms of cooperative behavior. This suggests that the evolutionary processes that fostered the emergence of gaze following, perspective-taking, and knowledge attribution—abilities that are widely shared with many primates—may be distinct from the evolutionary processes that fostered level-2 perspective taking, false belief reasoning, and share intentionality. One way to test this claim is through use of the comparative method (Harvey & Purvis, 1991; MacLean et al., 2012; Many Primates et al., 2019; Rosati, 2017). In particular, by comparing the distribution of theory of mind and related abilities across primate species that vary in their degree of cooperation versus competition in their natural social groups, it is possible to more formally test which abilities tend to arise in different social contexts. In particular, comparison of cognitive abilities that are more frequently present in cooperative species, versus more competitive species, can elucidate which abilities facilitate cooperation behaviors, including those in humans. This approach further can help pinpoint what new data is needed to assess the proposed link between social cognition and cooperation.

One target for large-scale comparative investigations is gaze-following. Attending to other's gaze direction is clearly useful in competitive interactions, as knowing the direction of another individual's gaze may allow individuals to find contested food or other useful stimuli. According, gaze-following is found across a wide and diverse range of primate species (Rosati & Hare, 2009; Shepherd, 2010). However, social attention appears to take on additional functions in cooperative contexts, such as signaling positive, helpful intentions (Csibra & Gergely, 2009; Siposova et al., 2018; Tomasello, Hare, Lehmann, & Call, 2007). Thus, one prediction is that species that exhibit high levels of cooperation may demonstrate more robust sensitivity to some aspects of others' attention. For example, both socially tolerant bonobos and more competitive chimpanzees follow other's gaze, but bonobos make more eye contact than do chimpanzees (Kano, Hirata, & Call, 2015), follow the gaze of a wider range of demonstrators (Kano & Call, 2014a), and in some cases follow gaze more robustly than chimpanzees (Herrmann, Hare, Call, & Tomasello, 2010). Along the same lines, more socially tolerant Barbary macaques sustain more robust social attention into adulthood compared to despotic rhesus macaques (Rosati & Santos, 2017). Given the broad distribution of gaze following across the primate order, testing whether this relationship holds up across other taxonomic groups will provide a key test of the cooperative hypothesis.

The ability to attribute goals and intentions is another good target for broader comparative investigations. A basic ability to organize other's actions in terms of underlying goals also seems widely shared across primates, in line with the fact that being able to infer what others want is crucial to be able to predict how another individual will behave in order to outcompete them (Byrne & Whiten, 1990; Flombaum & Santos, 2005; Hare et al., 2000, 2001). Yet understanding other's goals can also foster mutualistic cooperative interactions—and while there is little evidence that nonhumans can understand cooperative intentions, most of this work comes from chimpanzees (Hare & Tomasello, 2004, 2005; Herrmann & Tomasello, 2006; Jensen et al., 2007a). Thus, it is crucial to see if a broader array of species, comprising both despotic and tolerant species, also preferentially attribute 'competitive' goals to others. A key prediction is that competitive species may be especially adept at attributing agonistic goals to others, and will concordantly seek to conceal cues to their own underlying goals that would allow others to exploit them. In contrast, more cooperative species might more readily assume others have cooperative intentions, and also more readily reveal their own mental states to others. In line with this, cooperatively-breeding marmosets are able to utilize a demonstrator's helpful social cues to find hidden food (Burkart & Heschl, 2006), while a number of more competitive species including chimpanzees (Hare & Tomasello, 2004, 2005; Herrmann & Tomasello, 2006), rhesus macaques (Anderson, Montant, & Schmitt, 1996), and capuchins (Anderson, Sallaberry, & Barbier, 1995; Vick & Anderson, 2000) fail this task. Furthermore, several domesticated species characterized by high levels of tolerance, such as dogs (Hare & Tomasello, 2005) and goats (Kaminski, Riedel, Call, & Tomasello, 2005), are also more adept at attributing cooperative motives.

Finally, perspective-taking and false-belief attribution can play important roles in both competitive and cooperative behavior. Most work in primate cognition to date has focused on competitive interactions, and many despotic primate species like chimpanzees, rhesus macaques, and ring-tailed lemurs seem especially adept in perspective-taking tasks that involve competition with conspecifics and humans. However, there appears to be a crucial distinction between simpler forms of perspective-taking (involving awareness of the presence or absence of an object from another's perspective) which may allow individuals to outwit others—and more complex forms of perspective-taking that involves awareness of how things *appear* to others. This form of perspective-taking seems to have higher representational demands, and may facilitate cooperation by taking a 'birds eye view' on joint activities. False-belief-reasoning can similarly facilitate more complex forms of cooperation (Tomasello, 2014; Yoshida, Dziobek, et al., 2010). Yet while there is little evidence for either level-2 perspective taking or explicit false-belief attribution in nonhumans, most evidence comes from chimpanzees (Call & Tomasello, 1999; Kaminski et al., 2008; Karg et al., 2014; Krachun et al., 2010; Krachun et al., 2009). As such, tests of level-2 perspective-taking and false belief reasoning in species that have strong representational abilities, but are more tolerant, would be especially useful for testing this claim. For example, bonobos succeed in tasks requiring appearance-reality distinctions and anticipating false belief (Karg et al., 2014; Krupenye et al., 2016), and they also show greater tolerance in cooperative contexts than do chimpanzees (Hare et al., 2007). Accordingly, they may be more successful at level-2 perspective taking and explicit false-belief reasoning than are chimpanzees. On the other hand, if these abilities are unique to humans due to their dependence on language, no other primate—even those with a more tolerant social system and a demonstrated facility with tasks involves higher representational demands—should demonstrate that ability. In this way, evolutionary reasoning can pinpoint novel tests of the link between cooperation, social cognition, and language.

Conclusions

We have argued that comparative data provides unique insights into the emergence of human-like theory of mind, as well as the links between theory of mind and other cognitive abilities like language. Currently, there is strong evidence that many important components of theory of mind are shared with other primates, including sensitivity to the attentional states of others, goal understanding, visual and auditory perspective taking, and the ability to attribute knowledge and ignorance to others. The fact that many nonhumans species exhibit these abilities indicates that these abilities can emerge in the absence of language or the capacity for language, even if language may facilitate their emergence in humans. Yet other theory of mind abilities may be unique to humans, including understanding other's subjective perspective, attributing false beliefs to others, and shared skills and motivations for cooperative behavior. Accordingly, these abilities are strong candidates for skills that may be dependent upon language.

We have further argued that one key difference between human theory of mind and nonhuman theory of mind may lie in the distinct evolutionary functions of these different sets of capacities. A demonstration that at least one other nonhuman species possesses a given cognitive skill (such as knowledge attribution) provides strong evidence that this skill does not intrinsically require language. To date there have been great successes in tested whether a broad range of species exhibit a variety of theory of mind components—with skills like gaze following and visual perspective taking being especially well-explored across many primate taxa. This wealth of comparative data sets the stage for a new wave of research in comparative social cognition that aims to understand not just whether any animal has a given ability, but rather how and why different social cognitive abilities emerge in different contexts. Here we have specifically proposed that different theory of mind capacities may differ in their utility across different behavior contexts: whereas many aspects of social cognition that are shared across other primates seem to serve a competitive function, humans very often use theory of mind to support cooperative interactions. This theoretical framework provides a pathway for testing the role of cooperation in human social cognitive evolution, as well as the linked between theory of and language. Ultimately, understanding the origins of human social cognition must involving situating humans in the natural world and relating our species' special cognitive traits to the species behavioral problems that humans uniquely face in our social lives.

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