The Evolution of Social Intelligence in Macaques

by

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Dedication

This thesis is dedicated to my family, for their unwavering support.

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Abstract

Primates lead complex social lives, and this complexity is thought to drive the evolution of social intelligence, including social cognitive abilities that are thought to be especially sophisticated in humans. However, it remains unclear (1) how different social styles promote the emergence of these abilities, and (2) how social cognition alters naturalistic patterns of social behavior. My PhD research examines the social cognition and social behavior of two closely related primate species that have different social styles—despotic rhesus macaques (*Macaca mulatta*) and socially tolerant Barbary macaques (*Macaca sylvanus*), to characterize the processes shaping social cognition and test several major hypotheses about the evolutionary contexts that support the emergence of complex cognition.

The first focus of my dissertation is to characterize complex social cognition in primates. In Chapters 2 and 3, I assess whether rhesus and Barbary macaques—like humans—have a sophisticated understanding of others' gaze, that accounts for their line-of-sight. In Chapter 4, I further assess whether rhesus macaques are sensitive to gaze as a communicative cue, which has been proposed to have been especially important during human evolution (Csibra & Gergely, 2011). Finally, I review evidence for different social cognitive abilities across primates in Chapter 6, and argue that human-unique social cognitive abilities may be linked to cooperation.

The second focus of my dissertation is to test the role of social style in promoting sophisticated social cognition. In particular, while much work on primate social cognition has suggested that high rates of social competition drive social cognitive evolution (Byrne & Whiten,

1989; Dunbar, 1998), other work has argued that tolerance promotes sophisticated social cognition—and that despotic primate species are actually constrained to utilizing sophisticated social abilities within competitive contexts (Hare, 2001; Lyons & Santos, 2006).

Chapters 2, 3, and 5 test these hypotheses, by assessing whether despotic rhesus macaques can flexibly use a sophisticated understanding of others' gaze even in a non-competitive context (Chapter 2), testing whether tolerant Barbary macaques or rhesus macaques show greater skill in this task (Chapter 3), and examining the link between social behavior and cognition (Chapter 5).

The final focus of my thesis is to examine how social cognition predicts natural social behavior. The social intelligence hypothesis posits that primate sociality selected for cognitive skills which allow individuals to respond adaptively to others' behavior (Byrne & Whiten, 1989; Hare, 2017; Humphrey, 1976; Jolly, 1966), yet has not been empirically tested despite intense theoretical interest. In Chapter 5, I utilize a novel approach that combines both experimental assessments of cognitive abilities with naturalistic social behavior upon Barbary macaques. I then contrast three influential hypotheses about the relationship between intelligence and behavior: (1) does social intelligence enable interaction with a larger number of individuals (Dunbar 1998); (2) does social intelligence facilitate strong social bonds or other prosocial behavior (Cheney, Seyfarth, and Smuts 1986; Hare 2017; Dunbar and Shultz 2007); and (3) does social intelligence facilitate sophisticated competitive behavior? (Byrne and Whiten 1989).

Overall, this dissertation examines the evolution of social intelligence in macaques, by contrasting cognition and behavior across two closely related species that vary in social tolerance. This will provide new insights into how complex social intelligence evolves across species, including humans.

Chapter 1: Introduction

Social cognition is necessarily complex: the ability to correctly infer what others are thinking is crucial to navigating the human social world, but this is a difficult challenge. Within a given interaction, we attend to the expression of another individual and attribute emotions to them, assess whether the words they are telling us are true, or whether they might be lying. We use information including their personality characteristics, past behavior, and current intentions to do this—human social cognition is extremely computationally challenging (Saxe, 2006). Without these skills we would struggle to skillfully interact with other people, as so many of our social behaviors depend on the ability to interpret or even modify the mental states of other individuals. For example, teaching entails modifying someone's knowledge by giving them new information—and the act of teaching requires the ability to recognize what that person already knows and is ignorant about. Cooperating with someone is a lot easier if you can recognize that they share a goal with you, and many forms of cooperation (such as moving furniture down a steep staircase together, or hunting a bison) are further enabled by the ability to imagine what someone sees from their perspective. As well as being commonplace throughout our everyday lives, these impressive social cognitive abilities enable behaviors that are novel to humans and critical to our evolutionary history—such as flexible cooperation, altruistic concern, and cultural learning (Boyd & Richerson, 2009; Henrich & Henrich, 2007; Herrmann et al., 2007b; Moll & Tomasello, 2007; Saxe, 2006).

Despite these links to human uniqueness, some of these social intelligence abilities are shared with other primate species. In fact, species such as great apes and rhesus macaques have demonstrated sophisticated social cognitive abilities including the ability to track others' knowledge (Kaminski et al., 2008; Marticorena et al., 2011), intentions (Call & Tomasello, 2008; Rochat et al., 2008), and perspective (Flombaum & Santos, 2005; Hare et al., 2000). In contrast, some other primate species, such as many lemur species (Sandel et al., 2011) and marmosets (Burkart & Heschl, 2007), struggle in similar situations. This cognitive variation across species is analogous to that exhibited by physical traits, and can thus be studied to examine how social intelligence evolves (MacLean et al., 2014; Shettleworth, 2009; Thorndike, 1911). Understanding the factors that promote the evolution of sophisticated social cognition across primates will provide new insights into the cognitive mechanisms underlying social behavior across primates, as well as to how these abilities became so exaggerated in humans.

This work therefore examines how variation in social intelligence evolves across primates, and focuses upon two main questions. First, I examine how differences in social style across different primate species shape social cognition. On the one hand, a prominent theory is that high rates of competition drive social cognitive evolution: the idea is that individuals have to outwit each other to gain access to food and mates in such environments, promoting a kind of 'social cognitive arms race' (Byrne & Whiten, 1990). This therefore predicts that highly despotic primate species, who are characterized by high rates of aggression and a strict dominance hierarchy, should have stronger social cognitive abilities. On the other hand, alternate theories have instead highlighted the role of social tolerance, which is thought to permit the emergence of cooperative interactions—allowing selection to then act upon cognitive abilities that promote successful cooperation (Hare, 2017). This thus predicts that more tolerant primate species may have superior social cognitive skills. Adding a final layer of complexity, some proposals have argued that primate cognitive evolution in general was driven via competitive interactions, but uniquely human cognition was promoted via its beneficial effects for cooperation (Moll & Tomasello, 2007).

Second, I examine how social cognition predicts patterns of natural social behavior. While social cognitive evolution theories all hold the underlying assumption that cognition affects natural behavior (Byrne & Whiten, 1990; Dunbar, 1998; Hare, 2017; Jolly, 1966; Tomasello, 2019), the relationship between social intelligence and social behavior is unclear—different proposals have suggested that social intelligence facilitates sophisticated aggression (Byrne & Whiten, 1990), affiliation or other prosocial behavior (Cheney et al., 1986; Hare, 2017), or keeping track of an increasing number of individuals in a larger social network (Dunbar, 1998). Understanding how social cognition predicts natural behavior is also a secondary test of the effect of tolerance upon social cognition. For example, if social cognitive ability predicts aggressive behavior but not affiliative behavior, this suggests that despotism promotes sophisticated social cognitive evolution—because despotic species exhibit a higher frequency of aggressive behavior, and so there is more of an opportunity for selection to act (Thierry, 2000). Thus, the goal of this dissertation is therefore to (1) test the role of social style in shaping social cognitive evolution, and (2) to test how social cognitive ability predicts natural patterns of behavior. This combination of goals will have further explanatory power, as they are 'flipsides of the same coin'. That is, my first goal seeks to analyze how existing cognitive variation is linked to difference in social styles, in order to identify a selective pressure. My second goal seeks to understand how cognition predicts behavior, in order to infer areas of behavioral variability for selection to act upon.

How does social cognition evolve?

Social intelligence encompasses social cognitive abilities such as theory of mind; the ability to understand the subjective mental states of other individuals, such as their knowledge, intentions, and beliefs. Given that these skills are inherently social, they are thought to have evolved in response to social challenges (Byrne & Whiten, 1990; Call & Tomasello, 2008; Dunbar, 1998; Hare, 2017)—where the ability to correctly interpret and respond to another individual is enabled by social cognition, and carries a fitness benefit. While species such as corvids (Clayton, 2012; Emery & Clayton, 2004), elephants (Byrne et al., 2009) and dogs (Hare & Tomasello, 2005; Miklósi et al., 2004) have demonstrated impressive social intelligence capacities, primate—and especially human—social intelligence seems to be especially sophisticated. In particular, there is strong evidence that primate species such as great apes and rhesus macaques demonstrate theory of mind abilities such as perspective-taking, knowledge attribution and understanding others' intentions (Call & Tomasello, 2008; Krupenye & Call, 2019), and human theory of mind encompasses abilities such as understanding what others see and hear from their perspective, and rich forms of false belief understanding—neither of which have been demonstrated outside of primates.

The social intelligence hypothesis

How have primate social intelligence abilities emerged? A striking characteristic of the primate order is our intense sociality. While many mammalian species are nonsocial (Müller & Soligo, 2005), all living primate species are classified as social—even primate species that are typically regarded as less social, such as nocturnal prosimians and orangutans, actually live in dispersed social networks (Altmann, 1962; Mueller & Thalmann, 2000). Further, primates also demonstrate social behaviors that appear especially complex relative to other mammals, as evidenced by the presence of intense social hierarchies, consequent political maneuvering, reconciliation patterns and unusual kinship systems (de Waal, 1991). Consequently, a key proposal is that primate sociality has selected for social intelligence abilities that enable skillful social behavior (Cheney et al., 1986; Dunbar, 1998; Hare, 2017; Jolly, 1966; Whiten & Byrne, 1988): a proposal that has broadly been termed the *social intelligence hypothesis*. While different formulations of this hypothesis have alternately emphasized different potential functions of social intelligence, all hold in common the idea that the challenge of primate social life exerts a selective pressure upon individuals that has resulted in enhanced social intelligence abilities.

The social intelligence hypothesis has proved hugely influential in understanding the evolution of social intelligence in primates, including in humans (Hare, 2017). However, it has proved difficult to empirically test. Some of the most well-known evidence for the social intelligence hypothesis are the correlations between social complexity (indexed by social group size) and brain size in taxa including primates (Barton, 1996; Dunbar, 1998; Dunbar & Shultz, 2007), carnivores (Dunbar & Bever, 1998) and cetaceans (Marino, 1996)—but brain size is an indirect proxy for social intelligence, that may not reflect actual cognitive abilities (Healy & Rowe, 2007; Holekamp, 2007). In particular, social cognitive abilities such as theory of mind have been linked to specific areas of the brain such as the tempero-parietal junction (TPJ) (Saxe & Kanwisher, 2003); one possibility is that these brain regions increase in size independently of other regions (Barton & Harvey, 2000; Healy & Rowe, 2007). Additionally, it should be noted that increasingly complex social cognitive abilities are thought to have been a result of result of rearrangements of the cortical regions within the TPJ, rather than merely an expansion in its size (Patel et al., 2019). Furthermore, subsequent analyses of brain size have also found support for the alternative hypothesis that ecological complexity—rather than social complexity—better correlates with brain size (DeCasien et al., 2017).

Another line of evidence to understand how sociality affects cognition comes from contrasting cognitive abilities across species with different social structures; many species living in complex groups have demonstrated aptitude in social cognitive tasks. For example, species including chimpanzees, capuchins, rhesus macaques and ring-tailed lemurs live in relatively complex groups—their social groups are large, and hierarchical. These species appear to be fairly successful at attributing goals to others (Kano & Call, 2014b; Uller & Nichols, 2000), taking other's perspective (Flombaum & Santos, 2005; Hare et al., 2000; Sandel et al., 2011), and attributing knowledge to others (Hare et al., 2001; Kaminski et al., 2008; Marticorena et al., 2011). In contrast, species that live in smaller and less hierarchical groups, such as mongoose, ruffed and black lemurs (Sandel et al., 2011), and marmosets (Burkart & Heschl, 2007), have struggled in similar paradigms—although note that chimpanzees, rhesus macaques and ring-tailed lemurs have also been especially well-tested, potentially providing more opportunity to demonstrate these complex abilities (Many Primates et al., 2019). Furthermore, these tasks have typically occurred in captivity, and have not tested whether variation in cognitive abilities is linked to real-life social behavior, a key prediction of the social intelligence hypothesis.

A final approach to examining the social intelligence hypothesis has tested how primate sociality is linked to fitness in wild primate populations. Many primates form close social bonds (Langergraber et al., 2009; Mitani, 2009; Silk et al., 2006), and these social bonds are associated with greater fitness. For example, female baboons with closer social bonds experience higher offspring survival and longevity (Archie et al., 2014; Silk et al., 2009, 2010). In prime-aged female rhesus macaques (not older macaques) the number of close adult female relatives predicts survival—given that older macaques receive less aggression, the authors postulate that the presence of these relatives helps to protect against aggression (Brent et al., 2017). Social bonds have also been linked to fitness in male primates, for example in Assamese macaques: strong bonds are linked to coalitionary support during aggressive encounters, which in turn affects fitness (Ostner & Schuelke, 2018; Schülke et al., 2010). Social bonds in male chimpanzees have been linked to increased fitness through several pathways: individuals who form strong bonds with the alpha male have greater siring success, and individuals who have a large number of social connections overall also have greater siring success (Feldblum et al., 2021). Overall, there is strong evidence that social bonds are associated with reproductive success across both sexes in primates, but the social cognitive abilities that underlie the formation of these social bonds remain unclear—it is unknown whether the individuals with particularly strong social bonds have greater social intelligence.

The competition hypothesis

Building on the social intelligence hypothesis, many proposals have highlighted the role of competitive interactions in driving the evolution of sophisticated social cognition. According to the view of the *competition hypothesis*, individuals with greater social intelligence may be better able to socially outmaneuver conspecifics to get access to valuable resources such as food and mates. That is, social intelligence may have emerged to enable individuals to outcompete or deceive group-mates (Byrne & Corp, 2004; Hare, 2001; Lyons & Santos, 2006; Whiten & Byrne, 1988).

In support of the competition hypothesis, observations of wild primates suggest that competitive behaviors such as tactical deception may depend on theory of mind abilities (Kummer, 1982; Whiten & Byrne, 1988), and the presence of these competitive deceptive interactions within natural behavioral repertories shows a positive relationship with brain size (Byrne & Corp, 2004). This suggests that species with greater social intelligence might utilize these abilities to engage in ‘cognitively taxing’ forms of aggression, such as deception, alliance formation and manipulation. These behaviors are linked to advanced social intelligence abilities—while the exact cognitive mechanisms underlying behaviors such as deception are unclear, at minimum individuals must be able to recognize opportunities to deceive others, and they may utilize a rich understanding of what the other individual knows and perceives (Whiten & Byrne, 1988).

Second, experimental studies indicate that many of the most impressive demonstrations of social cognitive abilities in primates have come from experiments that have utilized competitive interactions. This includes demonstrations of visual perspective-taking and knowledge in chimpanzees (Hare, 2001; Hare et al., 2000; Kaminski et al., 2008), rhesus monkeys (Flombaum & Santos, 2005) and ring-tailed lemurs (Bray et al., 2014; Sandel et al., 2011) facing competition from conspecifics or human actors. Along the same lines, while many primates struggle to use cooperative social cues such as gaze or pointing to locate hidden food (capuchins; Anderson et al., 1995, chimpanzees; Call et al., 1998, 2000; Hare & Tomasello, 2004; Herrmann & Tomasello, 2006; Povinelli et al., 1999, rhesus macaques; Anderson et al., 1996, orangutans; Itakura & Tanaka, 1998), they may be more successful at using social cues in matched competitive situations where an individual is actively reaching for food instead (Hare & Tomasello, 2004; Herrmann & Tomasello, 2006).

Finally, many of the species showing sophisticated social cognitive abilities—such as chimpanzees, rhesus macaques and ring-tailed lemurs—also exhibit higher levels of competition in their natural groups (Flombaum & Santos, 2005; Kaminski et al., 2008; Marticorena et al., 2011;

Sandel et al., 2011) whereas more tolerant species may not in similar setups (capuchins; Costes-Thiré, Levé, Uhlrich, Pasquaretta, et al., 2015; Hare et al., 2003, common marmosets; Burkart & Heschl, 2007, Tonkean macaques; Costes-Thiré, Levé, Uhlrich, De Marco, et al., 2015; Costes-Thiré, Levé, Uhlrich, Pasquaretta, et al., 2015).

The tolerance hypothesis

A related but distinct proposal focuses specifically on the role of social tolerance in the emergence of sophisticated social cognitive abilities (Burkart et al., 2009; Cieri et al., 2014; Hare, 2017). These proposals are similar to the social intelligence hypothesis in that they seek to explain how primates have evolved sophisticated social cognitive abilities, but they focus upon the role of tolerance in 'opening the door' to the evolution of these abilities. That is, according to the *tolerance hypothesis*, an increase in tolerance permits cooperative behaviors to occur, which utilize complex social cognitive mechanisms. Evolution may subsequently act upon these social cognitive mechanisms which are now expressed in a cooperative context—a process that is proposed to be especially important for human evolution (Hare, 2017). The tolerance hypothesis is therefore similar to other proposals that emphasize the selective benefit to maintaining affiliative social bonds for social cognitive evolution (Cheney et al., 1986), but goes beyond this by stressing how social tolerance permits expressly cooperative social behaviors.

There are several lines of evidence that support the tolerance hypothesis. First, studies across a range of primate species have demonstrated that inter-individual tolerance is critical to effective cooperation (chimpanzees; Melis et al., 2006; Suchak et al., 2014, Japanese macaques; Kaigaishi et al., 2019, marmosets; Werdenich & Huber, 2002). In a cross-species comparison, more tolerant bonobos were able to sustain mutualistic cooperation in contexts where chimpanzees could not, such as when the food reward was highly monopolizable (Hare et al., 2007).

Experimental evidence also indicates that socially tolerant primate species may be predisposed to be attentive to social cues such as eye contact and gaze, even when these cues are neutral rather than framed as explicitly cooperative. For example, more tolerant bonobos pay more attention to the faces and eyes of conspecifics (Kano et al., 2015) and follow the direction of a demonstrator's gaze more frequently than do more chimpanzees (Herrmann et al., 2010). Similarly, competitive rhesus macaques make less eye contact than do more tolerant stump-tailed and crab-eating macaques (Thomsen, 1974), and show age-related declines in gaze-following unlike more tolerant Barbary macaques (Rosati & Santos, 2017).

Finally, more tolerant species may be more skilled at utilizing communicative cues. In particular, tolerant macaque species outperform intolerant species in a 'pointing cups' task, where they must produce communicative cues towards the demonstrator in order to succeed (Joly et al., 2017). Along similar lines, dogs and experimentally-domesticated foxes—which tend to show more tolerant and less aggressive reactions to humans than their wild-type sister taxa—are able to successfully utilize social communicative cues, whereas wolves and control-line foxes do not (Hare et al., 2002; Hare & Tomasello, 2005; Kaminski & Nitzschner, 2013; Topál et al., 2009). However, note that we do not know what the cognitive mechanism is that underlies these cooperative behaviors and reading of social communicative cues in the more tolerant species. Perhaps the individuals are not successfully performing the tasks by understanding the experimenter's underlying cooperative intention (a mental state attribution) but instead are simply more likely to follow attentional cues such as pointing and gaze direction, which could have been strongly associated with food and other rewards in a domesticated species' evolutionary history.

Humans may represent an extreme example of the tolerance proposal, as humans exhibit high levels of social tolerance alongside highly complex social cognitive abilities (Boyd & Richerson, 2009; Csibra & Gergely, 2011; Henrich & Henrich, 2007; Moll & Tomasello, 2007; Siposova et al., 2018). Indeed, high levels of basic gaze sensitivity is linked to more sophisticated social cognitive abilities in humans (Csibra & Gergely, 2011; Flom et al., 2017; Senju & Johnson, 2009).

Reconciling these competing accounts requires further research, but a crucial distinction may be between *motivations* or interest to attend and respond to others' social cues, versus *cognitive* abilities to represent and act upon other's mental states (Kano et al., 2015). That is, while there is good evidence that more tolerant species preferentially attend and respond to social stimuli (chimpanzees versus more tolerant bonobos: Herrmann et al., 2010; Kano et al., 2015; Kano & Call, 2014a, macaques; Rosati & Santos, 2017; Thomsen, 1974) it is unclear if tolerant species actually have more robust social cognitive abilities to reason about this social information, or are simply more motivated to respond to social cues.

Methodological approaches to cognitive evolution

How can researchers test between these different hypotheses about cognitive evolution? A critical method to study adaptation is the comparative method, where researchers contrast a given trait across multiple species to make inferences about its evolution (Clutton-Brock & Harvey, 1979; Felsenstein, 1985; Garamszegi, 2014; Harvey & Pagel, 1991; Martins, 2000; Nunn & Barton, 2001). This method can utilize comparisons across a broad range of species, or specifically target comparison species that provide a key test of a given hypothesis. Another approach—that has not been utilized as frequently within social cognitive evolution—it to focus on particular traits within a given species, to understand how these traits influence fitness (Baum & Larson, 1991;

Martins, 2000). Both methods are applicable to testing hypotheses about cognitive evolution, and can provide key explanatory power when used in conjunction with each other.

The comparative approach

An important method for testing hypotheses about adaptation is the comparative method: testing whether traits tend to covary with particular social or ecological characteristics, suggesting that they are adaptations for that particular characteristic (Clutton-Brock & Harvey, 1979; Felsenstein, 1985; Garamszegi, 2014; Harvey & Pagel, 1991; Martins, 2000; Nunn & Barton, 2001). To give an example, echnidas, European hedgehogs and African pygmy hedgehogs all share one characteristic in common across their natural environments—the presence of terrestrial predators. Consequently, they have all have spines as an adaptation to avoid predation. An important caveat is that it necessary to account for shared phylogeny between species; since European and African pygmy hedgehogs are closely related, they likely inherited their spines via common ancestry rather than both independently evolving spines, whereas distantly-related echnidas evolved spines independently. By using this method, which identifies covariation between particular environmental characteristics and the existence of certain traits while accounting for phylogeny, it is possible to identify the evolutionary drivers of particular traits.

The comparative approach has been used extensively to understand physical traits (e.g. Darwin, 1845), and has more recently also been applied to understanding cognitive traits. One of the first examples of this came from work examining food caching birds: there is now strong evidence that bird species that cache food, such as chickadees, nuthatches and jays, have independently evolved spatial cognitive abilities that are more sophisticated than those in non-food-caching species (Hampton & Shettleworth, 1996; Pravosudov & Roth II, 2013; Sherry et al., 1989, 1992). Along similar lines, frugivory and extractive foraging have been linked to larger brain size across the primate order relative to foliovory, which is congruent with the idea that these modes of foraging are especially cognitively demanding (Clutton-Brock & Harvey, 1980; DeCasien et al., 2017; Gibson, 1986; Parker & Gibson, 1977).

A key source of variation for studies that have examined cognitive evolution using the comparative approach has come from the type of species comparison used. One approach is to use broad-scale comparisons, that test a large number of species and account for common ancestry. That is, a given cognitive trait is tested across an array species, enabling the examination of socioecological correlates of this ability. An advantage of this approach is that there is more statistical power to identify correlations between socioecological factors and cognition, since there are more data points overall (MacLean et al., 2012; Martins, 2000). Consequently, this approach has been very successful in examining the evolution of physical traits in species which have great variation within given socioecological groups, such as birds (Lack, 1968).

However, it has proved challenging to apply this approach to primate cognition: it is often impractical to test cognitive abilities using the same methods across a large number of species. One issue is the practical problem of access and resources to these species (Many Primates et al., 2019). Further, the same cognitive task must be used across species to assess comparison; but species' performance can be very variable, introducing the problem of ceiling effects. Take the example of knowledge attribution, or the ability to understand that individuals can have knowledge and ignorance states: while there is strong evidence for this ability in chimpanzees (Hare et al., 2001; Kaminski et al., 2008), at present there is no evidence for this ability in lemurs. If chimpanzees and lemurs were tested in the same knowledge attribution paradigm, one possibility is that the chimpanzees would score very highly while the lemurs would score at zero.

Consequently, existing examples of this approach have generally often occurred within a relatively small number of taxa. An example comes from Sandel et al. (2011), who found that social cognitive abilities appear correlate with social group complexity within lemurs. Outside of the social realm, broad-scale comparisons have found that brain volume and dietary breadth predicts self-control abilities across primates (MacLean et al., 2014).

Targeted species comparisons

An alternative approach, that will be used within this dissertation, is to use targeted comparisons, or to collect data on species that provide a strong comparative test of a particular hypothesis (MacLean et al., 2012). These methods are especially useful for cognitive research, since they do not require a large number of species to be tested.

First, a number of studies have tested species that are distantly related yet share important aspects of their socioecology. In this way, if these species share a given cognitive trait it is unlikely that this is due to common descent— a more likely possibility is that this trait has evolved due to convergent evolution, in response to the shared social or ecological characteristic (De Petrillo & Rosati, 2019). One example of this comes from chimpanzees and capuchins: both species share similar ecological characteristics, in that both species feed primarily on variable and unpredictable food sources, exhibit extractive foraging behaviors, and frequently invest energy to obtain uncertain outcomes while hunting. In accordance with these similarities, both species show high levels of delay tolerance and similar risk-seeking strategies—cognitive traits that are not shared with their closer phylogenetic relatives (De Petrillo & Rosati, 2019). Another example comes from work that has compared social intelligence abilities between corvids and apes, which proposes that shared social intelligence abilities evolved via convergent evolution; like apes, corvids live in complex social environments characterized by large effective group sizes (Clayton, 2012; Emery, 2004).

Second, an alternate 'targeted species' approach is to test species that are closely related, but which display key differences in their socioecology. If these species then demonstrate differences in their cognitive abilities, it is possible to narrow in and make inferences about how this cognitive ability is related to those particular aspects of their socioecology. This method can powerfully tease apart how different social and ecological characteristics shape cognition, because species that are closely related (yet display a key difference in their socioecology) are less likely to have confounding factors relative to broader comparisons (Huey & Pianka, 1981). That is, it is less likely that there will be factors other than the socioecological characteristic in question that could be driving the evolution of different cognitive abilities between the two species.

This approach has provided key insights into social cognitive evolution. A first example comes from work that has assessed the effects of domestication upon social cognition: while dogs and wolves are closely related, dogs have undergone an extensive domestication process (Larson et al., 2012). Work has found that dogs are especially sensitive to human communicative cues, relative to the abilities found in wolves. Dogs are able to successfully follow human cues such as pointing and eye gaze towards objects, whereas wolves typically struggle in the same paradigm—these results hold true even when the wolves are hand-reared, and when dogs and wolves are tested very early in development, making it implausible that these results are the effect of different rearing conditions (Hare & Tomasello, 2005; Topál et al., 2009; Virányi et al., 2008). These differences in cognitive ability to understand social communicative cues are therefore thought to be a result of selection to successfully interpret human cues and bond with humans (Hare et al., 2002; Kaminski & Marshall-Pescini, 2014).

A second line-of-work that has utilized targeted comparisons of closely related species has contrasted the cognitive abilities of chimpanzees and bonobos, who are closely related and diverged from each other less than 1 mya (Prüfer et al., 2012). While these species share many facets of their socioecology, they have divergent methods of foraging; chimpanzees eat seasonably variable fruit, occasionally participate in hunting, and use tools to extract food (Malenky & Wrangham, 1994; Uehara, 1992; Van Lawick-Goodall, 1971). In contrast, bonobos depend on herbs that are homogenously distributed, rarely hunt, and do not use tools in the wild (Gruber et al., 2010; Surbeck & Hohmann, 2008). Thus, it follows that chimpanzees require enhanced skills to be able to wait for food resources relative to bonobos, and to invest in uncertain outcomes—this is because fruit and meat are not reliably available, relative to terrestrial herbs. Accordingly, experimental paradigms have found that chimpanzees are able to wait longer to obtain larger food rewards than bonobos (Rosati et al., 2007; Rosati & Hare, 2013), and are also more risk seeking than bonobos (Heilbronner et al., 2008; Rosati et al., 2007; Rosati & Hare, 2012, 2013). In the social realm, chimpanzee and bonobo comparisons have also been utilized to assess the impact of social tolerance upon social cognition: bonobos are considered to be more socially tolerant than chimpanzees. This is because they exhibit lower rates of aggression, and less severe aggression (Gruber & Clay, 2016; Stanford, 1998), and are better able to feed in proximity to one another in experimental contexts (Hare et al., 2007). In cognitive tasks, there is strong evidence that bonobos pay more attention to particular attention to gaze cues (Herrmann et al., 2010; Kano et al., 2015), and some evidence that they also perform more robustly in theory of mind tasks (Herrmann et al., 2010)—these results have been argued to be a result of selection for increased tolerance in the bonobo lineage (Hare, 2017b; Herrmann et al., 2010).

Linking cognition to behavior

The comparative method, including the targeted comparison method, compares traits across species to gain insight into its evolution. An alternative approach to studying adaptation is to focus upon the particular trait in question within a single species, and to assess how that trait functions to increase fitness (Baum & Larson, 1991; Martins, 2000). An example of this approach comes from Bernard Kettlewell's famous work with peppered moths, whose color can vary from near-black to grey. He found that the darker coloring increased camouflage and lowered predation risk, in areas of high pollution (Kettlewell, 1955).

Overall, this method relies upon examining the link between the trait in question, and its affect upon fitness. Can such an approach be applied to cognition? A key difference between cognition and other traits is that cognitive mechanisms exert their affect through behavior, which is the level that selection can actually act upon (Kamil, 1998; Shettleworth, 2009). For instance, improved understanding of others' goals and perspective might enable a monkey to surreptitiously steal a food item, resulting in a fitness benefit. Selection may therefore act to improve these goal attribution and perspective-taking abilities, over many successive generations. In contrast, selection can act directly upon physical traits, rather than through an intermediary such as behavior. An example would be selection acting to increase leg length in macaque, to enable especially fast running abilities. Consequently, utilizing a trait-based approach to understand cognitive evolution requires an understanding of how cognition predicts behavior, as well as how patterns of social behavior predict fitness.

Understanding how primate social behavior predicts fitness is an area of intense research interest. Behaviors such as aggression clearly incur fitness costs and benefits: winning an aggressive bout might push an individual up a social hierarchy, yet losing an aggressive bout may result in severe injury or even death (Martínez-Íñigo et al., 2021; Wilson & Wrangham, 2003; Wrangham, 1999). Recent work has also elucidated how affiliative behaviors, such as social bond formation, affect fitness. In particular, female baboons who form strong and stable social bonds live significantly longer than other female baboons (Silk et al., 2010), and their offspring live significantly longer (Silk et al., 2009).

While there is thus convincing evidence that links behaviors such as aggression and social bond formation to fitness in primates, the cognitive mechanisms that facilitate these fitness-relevant behaviors remain unclear. Skillful aggression could be enabled by knowledge of the other individual's intent and knowledge, as well as the social skills to attract coalitionary partners. Social bond formation may be facilitated by the ability to recognize others' affiliative intent, and sensitivity to others' knowledge of social relationships. Understanding this link between cognition and behavior is a 'missing piece of the puzzle' towards understanding how social cognition evolves.

Target species

This dissertation will focus on two species from the *Macaca* genus: rhesus macaques (*Macaca mulatta*) and Barbary macaques (*Macaca sylvanus*). The macaque radiation is notable for displaying highly divergent social styles (Thierry, 2000, 2007). In particular, intolerant macaque species (such as rhesus macaques) demonstrate behavioral patterns including a steep dominance hierarchy, strong kinship bias, presence and use of subordinate signals, and higher rates of aggression (Thierry, 2000). Contrastingly, tolerant macaque species (such as Barbary macaques) demonstrate behavior such as a flatter dominance hierarchy, high rates of reconciliation after aggression, use of affiliative signals, and lower rates of aggression (Thierry, 2000). It is possible to place the 22 macaque species into social grades, along this tolerance continuum: these interrelated set of traits cluster into four different grades of tolerance.

Importantly, macaques otherwise have very similar patterns of sociality and ecology. With regards to sociality, macaques live in multimale-multifemale groups, where males disperse and females inherit rank from their mother (Fa & Lindburg, 1996). Regarding ecological characteristics, macaques are generalist omnivores (Cui et al., 2019; Sengupta & Radhakrishna, 2016): both species typically feed upon seeds, buds, leaves and herbs (Menard, 2004). Given their difference in social style, yet similarity in other socioecological characteristics, macaques are an ideal taxon in which to contrast social cognition theories about social tolerance as well as differences in social behavior (such as rates of aggression versus affiliation) more broadly.

Within the macaque genus, rhesus and Barbary macaques are an ideal species comparison to test hypotheses about the evolution of social cognition and behavior. First, these species are at different ends of the spectrum with regards to their social behavior; rhesus macaques are regarded as being highly intolerant, Barbary macaques are highly tolerant. While no one research has directly contrasted rhesus and Barbary social behavior, rhesus macaques display rates of aggression that are higher and more unidirectional (the victim flees rather than engaging in counter-aggression) than other macaque species that are considered to be similarly or less tolerant than Barbary macaques, such as tonkean macaques (*Macaca tonkeana*) and crab-eating macaques (*Macaca fascularis*) (Thierry, 1985). Aggression also appears to be more severe in rhesus than Barbary macaques; severe biting is not rare in rhesus macaques, whereas it is in Barbary macaques (De Waal & Luttrell, 1989; Thierry, 2000). In line with these patterns of aggression, dominance rankings in rhesus macaques are far steeper than those in Barbary macaques, and reconciliation after aggression is a much rarer event (Thierry, 2007). Facial expressions that denote submission in rhesus macaques, such as retracting the lips and exposing teeth, also denote affiliation in Barbary macaques (Preuschoft & van Hooff, 1995). By a variety of measures, rhesus are far more despotic than tolerant Barbary macaques.

In addition to these marked differences in social behavior, it is possible to study both species within a similarly matched free-ranging context: this makes it possible to run cognitive tasks, as well as to conduct observations of natural social behavior. Specifically, rhesus macaques at Cayo Santiago range through a 38-acre forested island. At the Trentham Monkey Forest, Barbary macaques roam through a 60-acre forested area. Macaques at both sites live in large social groups, are provisioned daily, and are habituated to the presence of humans. Consequently, both cognitive experiments (Arre et al., 2021; Drayton & Santos, 2017; Flombaum & Santos, 2005; Marticorena et al., 2011; Rosati et al., 2016; Rosati & Santos, 2017) and studies of natural social behavior (Berthier & Semple, 2018; Brent et al., 2017; Carne et al., 2011; Faraut et al., 2015; Semple et al., 2013; Widdig et al., 2004, 2004) have been successfully completed at both sites.

Overall, since rhesus and Barbary macaques are closely related yet demonstrate different patterns of social tolerance, they provide a key test for hypotheses concerning the role of social style in cognitive evolution. Importantly, these species are otherwise live in similar ecological and social environments. Furthermore, studying free-ranging and habituated animals presents a unique opportunity to uniquely combine behavioral and cognitive methods.

Research goals

Overall, this thesis aims to test several key theories regarding the evolution of social intelligence. To do this, I will use a targeted comparison to contrast the cognitive abilities of two macaque species with different social styles: despotic rhesus macaques at Cayo Santiago and tolerant Barbary macaques at the Trentham Monkey Forest.

First, I will characterize complex social cognition in primates. In particular, I will focus on how macaques interpret gaze cues, as gaze-following is common across primates yet has also been linked to sophisticated social cognitive abilities in humans (Flom et al., 2017; Rosati & Hare, 2009; Shepherd, 2010). In Chapters 2 and 3, I assess whether rhesus and barbary macaques—like humans—have a sophisticated understanding of others' gaze, that accounts for their line-of-sight. In Chapter 4, I further assess whether rhesus macaques are sensitive to gaze as a communicative cue, which has been proposed to have been especially important during human evolution (Csibra & Gergely, 2011). Finally, I review evidence for different social cognitive abilities across primates in Chapter 6. In particular, I argue that social cognitive abilities that are unique to humans may be critically enabled by language, and that these abilities may have evolved in response to selection for effective cooperation—even if primate social cognition in general evolved to support competition.

My next goal is to test the role of social style in promoting sophisticated social cognition: in Chapter 2, I assess whether despotic rhesus macaques can flexibly use a sophisticated understanding of others' gaze even in a non-competitive context—in contrast to proposals arguing that despotic species are constrained to utilizing sophisticated social cognitive abilities specifically within competitive contexts. In Chapter 3, I then compare rhesus and Barbary macaques' ability within this task, to test whether either the tolerant or despotic species shows more sophisticated gaze-following abilities.

The final focus of my thesis is to examine how social cognition predicts natural social behavior. The social intelligence hypothesis posits that primate sociality selected for cognitive skills which allow individuals to respond adaptively to others' behavior (Byrne & Whiten, 1990; Hare, 2017; Humphrey, 1976; Jolly, 1966), yet has not been empirically tested despite intense theoretical interest. Overall, this research provides novel insights into the role of social style in shaping social cognition, and into how cognition generates patterns of behavior that selection acts upon—a key component towards understanding social cognitive evolution.

In Chapter 5, I utilize a novel approach that combines both experimental assessments of cognitive abilities with naturalistic social behavior upon Barbary macaques. I then contrast three influential hypotheses about the relationship between intelligence and behavior: (1) does social intelligence enable interaction with a larger number of individuals (Dunbar 1998); (2) does social intelligence facilitate strong social bonds or other prosocial behavior (Cheney, Seyfarth, and Smuts 1986; Hare 2017; Dunbar and Shultz 2007); and (3) does social intelligence facilitate sophisticated competitive behavior? (Byrne and Whiten 1990).

Overall, this dissertation examines the evolution of social intelligence in macaques, by contrasting the cognition and behavior across two closely related species that vary in social tolerance. This will provide new insights into how complex social intelligence evolves across species, including humans.

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Chapter 2: Flexible Gaze Following in Rhesus Monkeys[1]

Abstract

Humans are characterized by complex social cognitive abilities that emerge early in development. Comparative studies of nonhuman primates can illuminate the evolutionary history of these social capacities. We examined the cognitive skills that rhesus monkeys (*Macaca mulatta*) use to follow gaze, a foundational skill in human social development. While rhesus monkeys can make inferences about others' gaze when competing, it is unclear how they think about gaze information in other contexts. In Study 1, monkeys (n = 64) observed a demonstrator look upwards either in a *barrier* condition where a box was overhead so that monkeys could not see the target of her gaze, or a *no barrier* condition where nothing blocked her view. In Study 2, monkeys (n = 59) could approach to observe the target of the demonstrator's gaze when the demonstrator looked behind a *barrier* on the ground or, in the *no barrier* condition, behind a window frame in the same location. Monkeys were more likely to directly look up in Study 1 if they could initially see the location where the demonstrator was looking, but they did not preferentially reorient their bodies to observe the out-of-view location when they could not see that location. In Study 2, monkeys did preferentially reorient, but at low rates. This indicates that rhesus monkeys can use social cognitive processes outside of competitive contexts to model what others can or cannot see, but may not be especially motivated to see what others look at in non-competitive contexts, as they reorient

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[1] This research was previously published in *Animal Cognition* (Bettle & Rosati, 2019).

infrequently or in an inconsistent fashion. These similarities and differences between gaze-following in monkeys and children can help illuminate the evolution of human social cognition.

Introduction

Many eyes are better than one: gaze-following, or looking in the direction that another individual is looking, can provide important information about the environment as well as about what others are seeing and thinking. In humans, gaze-following is an important social milestone that emerges early in development (Butterworth & Jarrett, 1991; Flom, Lee, & Muir, 2017). Gaze-following scaffolds the development of other important human social cognitive abilities such as language (Brooks & Meltzoff, 2005; Morales, Mundy, & Rojas, 1998) and theory of mind (the ability to ascribe subjective mental states to others; Baldwin & Moses, 1994; Flom et al., 2017; Lee, Eskritt, Symons, & Muir, 1998; Moll & Meltzoff, 2011; Moll & Tomasello, 2007). Yet gaze-following is also important for other species, as it can provide clues to the direction of food, predators and mates in the external environment. Accordingly, basic co-orienting responses—where individuals match the head or eye position of others—are phylogenetically widespread (Rosati & Hare, 2009; Shepherd, 2010). Since other species do not display human-like social cognition or language, an important question concerns the differences between human and nonhuman gaze-following. We therefore examined whether rhesus monkeys (*Macaca mulatta*) can flexibly control their gaze-following responses like humans.

A crucial distinction for considering comparative patterns of gaze-following concerns the psychological mechanisms different species use to follow gaze. One potential mechanism is termed ‘reflexive’ gaze-following: shifting where one is looking in response to external stimuli, such as simple directional eye and head cues that automatically capture attention, without further reasoning about the social context (Deaner & Platt, 2003; Friesen & Kingstone, 1998; Shepherd, 2010). This kind reflexive co-orienting has been documented in humans and many other species (Butterworth & Cochran, 1980; Davidson, Butler, Fernández-Juricic, Thornton, & Clayton, 2014;

Friesen & Kingstone, 1998; Ricciardelli, Carcagno, Vallar, & Bricolo, 2013; Ruiz, Gómez, Roeder, & Byrne, 2009). However, this reflexive mechanism breaks down in some contexts. For example, if the other individual's line-of-sight is blocked by a barrier, reflexive matching of gaze direction will not allow individuals to actually perceive what the actor sees. Yet humans and at least some other primate species can also engage in more 'cognitive' gaze-following responses, that involve reasoning about the social or physical context to assess what the other agent actually sees. For example, humans and great apes habituate to repeated looks, reorient their body to observe the target of another's gaze, and check back to reassess where that individual is looking—indicating their responses are not purely reflexive (Bräuer, Call, & Tomasello, 2005; Butterworth & Jarrett, 1991; Okamoto-Barth, Call, & Tomasello, 2007; Tomasello, Hare, & Fogleman, 2001). This kind of mechanism enables individuals to accurately detect the location that others look at across a broader range of situations than purely reflexive gaze following. In humans, more cognitive forms of gaze-following may further enable shared visual attention, a common frame-of-reference that is thought to promote the development of human social cognitive capacities in infancy (Tomasello, 2014). Understanding what mechanisms different species use to follow gaze can therefore contextualize the patterns of human social cognitive development.

While basic gaze-following responses are common across species, the particular psychological mechanisms underlying these behaviors appear to vary (Rosati & Hare, 2009; Shepherd, 2010). A common test to distinguish between more reflexive versus more cognitive mechanisms for gaze-following comes from studies of visual perspective-taking, generally involving competitive interactions. For example, chimpanzees (*Pan troglodytes*) can infer other's visual perspective to outcompete both conspecifics and humans by targeting hidden food in scramble competition (Bräuer, Call, & Tomasello, 2005; Hare, Call, Agnetta, & Tomasello, 2000;

Hare, Call, & Tomasello, 2001, 2006; Kaminski, Call, & Tomasello, 2008; Melis, Call, & Tomasello, 2006). Similarly, rhesus monkeys (Flombaum & Santos, 2005; Lyons & Santos, 2006; Santos, Nissen, & Ferrugia, 2006) and ring-tailed lemurs *(Lemur catta)* (Bray, Krupenye, & Hare, 2014; MacLean et al., 2014; Sandel, MacLean, & Hare, 2011) will preferentially try to steal food that a human competitor cannot perceive. In contrast, many of these same species do not use information about other's perspective in 'cooperative' paradigms that involve similar inferences but hinge on cooperative motives such as sharing food (Anderson, Montant, & Schmitt, 1996; Anderson, Sallaberry, & Barbier, 1995; Call, Agnetta, & Tomasello, 2000; Call, Hare, Carpenter, & Tomasello, 2004; Call, Hare, & Tomasello, 1998; Itakura & Tanaka, 1998; Vick & Anderson, 2000). Thus, one proposal is that nonhuman primates can utilize 'cognitive' mechanisms to reason about what the others can see primarily in competitive contexts, either because they are more motivated during competition or because their abilities are actually constrained to competitive contexts (Byrne & Whiten, 1989; Call et al., 2004; Hare, 2001; Lyons & Santos, 2006). In contrast, humans can use these abilities more flexibly across many contexts (Bettle & Rosati, 2016; Rosati, Arre, Platt, & Santos, 2016).

Another approach to understanding gaze processing in primates comes from work using 'geometric' gaze-following tasks. Here, a demonstrator looks at an object that is behind a barrier and thus outside of the subject's line-of-sight, so individuals must actually reorient from their initial position, rather than just match their head to the demonstrator's direction of gaze, to see what the demonstrator sees. In fact, both children and other great apes will actively move to look behind a barrier that a demonstrator is looking behind in this context (Bräuer et al., 2005; MacLean & Hare, 2012; Moll & Tomasello, 2004; Okamoto-Barth, Call, & Tomasello, 2007; Tomasello, Hare, & Agnetta, 1999). Since children and apes move to look behind the barrier, their responses cannot stem from a purely reflexive co-orientation process; such a response would lead them to simply match the gaze direction of the demonstrator and therefore incorrectly look past the barrier and miss the true target location of the actor's attention. Instead, these species exhibit a more cognitively controlled response by moving their bodies to see where the other is looking, accounting for some aspect of the other's line of sight. Crucially these interactions do not entail any obvious competitive motives like visual perspective-taking paradigms, such as contested food or initial agonistic displays. This suggests that apes can make inferences about where others are looking in a flexible manner, using cognitive gaze-following abilities even in the absence of competition. This aligns with accumulating evidence that great apes, like children, exhibit a broad spectrum of social cognitive abilities across competitive and non-competitive social contexts (Bulloch, Boysen, & Furlong, 2008; Hopkins, Taglialatela, & Leavens, 2007; Hostetter, Russell, Freeman, & Hopkins, 2007; Krupenye, Kano, Hirata, Call, & Tomasello, 2016).

Can other primate species also reason about gaze across different social contexts, or do they show most robust skills specifically in competitive contexts (Byrne & Whiten, 1989; Call et al., 2004; Hare, 2001; Lyons & Santos, 2006)? Rhesus macaques provide a strong test of this proposal. First, rhesus monkeys are characterized as a strongly despotic species, exhibiting high rates of agonism in their natural behaviour. Long-term behavioural observations indicate reduced levels of affiliative interactions compared to other macaque species (Brent et al., 2013; Thierry, 2000; Widdig, Nürnberg, Krawczak, Streich, & Bercovitch, 2002), and most clear examples of rhesus cooperation in natural interactions involve providing support during aggressive interactions or rank disputes (Cheney, 2011; Higham & Maestripieri, 2010; Widdig et al., 2006). Although there have been few experimental assessments of rhesus cooperation, comparisons with other closely-related macaque species also reveal that dyads of rhesus monkeys collaborate much less frequently than more tolerant species (Petit, Desportes, & Thierry, 1992). Thus, rhesus monkeys are characterized by extreme despotism, and competition is central to their natural social behaviors.

Currently, the strongest evidence that rhesus monkeys can make inferences about other's gaze comes from competitive interactions. For example, rhesus monkeys will preferentially try to steal food from a human competitor that cannot see their approach, compared to one who can (Flombaum & Santos, 2005), and will preferentially steal in a 'quiet' fashion to avoid alerting a human competitor to theft (Santos et al., 2006). This suggests that monkeys can deduce what others perceive and use it to outcompete them. Work using expectancy looking time methodologies, involving measures of looking to index cognitive processes, has further shown that monkeys understand other's knowledge states based on what the other individual previously saw (Marticorena, Ruiz, Mukerji, Goddu, & Santos, 2011; Martin & Santos, 2014). For example, rhesus monkeys look longer when a demonstrator searching for hidden food searches in an empty box versus where the food is located—indicating surprise at this unexpected action (Marticorena et al., 2011; Martin & Santos, 2016). While these looking time tasks do not involve direct competition, the ability to track where individuals are searching for food is highly relevant to competitive scenarios. Finally, rhesus show basic co-orientation responses to both conspecifics and humans (Call et al., 1998; Emery, Lorincz, Perrett, Oram, & Baker, 1997; Itakura, 1996; Rosati et al., 2016; Rosati & Santos, 2017; Shepherd, 2010; Shepherd, Deaner, & Platt, 2006; Tomasello, Hare, & Fogleman, 2001), and are sensitive aspects of social context when doing so. For example, when a demonstrator looks at a distantly located object in a surprised manner while vocalizing, monkeys look to this object. In contrast, when she has previously seen this object, the monkeys search longer to identify an alternative target of gaze (Drayton & Santos, 2017). However, rhesus macaques can use similar vocal signals in competitive contexts, such as during aggressive interactions (Lindburg, 1971; Partan, 2002). Thus, it is possible that they interpreted this as a competitive or agonistic situation. Consequently, evidence for cognitive gaze-following in rhesus comes primarily from interactions that are either clearly competitive or could be construed as so.

In the current work, we therefore examined rhesus monkeys' abilities to use cognitive gaze-following mechanisms in neutral, non-competitive interactions. Across two experiments, rhesus monkeys saw a human demonstrator look in a particular direction. Monkeys could either see the target location of the actor's attention by moving their head in the same direction as the actor, or it was necessary for the monkeys to reorient their bodies from their initial viewing position to see the target location, allowing us to distinguish reflexive responses (involving simple matching of head orientation) from more cognitive forms of gaze-following (involving reasoning about where others are specifically looking). In Study 1 we examined monkeys' responses when a human actor looked upwards (either at the sky or into an overhead box), and in Study 2 we examined monkeys' responses when a human actor looked down (either behind a window or behind a closed box). Importantly, these studies never involved contested food or agonistic emotional or vocal displays, key cues indicating a competitive context in prior work. These studies can shed light on how individuals from this highly competitive species use their social cognitive abilities across contexts.

Study 1: Overhead barrier

In Study 1, we examined monkeys' responses to a human demonstrator looking upwards. In the *barrier condition* the human's line-of-sight towards the sky was blocked by an overhead box, such that the target of her gaze was inside the box. In the *no barrier condition* she produced the same action but there was no box above her head. We predicted that if the monkeys understood the demonstrator's line-of-sight, they should preferentially look up at the sky in the *no barrier* condition where they could also see the demonstrator's target from their initial location compared to when the demonstrator looked inside the box, but rather reorient by approaching the apparatus in the *barrier* condition to see where the demonstrator was looking. In contrast, monkeys using reflexive mechanisms should match their head direction to the demonstrator's head direction similarly in both situations, and not reorient their body to see what the demonstrator was actually looking at in the barrier condition.

Methods

Subjects

Our final sample comprised 64 rhesus monkeys living at the Cayo Santiago Field Station (38 males and 26 females, ranging from 1.5 years to 21.3 years). Cayo Santiago is a 38 acre island off the coast of Puerto Rico (Rawlins & Kessler, 1986), with approximately 1500 semi-free-ranging monkeys that are highly habituated to humans and can be individually by unique chest tattoos and ear notches. While monkeys from this population have participated in prior studies of gaze-following (Drayton & Santos, 2017; Rosati et al., 2016; Rosati & Santos, 2017) and see a variety of natural barriers (such as trees and rocks), they were naïve to gaze-following tasks involving an overhead barrier used in the current study.

Apparatus and setup

Monkeys experienced one of two conditions in a between-subjects design in which they saw a demonstrator look upwards by rotating both her head and eyes (see Figure 1). In the *barrier* condition, the demonstrator looked upwards into a barrier above her head (a box 41 cm long, 31 cm wide, 15 cm deep; propped onto a stick attached to a tripod of total height 1.77 m). The demonstrator could see into the box from her position, but the monkey could not (see Fig. 1a). In the *no barrier* condition, the demonstrator performed the same actions next to the tripod, but her line-of-sight was not blocked (the box was removed). As such, the monkeys could observe her visual target from their initial position in this condition.

Following the methods of prior work (Rosati et al 2017; Rosati & Santos 2017; Tomasello et al. 200; Tomasello et al. 2001), there was no specific target stimulus in either condition that would cause the monkey to look up independently of the demonstrator's actions; rather the demonstrator either looked upwards with her line of sight unimpeded (*no barrier* condition) or she looked upwards into the box (*barrier* condition). To ensure that the gazing actions of E1 appeared plausible, the apparatus was always set up near a tree such that E1 could feasibly be gazing at something above (again following the methods of Rosati et al 2016; Rosati & Santos 2017). We always checked that there were no other monkeys above the apparatus who might attract the subject's attention. Finally, we used a human demonstrator to ensure tightly controlled behavior across conditions; previous research shows that macaques robustly follow the gaze of both humans and conspecifics at similar rates (Ferrari, Kohler, Fogassi, & Gallese, 2000; Rosati et al., 2016; Rosati & Santos, 2017; Teufel, Alexis, Clayton, & Davis, 2010; Tomasello et al., 2001).

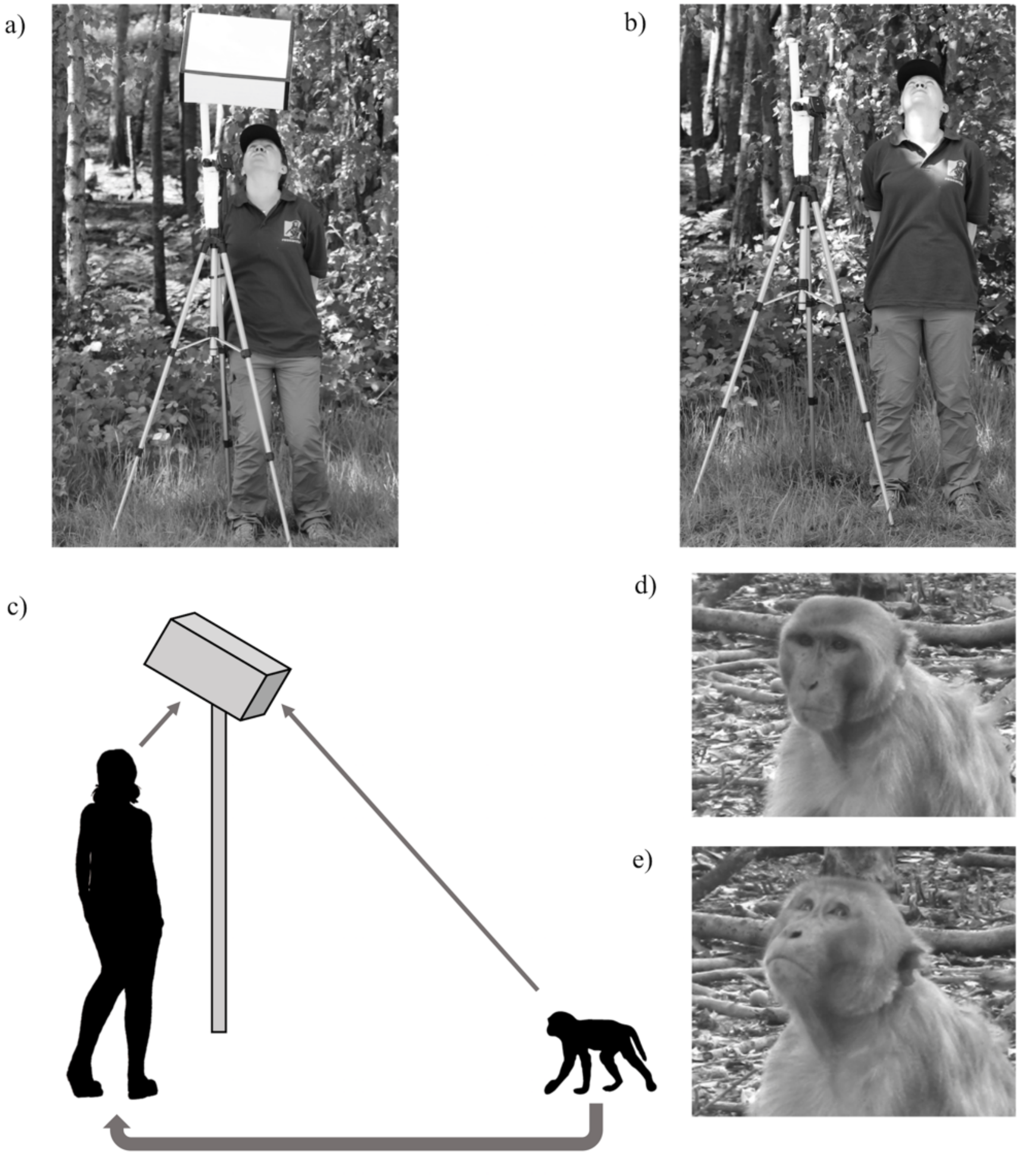

Figure 1: Setup for Study 1: Overhead barrier. (a) In the barrier condition, the demonstrator's line-of-sight is blocked by an overhead barrier. (b) In the no barrier condition, the demonstrator looked at the sky. (c) Diagram of setup. In order to see the target of the demonstrator's gaze in the barrier condition, monkeys had to approach the apparatus. (d) Video still example of the subject looking at the demonstrator at the start of a trial. (e) Video still of a monkey looking upwards.

Procedure

In sessions, Experimenter 1 (E1) identified a monkey who was sitting calmly. Condition was randomly assigned based upon a pre-designated list carried by Experimenter 2 (E2). Next, E1 placed the apparatus 2-3m from the monkey and stood to the side of the apparatus (see Figure 1). From their initial position, monkeys could observe the apparatus and E1, but could not see into the barrier. E2 stood approximately 6m away from the monkey, to film the monkey's response.

At the start of each trial, E1 attracted the monkey's attention by calling to them and snapping her fingers. When the monkey attended, she said 'now' and looked directly upwards (into the box in the *barrier* condition, or parallel to the stick in the *no barrier* condition; see Figures 1a-b). The 10 sec *looking phase,* timed with a stopwatch by E1, began when she said 'now'. This phase was used to assess if monkeys looked upwards after the demonstrator did (see Figure 1d-e for examples). After E1 looked up for ten seconds, the timer beeped and the *approach phase* began. This phase allowed us to assess if monkeys reoriented by approaching the apparatus, within a distance where they could see into the box in the *barrier condition*. Here, E1 turned around and walked approximately 7m away from the monkey (to stand behind E2), so the monkey could approach without being in close proximity to E1. Monkeys had one minute to approach. Subjects had to complete the initial 10s *looking phase* to be included.

Exclusions

Occasionally, monkeys who were approached for testing failed to produce scorable responses. For example, they sometimes failed to observe the demonstrator look up in the *looking phase,* or were displaced by other monkeys before they could approach. To assess this, a blind coder scored which sessions should be excluded. For the *looking phase,* five individuals were scored as not observing the demonstrator's looking demonstration (n=5); an additional 2 monkeys were excluded at time of test because of apparatus failure or experimenter error (e.g., the apparatus fell down). For the *approach phase*, 15 additional individuals were excluded during video coding (following similar criteria described in (Rosati & Santos, 2016) because another monkey displaced the subject before they made a response (n=1), another monkey tampered with the apparatus (n=11), or the subject left the testing area before the *approach phase* began (n=1); an additional 2 subjects were excluded due to apparatus failure. These individuals were included in the looking analyses. These exclusions resulted in a final sample of 31 subjects in the *barrier condition*, and 33 in the *no barrier condition* for looking phase analyses; and 25 monkeys in the *barrier* condition, and 24 in the *no barrier* condition for approach analyses.

Coding and reliability

Two independent coders scored responses of the final set of 64 subjects. We clipped out the 10s *looking phase* and the minute-long *approach phase* to code them separately. Each video clip was assigned a random trial ID, so coders could score looks blind to condition. The barrier was inherently visible in the *approach phase,* but coders were blind to the monkey's initial response in the *looking phase*. To code the *looking phase* responses, each coder marked the trial start (when E1 said 'now') and coded the subsequent 10s frame-by-frame. Following previous work (Rosati et al., 2016; Rosati & Santos, 2017), we coded:

(1) whether the individual *looked up* towards the sky or not from their initial starting position, as a binomial response. This is based on changes in monkey's head and/or eye direction (see Figure 1d-e). This was our key measure in the look phase. We predicted that the monkeys would look up

more in the *no barrier* condition, because they could see the target location of the demonstrator's gaze, but would be less likely to produce this response when it did not allow them to see the location where the demonstrator was looking.

(2) total *duration of looking* up in seconds; we predicted that monkeys would look up longer in the *no barrier* condition in order to better observe what the demonstrator was looking at.

(3) *latency to look up* in seconds; we predicted that the monkeys would look up sooner following the demonstrator's movements in the *no barrier* condition where monkeys could see the target location of demonstrator's gaze.

(4) the *number of discrete looks up* as a count response; we predicted that the monkeys would look up more times in the *no barrier* condition in order to better identify what E1 was looking at, since they could see the target location of the experimenter's gaze in this condition.

The reliability coder had high reliability with the primary coder for these measures (*looking up*: K = 0.94; *duration of looking*: r_p= 0.98; *latency to look*: r_p= 0.89; *number of looks*: r_s= 0.94).

For the *approach phase*, we examined whether the monkeys reoriented to a position where they could see what the demonstrator looked in the barrier condition. In this naturalistic context it was difficult to assess whether the monkey actually looked into the barrier, so we used approaches within arm's distance of the apparatus as a proxy for reorientation that could be scored in a comparable way in both conditions. We therefore coded each one-minute *approach phase* clip for:

(1) whether the monkey *approached* within arm's distance of the apparatus as a binomial response (see Movie S1). This was our key measure in the approach phase; we predicted that the monkeys would preferentially approach the apparatus in the *barrier* condition because reorientation was necessary to see the target location of the demonstrator's gaze in this condition.

(2) the *latency to approach* within an arm's distance of the apparatus in seconds; we predicted that if the monkeys' approach response reflected attempts to look at the target of E1's gaze, they would approach more quickly in the *barrier* condition. The reliability coder had high reliability with the primary coder for these measures (*approaching*: K = 1.0; *latency to approach*: r_p= 0.98)

Statistical analyses

We analyzed the data in R v3.4.1 (R Development Core Team, 2017). We used logistic regressions implemented with the *glm* function to examine propensity to look upwards or approach; linear regressions to examine total looking time and latency to approach; and Poisson regressions to analyze number of looks, a count measure. The looking latency data was heavily right skewed, so we used an inverse Gaussian distribution (inverse link function) in accordance with recommendations for skewed reaction time data (Harald Baayen & Milin, 2010; Lo & Andrews, 2015). For all analyses, we first constructed a base model that accounted for subject's *age* and *sex*, which have been shown to affect gaze-following responses in prior studies (Rosati et al., 2016; Rosati & Santos, 2017). We then added in condition as a predictor, and examined whether model fit improved using likelihood ratio tests (Bolker et al., 2009); here significant improvement in fit indicates the predictor should be included in the model. We also report *Akaike information criterion* (*AIC*); lower AIC values indicate relatively better model quality.

Data availability

Data from both studies are available on Dryad Digital Repository.

Results

We examined monkeys' propensity to look upwards across conditions. During the *looking phase*, M = 57.58% of monkeys looked up in the *no barrier* condition, whereas only 32.26% of monkeys looked up in the *barrier* condition (see Fig 2a). Including *condition* significantly improved model fit (LRT: 2 = 4.31, df = 1, p = 0.04; AIC = 85.21 compared to 87.82 in base model). The full model also showed a nonsignificant trend that more males than females looked up, and more younger monkeys than older monkeys looked up (see Table 1). Importantly, in addition to accounting for age and sex in the models, there were similar numbers of males in both conditions (19 in each), and there was no difference in subjects' age between conditions (mean age barrier = 7.69, mean age no barrier = 7.17; t_{62} = 0.39, p > 0.69). These demographic characteristics cannot account for the condition effect.

Next, we looked at the total duration of time that monkeys spent looking up. We included only trials where the monkey did look up (10 in *barrier* and 19 in *no barrier*): in the *barrier* condition, monkeys looked up for 1.65s on average, and for 2.52s in the *no barrier* condition. Adding *condition* did not significantly improve model fit (LRT: 2 = 2.28, df = 1, p = 0.35; AIC = 116.21 compared to 115.20 for the base model).

We found similar results for latency to look and number of total looks: including condition as a predictor did not improve model fit (latency to look: 2 = 0.53, df = 1, p = 0.21, AIC = 105.57 compared to 104.3 for the base model; number of looks: 2 = 0.00, df = 1, p = 0.98, AIC = 81.95 compared to 79.92 for the base model). Overall, these results indicate that the key difference across conditions concerned the monkeys' overall propensity to look up or not, not these other characteristics of their gazing response if they did look up.

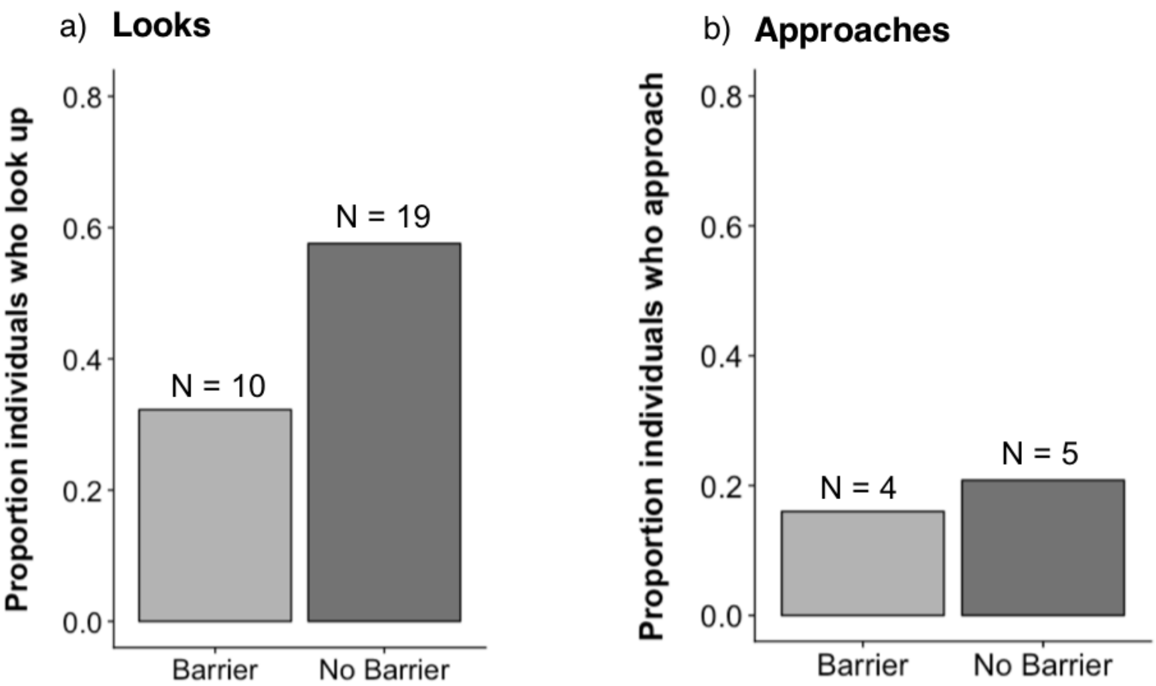

Figure 2: Looks upward and approaches in Study 1 (overhead barrier) (a). Proportion of individuals who looked upward during the looking phase. (b). Proportion of monkeys who approached the apparatus during the approach phase.

Predictor	**Estimate**	***Z***	**P-value**
Sex (reference: *female*)	1.071	1.826	0.068
Age (in years)	-0.109	-1.882	0.060
Condition (reference: *barrier*)	1.123	2.029	0.043

Table 1: Predictors of looking responses in Study 1 (overhead barrier). Parameters from the full model predicting looks upward as a binary response. This model was compared to a base model that included only sex and age as predictors. Baseline reference

We then analyzed the monkeys' approaches. In the *barrier* condition, monkeys approached on 16.00% of trials; and on 20.83% of trials in the *no barrier* condition. Including *condition* did not significantly improve model fit (2 = 0.19, df = 1, p = 0.66, AIC = 46.58 compared to 44.77 in base model; see Table 2). We also examined monkeys' *latency to approach.* For this analysis we only included those trials where the individual did approach; 4 in the *barrier* condition, and 5 in the *no barrier* condition. On average, monkeys took 17.12s to approach in the *barrier* condition, and 13.59s in the *no barrier* condition. Including condition did not improve model fit (2 = 0.00, df = 1, p = 1.00, AIC = 60.95 compared to 58.95 for the base model). Overall, monkeys did not preferentially reorient when their view of the demonstrator's visual target was blocked.

Predictor	**Estimate**	***Z***	**P-value**
Sex (reference: *female*)	-0.925	-1.057	0.290
Age as covariate	-0.206	-1.630	0.103
Condition (reference: *barrier*)	0.356	0.434	0.664

Table 2: Predictors of approaches in Study 1 (overhead barrier). Parameters from the full model predicting approaches to the apparatus upward as a binary response. Baseline reference for predictors indicated in table.

Discussion

These results indicate that rhesus monkeys were more likely to look upwards when they could see the target location of the demonstrator's attention from their initial position. This suggests that rhesus monkeys can utilize information about another individual's line-of-sight to modulate gaze-following. However, the monkeys did not preferentially reorient to view the target location by approaching in the *barrier* condition, and did not approach very frequently. One possibility is that monkeys were not motivated to view what the demonstrator was looking at, unlike children and apes tested in similar paradigms (Bräuer et al., 2005; Moll & Tomasello, 2004; Okamoto-Barth et al., 2007). However, note that our study differed from prior work by using an overhead barrier. This allowed us to examine propensity to look up and approaches as two different dependent measures, but could have made it more difficult for the monkeys to reorient to locate the demonstrator's visual target. From a motivational perspective, monkeys might be less likely to reorient to look into an overhead barrier, if they do not expect an interesting stimulus to be located there. They might expect any interesting stimuli to have ‘fallen out’ given the boxes’ orientation to the ground– although insects or hanging fruit could have been present, or items stuck to the inside of the box. Additionally, the overhead setup made it challenging to code looks into the box if they approached. In Study 2, we therefore developed a paradigm that was more analogous to prior work with apes.

Study 2: Reorienting around a barrier

In Study 2, we examined monkeys’ responses to a human demonstrator looking downwards behind an apparatus. In the *barrier* condition the monkey’s view of the demonstrator’s target of gaze was blocked by an occluder, whereas in the *no barrier* condition the demonstator looked behind a ‘window frame’ in the same location, so the monkeys also could already see where the demonstrator looked from their initial position. We predicted that if the monkeys understood the demonstator’s line-of-sight, they should preferentially approach and look behind the apparatus in the *barrier* condition in order to observe the location where the demonstrator had looked.

Methods

Subjects

Our final sample was 59 rhesus monkeys from the same population as Study 1 (41 males and 18 females, ranging from 0.84 to 18.41 years). Nine monkeys in our final sample also participated in Study 1, but were naïve to the particular procedure used here. To our knowledge there have been no prior studies of gaze-following utilizing these kinds of barriers in this population, although these monkeys have experienced studies involving boxes or other apparatuses placed on the ground (Marticorena et al., 2011; Martin & Santos, 2014; Santos et al., 2006).

Apparatus and setup

Monkeys experienced one of two conditions in a between-subjects design in which they saw a demonstrator look behind an apparatus on the ground (see Figure 3 for example.). The apparatus was a box (76 cm high, 27 cm wide, 28 cm deep; see Fig 3). In the *barrier* condition, the apparatus blocked the monkey's view of what she was looking at. In the *no barrier* condition, we removed the front panel of the apparatus facing the money so they could directly see where the demonstator looked from their starting position.

Procedure

In session, experimenter 1 (E1) first identified a calm monkey for testing, then condition was randomly assigned by experimenter 2 (E2) based upon a pre-assigned list. Next, E2 set up the apparatus approximately 2-3 m from the monkey, before standing approximately 6 m away from the monkey to film their response. E1 then approached the apparatus to stand beside it, such that the apparatus was close to E1 and oriented away from the subject. E1 then produced the looking demonstration. Each session then had two phases. In an initial 5s *looking phase* the demonstrator looked behind the apparatus; note that we did not code any responses from the monkey during this phase, unlike in Study 1. This was followed by a 30s *approach phase*. We used a 30s long approach phase, rather than a minute-long approach phase, as in Study 1, to minimize the possibility of interference by other monkeys. The average time to approach in Study 1 was 15.16s, so this gave sufficient time to approach. To start the trial, E1attracted the monkey's attention by calling and snapping her fingers. When the monkey attended to her, she turned her head and shoulders to gaze directly behind the apparatus, while bending at the waist (see Figure 3). E1 held her pose for 5 sec, and then turned around and walked to stand behind E2 so that the monkey could approach the apparatus. The *approach phase* began as she straightened up to turn around. After 30s, E2 stopped filming and the trial ended. During the session, E2 filmed the monkey so that the monkey and apparatus were both in the shot.

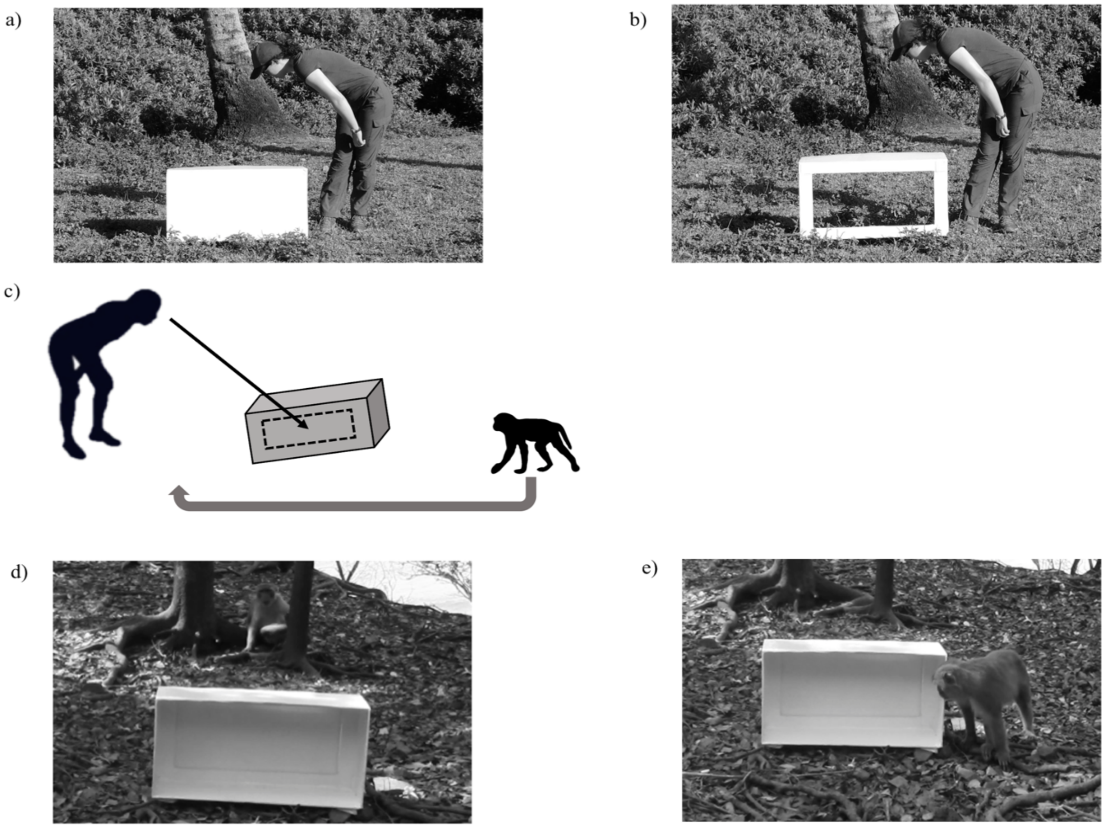

Figure 3: Setup for Study 2, Reorienting around a barrier. Demonstrator looking behind apparatus in the (a) barrier condition and (b) no barrier condition. (c) Diagram of setup. In order to look where the demonstrator had looked, the monkey has to approach behind the apparatus in the barrier condition. Monkeys in the no barrier condition could see the target location from their initial position because the front panel of the box was removed (dashed lines). Video stills of monkeys (d) in their initial position and (e) reorienting to look behind the apparatus.

Exclusions

Some of the monkeys that were approached for testing were not included in the final dataset, as in Study 2. A blind coder therefore watched all the sessions from videotape and scored whether such interferences made the session unusable. In total, 9 individuals were excluded from the approach measure because other monkeys displaced the subject (n=3) or tampered with the apparatus (n=6). This resulted in a final sample of 31 monkeys in the *barrier* condition, and 28 in the *no barrier* condition.

Coding and analyses

Two coders scored the sessions from video, using similar procedures to Study 1. We coded:

1. Whether the individual *approached* the apparatus (to within an arm's distance of the apparatus) or not as a binomial response. This was our key measure; we predicted that the monkeys should preferentially approach behind the apparatus to observe the target of her gaze in the *barrier* condition.
2. The *latency to approach* within an arm's distance of the apparatus; we predicted that if the monkeys' approach response reflected attempts to look at the target of E1's gaze, they would approach more quickly (shortly after the *looking phase* demonstration) in the *barrier* condition.
3. Whether individuals *looked* behind the apparatus or not as a binomial response; we predicted that if monkeys understand the demonstator's line of sight, they would preferentially look behind the apparatus in the *barrier* condition. We used looks behind the apparatus as a secondary code, and approaches as our primary measure. This is because

sometimes monkeys produced an approach response, but then another monkey interfered before they could produce a look response (2 of 10 trials with approaches).

The reliability coder had high reliability with the primary coder for all measures (*approaching*: K=0.94; *looking behind barrier*: K=0.91; *latency to approach*: r_P=1.0). We analyzed the data using the same general approach as for Study 1.

Results

In the *barrier* condition, 25.81% of the monkeys approached the apparatus, whereas only 7.14% approached in the *no barrier* condition (see Fig 4). Including *condition* as a predictor in our model significantly improved fit (LRT: 2= 4.31, df= 1, p= 0.04; AIC = 56.52 compared to 58.83 for the basic model): more monkeys approached when they could not see the target of the demonstrator's gaze from their initial position (see Table 3). As in Study 1, in addition to accounting for age and sex in the models we also randomly assigned subjects to condition while accounting for sex and age cohort. There were similar numbers of males in both conditions (20 in barrier, 21 in no barrier), and no difference in subjects' age between conditions (mean age barrier = 8.05, mean age no barrier = 8.31; t_{57}= 0.22, p > 0.82).

To analyze *latency to approach,* we only included trials where the individuals did approach. On average, monkeys took 12.66s to approach in the *barrier* condition (n = 8), and 26.27s to approach in the *no barrier* condition (n = 2). We found a non-significant trend for faster approaches in the *barrier* condition (LRT: 2 = 221.63, df = 1, p = 0.051; AIC = 73.89 compared to 76.81 for the base model).

Finally, we checked whether approaches did relate to looking behavior. For 7 of the 8 approach trials where looks were possible to code, the monkey clearly looked behind the apparatus, either by looking at this location from over the top of the apparatus (n=3) or by walking to one side and looking back behind the apparatus (n=3), or doing both (n=1). The main condition effect from the analysis of approach responses held when we analyzed looks instead of approaches (LRT: 2 = 4.98, df = 1, p = 0.03; AIC = 39.31 compared to 42.29 for the base model). This supports our interpretation of approaches as reflecting an attempt to observe the demonstrator’s visual target location behind the barrier.

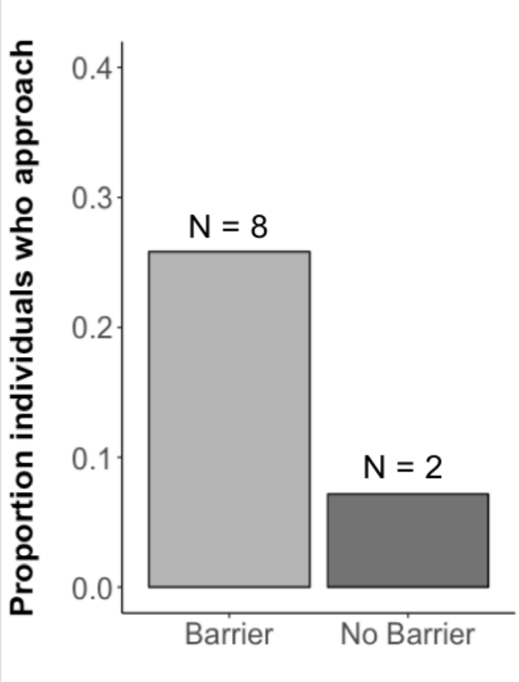

Figure 4: Approaches to the apparatus in Study 2 (reorienting around a barrier). Proportion of trials where monkeys approached the apparatus across conditions. Total number of individual monkeys showing each response per condition is indicated above the relevant bar.

Predictor	**Estimate**	***Z***	**P-value**
Age (as covariate)	0.034	0.408	0.684
Sex (reference: female)	0.808	0.910	0.363
Condition (reference: *Barrier*)	-1.605	-1.885	0.060

Table 3: Predictors for approaches in Study 2 (reorienting around a barrier). Parameters from the full model predicting approaches to the apparatus as a binary response. This model was compared to a base model that included only Sex and Age as predictors. Baseline reference for predictors indicated in table.

Discussion

Monkeys were more likely to approach and look behind an apparatus in the *barrier* condition when they could not initially see where the demonstrator was looking, compared to the *no barrier* condition where they could. This shows that rhesus monkeys can model other's the line-of-sight and use this information to re-orient. Notably, the monkeys in Study 1 did not preferentially approach the way they did in Study 2. One possibility is that reorienting in Study 1 was more difficult because the was overhead. By comparison, Study 2 used an apparatus placed upon the ground, more similar to past work with apes and children (Bräuer et al., 2005; Moll & Tomasello, 2004; Okamoto-Barth et al., 2007). Monkeys may also have more frequently experienced interesting stimuli upon the ground (such as food), so are subsequently more interested in approaching in that situation. Notably, however, approaches were infrequent in both studies. Thus, monkeys appear to understand that the target of the demonstrator's gaze was hidden by the barrier in that situation and responded accordingly, but were overall relatively unmotivated to actually approach to observe the target of her gaze.

General discussion

Across two studies, we found that rhesus monkeys accounted for whether they could see where others are looking, exhibiting cognitive control over their gaze following responses rather than just reflexively matching a shift in other's attention. In Study 1, more monkeys looked up in the *no barrier* condition when doing so enabled them to observe the same overhead location where the actor was looking, compared to a *barrier* condition where the actor's line-of-sight upwards was blocked. In Study 2, more monkeys approached an apparatus on the ground that a human had looked behind in the *barrier* condition when their initial view of the location was blocked, than a *no barrier* condition where the apparatus was a window frame. However, rhesus monkeys may not be especially motivated to see what other individuals are looking at in these contexts, as suggested by the low rates of approaches in both studies. Overall, these results show that gaze-following in rhesus macaques accounts for at least some aspects of what others actually see. The current work does not support the interpretation that monkeys engaged in reflexive gaze responses in response to simple directional head or eye cues (Friesen & Kingstone, 1998; Hood, Willen, & Driver, 1998; Shepherd, 2010), because this would have produced identical responses regardless of whether the actor's line of sight was blocked by a barrier. This builds on prior work showing that rhesus monkeys exhibit basic co-orienting responses (Deaner & Platt, 2003; Emery et al., 1997; Rosati et al., 2016; Rosati & Santos, 2017; Tomasello et al., 2001).

As such, our results indicate that even extremely despotic primate species can use cognitive abilities outside of competitive situations to infer where others look, in contrast to some theoretical proposals (Byrne & Whiten, 1989; Hare, 2001; Hare & Tomasello, 2004; Lyons & Santos, 2006). Unlike prior work with rhesus monkeys, our paradigm did not involve competitive cues, did not involve food, and did not invoke a scenario where the subject needed to 'outwit' the demonstrator.

This work thus adds to growing evidence that some primate species can use social cognitive abilities across many different social contexts (Bulloch et al., 2008; Crockford, Wittig, Mundry, & Zuberbühler, 2012; Grueneisen, Duguid, Saur, & Tomasello, 2017; Hopkins et al., 2007; Hostetter et al., 2007; Melis & Tomasello, 2013; Yamamoto, Humle, & Tanaka, 2012). However, we also found that rhesus monkeys did not seem particularly motivated to see where others were looking in this non-competitive context. While rhesus monkeys adjusted their gaze-following responses depending on whether they could also see where the demonstrator had looked, they reoriented at low rates in both studies. Importantly, the monkeys clearly used information about the actor's line-of-sight in both studies: more individuals looked up in the *no barrier* condition in Study 1, and more approached to view behind the barrier in Study 2. Thus, it is unlikely that they approached infrequently due to a (non-motivational) cognitive inability to assess where others look. Monkeys in this population also approach and search novel apparatuses at high rates when they think there is hidden food (Flombaum & Santos, 2005; Rosati & Santos, 2016; Santos et al., 2006). Moreover, both infants and apes will approach to look behind a barrier that a demonstrator looks behind in a similar situation (Bräuer et al., 2005; Butler, Caron, & Brooks, 2000; Moll & Tomasello, 2004; Okamoto-Barth et al., 2007). An important question is therefore why the rhesus monkeys were relatively unmotivated to approach and observe where the demonstrator was looking in these contexts.

One possibility is that monkeys were uninterested in approaching because the demonstrator was a human rather than a conspecific. However, this interpretation is inconsistent with the fact that monkeys did frequently follow the demonstrator's gaze in Study 1, demonstrating that they do pay attention to where humans look. More generally, macaques follow the gaze of both human and conspecific demonstrators (Ferrari et al., 2000; Rosati et al., 2016; Rosati & Santos, 2017;

Teufel et al., 2010; Tomasello et al., 2001), and most evidence that these rhesus can account for other's visual perspective or knowledge states comes from studies involving interactions with a human (Drayton & Santos, 2017; Flombaum & Santos, 2005; Marticorena et al., 2011; Martin & Santos, 2014; Santos et al., 2006). Moreover, prior work showing that great apes can follow gaze around barriers also involved human actors (Bräuer et al., 2005; Okamoto-Barth et al., 2007). Therefore, it is unlikely that the use of a human demonstrator alone can explain the rhesus monkeys' low motivation to approach and observe where the actor had looked.

Another possibility is that rhesus monkeys' low levels of social tolerance drives this response. Several proposals have argued that tolerant species exhibit more robust social cognitive abilities than do despotic species, the idea being that these social cognitive skills can facilitate cooperative or prosocial interactions (Burkart, Hrdy, & Van Schaik, 2009; Hare, 2017; Hare & Tomasello, 2005; Joly et al., 2017). For example, humans frequently use gaze as a cooperative cue to partake in joint attentional interactions (Tomasello, 1995; Tomasello & Carpenter, 2007) and when providing pedagogical information (Csibra & Gergely, 2009; Senju & Csibra, 2008). This raises the possibility that while competitive primate species can flexibly use social cognitive abilities, humans may be uniquely motivated to use these skills to engage in interactions where they share attention–for example, by looking at the same location or object. This shift may contribute to the development of human-unique social abilities.

One important question for future research therefore concerns how rhesus monkeys respond to the same gaze cues across different contexts. In this study, we tried to establish a neutral interaction, and therefore did not use cues that were either explicitly competitive or cooperative in nature. For example, the experimenters never handled food, and never produced emotional or vocal signals commonly used in either agonistic of affiliative contexts. Yet previous work has established that closely-related macaque species with different social style may respond differently to gaze cues depending on these kinds of signals, or have different reactions particular social contexts. For instance, competitive rhesus monkeys gaze-follow differentially according to rank (Shepherd et al., 2006), while more tolerant Barbary macaques (*Macaca sylvanus*) do not (Teufel et al., 2010). Crested macaques (*Macaca nigra*), another tolerant species, respond especially quickly to gaze cues from conspecific friends versus non-friends (Micheletta & Waller, 2012). In contrast, long-tailed macaques (*Macaca fascicularis),* a competitive species, follow gaze more frequently when an actor exhibits a submissive facial expression versus an affiliative expression (Goossens, Dekleva, Reader, Sterck, & Bolhuis, 2008). Future research should therefore compare how rhesus monkeys react to gaze cues in actively cooperative or affiliative situations, as well as how social tolerance across species may shape social cognitive processes more generally.

Finally, a key question invoked by our result is whether these kinds of gaze-following abilities scaffold later developing cognitive skills in primates: to what degree are the building blocks of human social cognitive development shared with other species? While rhesus macaques have demonstrated a sophisticated understanding of the mental states of other individuals (Drayton & Santos, 2016, 2017; Flombaum & Santos, 2005; Marticorena et al., 2011; Martin & Santos, 2014; Santos et al., 2006), their social cognitive abilities appear to be different from that of humans. For instance, rhesus monkeys do not demonstrate false belief understanding (Marticorena et al., 2011; Martin & Santos, 2014), suggesting that cognitive gaze-following is not a sufficient condition for the development of human-like social cognitive abilities. One possibility is that gaze-following follows a different developmental trajectory in rhesus monkeys, reflecting a different developmental role. While previous work has shown that basic co-orienting follow a similar developmental trajectory in rhesus monkeys and humans (Rosati et al., 2016), it remains unclear whether this is also true for other social cognitive abilities such as inferring other's line-of-sight, visual perspective-taking, or knowledge attribution. Analyzing the role of gaze-following in shaping the development of these abilities will shed light upon the origins of human-unique social cognitive abilities, and in particular how divergences in developmental trajectories influence mature social cognitive skills across species (Rosati, Wobber, Hughes, & Santos, 2014).

In conclusion, rhesus monkeys can flexibly model a demonstrator's line-of-sight in a neutral gaze-following context, and do not just reflexively shift attention to match the direction of other's gaze. Our findings demonstrate that even highly despotic primate species are not constrained to using social cognitive processes in competitive contexts. However, rhesus monkeys show a low motivation to move to observe what others can see. This highlights that the ability to infer where others are looking, and the motivation to engage in social interactions by using such skills, may be dissociated across species. This has important implications for our understanding of the interplay between tolerance and social cognition in the evolution of human-unique cognitive abilities that hinge on new forms of tolerant cooperative interactions in our own species.

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Chapter 3: Sensitivity to Line-of-Sight in Tolerant Versus Despotic Macaques

Abstract

Complex social life is considered important to the evolution of cognition in primates. One key aspect of primate social interactions concerns the degree of competition that individuals face in their social group. To examine how social tolerance versus competition shapes social cognition, we experimentally assessed capacities for flexible gaze-following in more tolerant Barbary macaques (*Macaca sylvanus*) and compared to prior data from despotic rhesus macaques (*Macaca mulatta*). Monkeys observed an actor look upwards either into an overhead *barrier*, so monkeys could not directly see the target of gaze without reorienting, or when *no barrier* was present, so monkeys could observe the target location by also gazing upwards. Both species (N= 58 Barbary macaques, 64 rhesus macaques) could flexibly modulate their gaze responses to account for the demonstrator's line-of-sight, looking up more often when no barrier was present, and this flexible modulation declined with age in both species. However, neither species preferentially approached to look inside the barrier when their view of the target location was obscured, although rhesus macaques approached more overall. This pattern suggests that both tolerant and despotic macaques exhibit similar capacities to track other's line-of-sight, and do not preferentially reorient their bodies to observe what an actor looks at in this situation. This contrasts with other work indicating that competitive primates are especially adept at some aspects of theory of mind. Thus, it is important to understand both the similarities and differences in the social cognitive abilities of primates with different social styles

Introduction

A dominant explanation for the evolution of social intelligence across primates concerns the critical role of complex social life (Byrne & Whiten, 1990; Dunbar, 1998; Hare, 2017; Humphrey, 1976; Jolly, 1966). That is, the demands of group living selected for cognitive skills which allow individuals to respond adaptively to others' behavior. Direct comparisons of cognitive abilities across species with different social characteristics are critical to establish how sociality shapes cognition. In particular, contrasting the cognitive abilities of species that are closely matched for other variables such as phylogenetic history, yet differ in regard to a particular social characteristic, can provide fine-grained insights into how certain aspects of sociality impact cognitive evolution (MacLean et al., 2012; Rosati et al., 2017).

A species' degree of tolerance versus despotism is one social characteristic hypothesized to shape the evolution of sophisticated social cognitive abilities. Many proposals have highlighted the role of competitive interactions in driving the evolution of sophisticated social cognition: individuals with greater social intelligence may be better able to socially outmaneuver conspecifics in order to get access to valuable resources such as food and mates. For example, social intelligence may have emerged to enable individuals to outcompete or deceive group-mates (Byrne & Corp, 2004; Byrne & Whiten, 1990; Hare, 2001; Lyons & Santos, 2006). Thus, this *competition hypothesis* predicts that species characterized by high levels of competition or aggression would demonstrate more robust complex social cognitive abilities. Yet competing proposals have instead highlighted the role of tolerant or cooperative interactions in driving sophisticated social cognition, enabling individuals to establish close social ties and accrue benefits from cooperation (Burkart et al., 2009; Cheney et al., 1986; Hare, 2017). That is, an increase in social tolerance is thought to 'open the door' to cooperative behavior such that new social cognitive abilities that facilitate effective coordination can emerge (Burkart et al., 2009; Hare, 2017). This *tolerance hypothesis* predicts that species characterized by more tolerant or affiliative interactions would demonstrate more robust complex social cognitive abilities, a function that is proposed to have been especially important in the evolution of uniquely-human social cognition (Hare, 2017).

Currently, there is some evidence to support both viewpoints. In terms of the competition hypothesis, observations of wild primates suggest that competitive behaviors such as tactical deception may depend on theory of mind abilities (Kummer, 1982; Whiten & Byrne, 1988), and the presence of these competitive deceptive interactions within natural behavioral repertories shows a positive relationship with brain size (Byrne & Corp, 2004). Second, experimental studies indicate that many of the most impressive demonstrations of social cognitive abilities in primates have come from experiments that have utilized competitive interactions. This includes demonstrations of visual perspective-taking and knowledge in chimpanzees (Hare et al., 2000, 2001; Kaminski et al., 2008), rhesus monkeys (Flombaum & Santos, 2005), and ring-tailed lemurs (Bray et al., 2014; Sandel et al., 2011) facing competition from conspecifics or human actors. Along the same lines, while many primates struggle to use cooperative social cues such as gaze or pointing to locate hidden food (capuchins; Anderson et al., 1995, chimpanzees; Call et al., 2000; Call et al., 1998; Hare & Tomasello, 2004; Herrmann & Tomasello, 2006; Povinelli et al., 1999; Tomasello et al., 1997, rhesus macaques; Anderson et al., 1996, orangutans; Itakura & Tanaka, 1998), they may be more successful at using social cues in matched competitive situations where an individual is actively reaching for food instead (Hare & Tomasello, 2004; Herrmann & Tomasello, 2006). Finally, many of the species showing sophisticated social cognitive abilities—such as chimpanzees, rhesus macaques and ring-tailed lemurs—also exhibit higher levels of competition in their natural groups (Flombaum & Santos, 2005; Hare et al., 2000, 2001; Kaminski et al., 2008; Sandel et al., 2011; Santos et al., 2006), whereas more tolerant species may not in similar setups (capuchins; Costes-Thiré, Levé, Uhlrich, Pasquaretta, et al., 2015; Hare et al., 2003, common marmosets; Burkart & Heschl, 2007, Tonkean macaques; Costes-Thiré, Levé, Uhlrich, De Marco, et al., 2015; Costes-Thiré, Levé, Uhlrich, Pasquaretta, et al., 2015).

Conversely, evidence for the tolerance hypothesis comes from studies of cooperative interactions. For example, studies across a number of species have demonstrated that inter-individual tolerance is critical to effective cooperation (chimpanzees; Melis et al., 2006, Suchak et al., 2014, Japanese macaques; Kaigaishi et al., 2019, hyaenas; Drea & Carter, 2009, marmosets; Werdenich & Huber, 2002, ravens; Massen et al., 2015, rooks; Seed et al., 2008, hyaenas; Drea & Carter, 2009, marmosets; Werdenich & Huber, 2002). In a cross-species comparison, more tolerant bonobos were able to sustain mutualistic cooperation in contexts where chimpanzees could not, such as when the food reward was highly monopolizable (Hare et al., 2007). Second, experimental evidence indicates that socially tolerant primate species may be predisposed to be attentive to social cues such as eye contact and gaze, even when these cues are neutral rather than framed as explicitly cooperative. For example, more tolerant bonobos pay more attention to the faces and eyes of conspecifics (Kano et al., 2015), and follow the direction of a demonstrator's gaze more frequently (Herrmann et al., 2010) than do more chimpanzees. Similarly, competitive rhesus macaques make less eye contact than do more tolerant stump-tailed and crab-eating macaques (Thomsen, 1974), and show age-related declines in gaze-following unlike more tolerant Barbary macaques (Rosati & Santos, 2017). Third, more tolerant species may be more skilled at utilizing communicative cues. In particular, tolerant macaque species outperform intolerant species in a 'pointing cups' task, where they must produce communicative cues towards the demonstrator in order to succeed (Joly et al., 2017). Along similar lines, dogs and experimentally-domesticated foxes—which tend to show more tolerant and less aggressive reactions to humans than their wild-type sister taxa—are able to successfully utilize social communicative cues, whereas wolves and control-line foxes do not (Hare et al., 2002, 2005; Hare & Tomasello, 2005; Kaminski & Nitzschner, 2013; Topál et al., 2009). Finally, humans may represent an extreme example of this proposal, as humans exhibit high levels of social tolerance alongside highly complex social cognitive abilities (Boyd & Richerson, 2009; Csibra & Gergely, 2011; Henrich & Henrich, 2007; Siposova et al., 2018; Tomasello et al., 2005, 2007; Tomasello & Carpenter, 2007). Indeed, high levels of basic gaze sensitivity is linked to more sophisticated social cognitive abilities in humans (Csibra & Gergely, 2011; Flom et al., 2017; Senju & Johnson, 2009; Siposova et al., 2018).

How can these competing accounts be reconciled? One critical distinction may be between *motivations* or interest to attend and respond to others' social cues, versus *cognitive* abilities to represent and act upon other's mental states (Kano et al., 2015). For example, while there is strong evidence that more tolerant species show attentional biases towards social stimuli (chimpanzees versus more tolerant bonobos: Kano et al., 2015; Kano & Call, 2014a; macaques: Thomsen, 1974), and preferentially respond to such stimuli (chimpanzees vs bonobos: Herrmann et al., 2010; macaques: Rosati & Santos, 2017), it is unclear if tolerant species actually have more robust social cognitive abilities to reason about this social information. In fact, studies contrasting specific theory of mind abilities have frequently found similar performance across species. For example, more tolerant bonobos and more competitive chimpanzees show similar evidence for intention understanding (Kano & Call, 2014b, although for bonobo advantage see: Herrmann et al., 2010); understanding others' visual access (Grueneisen et al., 2017); and implicit false belief reasoning (Krupenye et al., 2016), and chimpanzees can also outperform bonobos in some social cognition assessments (Girard-Buttoz et al., 2020, MacLean & Hare, 2012). In a cognitive battery contrasting the performance of several macaque species that differ in tolerance, these species all showed similar understanding of attentional states, intention-reading, and gaze following, although the tolerant species were better at producing communicative cues to attain food (Joly et al., 2017). Finally, both rhesus and Barbary macaques show similar predictions about how others will act based on what they previously saw (Arre et al., 2021). Accordingly, tolerance may promote abilities to produce and respond to other's basic social cues, as these cues can be used for mutual benefit (Tomasello et al., 2007), whereas sophisticated social cognitive abilities may be favored in competitive contexts as they can be used to outwit others (Byrne & Whiten, 1990).

In the current work, we compared social cognition in macaque species differing in social tolerance, using a 'geometric' gaze-following paradigm that can assess both basic propensities to respond to other's gaze cues, as well as the cognitive flexibility of this response. While some species exhibit fairly reflexive gaze-following responses where they seem to automatically match the direction of other's eye and head cues regardless of context (Deaner and Platt 2003; Friesen and Kingstone 1998; Ruiz et al. 2009; Shepherd 2010), other species are able to reason about social and physical factors (such as the presence of a barrier) that determine what the other individual can see and modulate their own responses accordingly. For example, all great apes account for the presence of barriers when following gaze, and thus will not simply match the gaze direction of others when doing so does not allow them to observe the target location (Bräuer et al. 2005; Butterworth and Jarrett 1991; Okamoto-Barth et al. 2007; Tomasello et al. 2001). Thus, this kind of sensitivity indicates that animals are not only reflexively following other's gaze (Bettle & Rosati, 2019; Rosati and Hare 2009; Shepherd 2010).

We therefore tested the flexibility of gaze-following responses (whether monkeys could account for the presence of a barrier), as well as overall responsivity to gaze cues. We tested a sample of semi-free-ranging Barbary macaques, and compared this to prior data from rhesus macaques tested in the same paradigm (Bettle & Rosati, 2019). While Barbary macaques are characterized by high levels of social tolerance, exhibiting a relaxed dominance hierarchy, more affiliative interactions and reconciliation after aggression, rhesus macaques are highly despotic with a steep dominance hierarchy and severe aggression (Thierry, 2000, 2007). Prior work indicates that while both rhesus macaques and Barbary macaques follow others' gaze (Drayton & Santos, 2017; Rosati et al., 2016; Teufel et al., 2010; Tomasello et al., 2001), Barbary macaques maintain a higher propensity to respond to basic gaze cues over the lifespan than do rhesus (Rosati & Santos, 2017). Yet while rhesus monkeys are also sensitive to other's line-of-sight (Bettle & Rosati, 2019), as well as to other's knowledge state (whether or not she has previously seen the object she is looking towards (Drayton & Santos, 2017), and can engage in both visual perspective-taking and knowledge-attribution (Flombaum & Santos, 2005; Horschler et al., 2019; Marticorena et al., 2011; Martin & Santos, 2014; Santos et al., 2006), there has been no work examining whether Barbary gaze-following also engages these more flexible, mentalistic mechanisms. Notably, while rhesus monkeys are able to account for other's line-of-sight, they do not appear particularly willing to re-orient their bodies to view what others see (Bettle & Rosati, 2019), which accords with this potential distinction between motivations to engage with others and cognitive flexibility of responses.

In the task, monkeys observed a human actor looking upwards in one of two situations. In the *no barrier* condition, the actor looked upwards towards the sky, so a monkey who also looked up could see the target location from their position. In the *barrier* condition, in contrast, the actor produced the same behavior, but her line-of-sight was blocked by an overhead barrier, so the only way for the monkey to see the target location was to move towards the apparatus to look inside the barrier. As in prior work, monkeys were presented with a neutral gaze cue that was not framed as an explicitly competitive or cooperative interaction (Bräuer et al. 2005; Butterworth and Jarrett 1991; Okamoto-Barth et al. 2007; Rosati et al., 2016; Rosati & Santos, 2017; Tomasello et al. 2001). For practical reasons, we utilized a human demonstrator in our task rather than a conspecific. Current work indicates that macaques follow the gaze of both human and conspecific demonstrators at similar rates (Ferrari et al. 2000; Rosati et al. 2016; Rosati and Santos 2017; Teufel et al. 2010; Tomasello et al. 2001). Further, most work demonstrating more sophisticated social cognitive skills in macaques, such as perspective-taking, have also used a human demonstrator (Arre et al., 2021; Drayton and Santos 2017; Flombaum and Santos 2005; Marticorena et al. 2011; Martin and Santos 2014; Santos et al. 2006). Use of a human demonstrator also allowed us to tightly control the actor's behavior across conditions, in a way that would not be feasible with conspecific demonstrators.

We used this setup to compare macaques' (1) overall *responsiveness* to other's gaze direction; (2) the cognitive *flexibility* of their responses accounting for other's line of sight; and (3) their tendency to *reorient* to view the actor's gaze target. To assess responsiveness to other's gaze, we examined how frequently each species looked up across conditions. To assess the cognitive flexibility of their gaze-following abilities, we examined whether these responses accounted for the demonstrator's line-of-sight by looking up more often in the *no barrier* condition. Finally, we assessed if either species were more like to preferentially approach to look into the box in the *barrier* condition, where reorientation is necessary to observe the target of the demonstrator's gaze. We predicted that the tolerant Barbary macaques would show more responsiveness to gaze cues and more motivation to approach compared to rhesus, but that both would demonstrate a similarly flexible response that accounted for the actor's line-of-sight.

Methods

Ethics statement

All applicable guidelines for the care and use of animals were followed, adhering to site-specific guidelines for animal research. All behavioral tests at Trentham Monkey Forest were approved by University of Michigan's Institutional Animal Care and Use Committee (IACUC protocol 8302). Behavioral tests at Cayo Santigao were approved by University of Puerto Rico Medical Sciences Campus' IACUC (protocol #A140116).

Subjects

Our final sample comprised 58 Barbary macaques living at the Trentham Monkey Forest, UK (34 males and 24 females; mean age 9.4 years ± SD = 7.2 years, ranging from 1 to 31 years old). These were compared to a sample of 64 rhesus monkeys living at the Cayo Santiago Field station, Puerto Rico (38 males and 26 females; mean age 7.4 years ± 5.3 years, ranging from 1.5 to 21.3 years). Both species had similar age distribution across conditions. The rhesus data was previously reported as part of prior work (see Bettle & Rosati, 2019). Monkeys at both sites can be identified via unique tattoos and facial and body features, as well as by ear notches at Cayo Santiago. At both sites, monkeys are semi-free-ranging and well-habituated to humans. For example, at Trentham Monkey Forest, monkeys range through a 60 acre forested area. They are habituated to staff who walk through the forest and provision food, as well as to researchers who observe the monkeys, and to tourists who walk through the area on defined paths that run around the site. At Cayo Santiago, monkeys range through the 38-acre forested island and are habituated to the presence of staff who walk through the forest and provision food, and to researchers who observe the monkeys. Thus, both populations of monkeys experience human observers walking through the site since their birth. Accordingly, monkeys from both populations have successfully participated in multiple prior cognition studies, including tasks involving gaze-following (Arre et al., 2021; Drayton & Santos, 2017; Rosati et al., 2016; Rosati & Santos, 2017), but both were naïve to the particular overhead barrier apparatus used in this study.

Apparatus and setup

Monkeys experienced one of two gaze-following conditions in a between-subjects design. In both conditions, the demonstrator looked upwards by rotating both her head and eyes (see Fig. 1). In the *barrier* condition, the demonstrator's line-of-sight was blocked by a barrier above her head (a box 40 cm long, 31 cm wide, and 15 cm deep that was propped on a stick atop of a tripod; total height 1.77 m). When the demonstrator looked upwards in this condition, she could see into the box, but the monkey could not from their position (see Fig 5a). In the *no barrier* condition, the demonstrator produced the same actions next to the tripod, but her line-of-sight was not blocked. As such, in this condition the monkeys could observe where she was looking without moving from their initial position. Following the methods of prior work (Bettle & Rosati, 2019; Rosati et al., 2016; Rosati & Santos, 2017), the apparatus was always set up close to a tree such that the demonstrator could feasibly be looking at something above her head.

Procedure

Procedures were identical to those reported in prior work (Bettle & Rosati, 2019). In test sessions, the demonstrator (experimenter 1, E1) and the camera person (experimenter 2, E2) approached a calmly-sitting monkey. Once a potential monkey was located, condition was randomly assigned based upon a pre-designated list carried by E2. Next, E1 set up the apparatus approximately 2-3 m away from the monkey. E2 stood approximately 6 m away from the monkey, behind E1, in order to film the monkey's behavior.

To begin the trial, E1 attracted the monkey's attention by calling or snapping her fingers. When she had the monkey's attention, she said 'now' and looked directly upwards for 10s (into the box in the *barrier* condition, or parallel to the stick in the *no barrier* condition). She started a stopwatch at the same time as saying 'now' to time this *looking phase*. During this phase, E2 filmed whether the monkey looked upwards (see Fig 5e for example upwards look). After 10s, the stopwatch beeped to mark the start of the *approach phase*. Here, E1 turned around and walked to stand behind E2. This allowed the monkey to approach the apparatus without being in close proximity to E1. Monkeys were filmed for 1 minute, to assess whether they approached the apparatus.

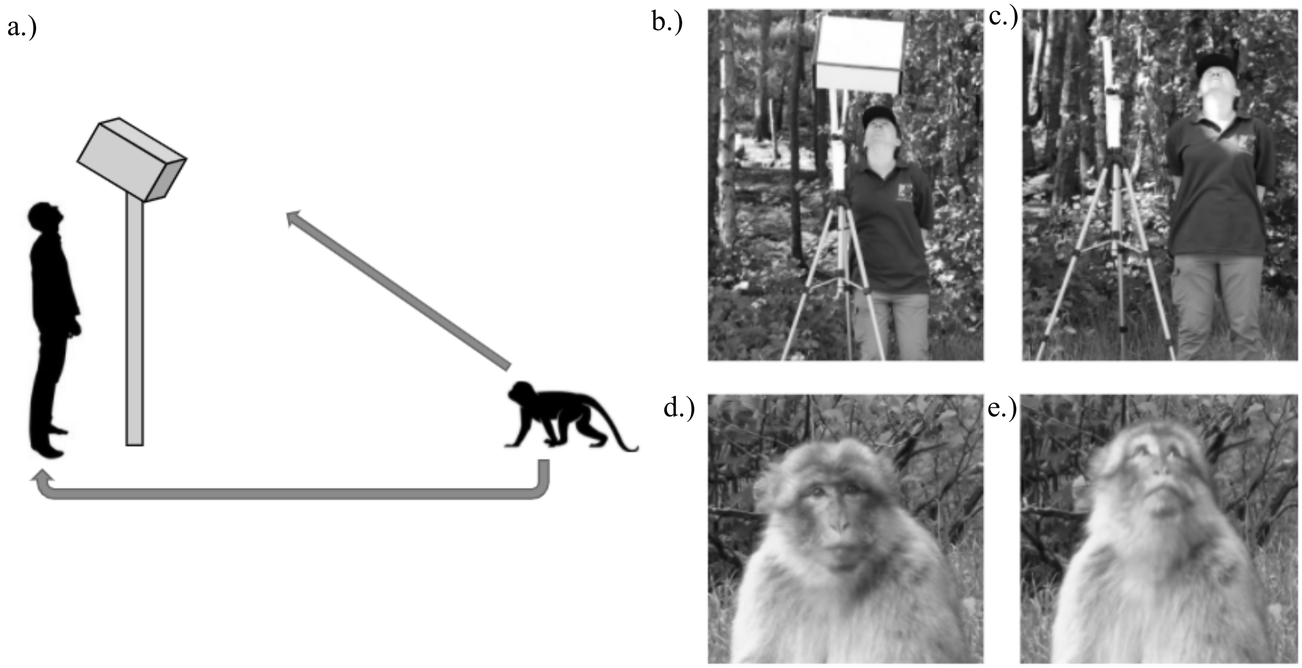

Figure 5: Experimental setup. (a) Diagram of setup. While monkeys could see the actor's target of attention from their starting position in the no barrier condition, they had to reorient by approaching the apparatus to do so in the barrier condition depicted here. (b) Video still demonstrator looking upwards in the barrier condition. (c) Video still of demonstrator looking upwards in the no barrier condition. (d) Video still of a Barbary macaque looking at the demonstrator at the start of a trial. (e) Video still of a Barbary macaque looking upwards to produce a gaze-following response.

Exclusions

On occasion, a monkey would be approached for testing but would fail to produce a scoreable response. For instance, some monkeys did not actually see the demonstrator's upwards look in the looking phase, or were displaced by other monkeys before they could approach in the approach phase. A blind coder therefore scored whether sessions should be excluded for these reasons. In addition to our final analyzed sample, four Barbary macaques were excluded from video because they did not see the demonstrator's upwards look. The same coder has previously assessed the rhesus data, and 5 rhesus monkeys were excluded for not seeing the look; an additional 2 monkeys were excluded due to apparatus failure or experimenter error (reported in Bettle &

Rosati, 2019). Overall, a total of 60 monkeys were included in the final sample for the looking phase in the *barrier* condition (29 Barbary, 31 rhesus), and 62 monkeys in the *no barrier* condition (29 Barbary, 33 rhesus). Additional monkeys that were included in the looking phase analyses were then excluded from analyses of the approach phase, for example because another monkey interfered during the one-minute approach period. Two Barbary macaques were excluded because they were displaced, and one was excluded because they left the testing area. The same coder has previously assessed the rhesus data, and 11 monkeys were excluded because another individual tampered with the apparatus, 1 was excluded because they were displaced, 1 was excluded because they left the area, and 2 were excluded due to apparatus error (as reported in Bettle & Rosati 2019).

Coding and reliability

For monkeys included in the final sample, independent coders scored monkey's responses (the same coders for both species). To code responses blind to condition, we clipped the 10s long looking phase and the 60s long approach phase out of the longer videos. Every clip was assigned a random trial ID, to enable coding blind to condition. While the barrier was inherently visible in the approach phase videos, coders were blind to condition in the initial looking phase and blind to a monkey's initial looking response when coding the approach responses.

To code the looking responses, our primary measure of gaze propensity and flexibility, both coders identified the start of the trial (where E1 said 'now') and coded the next 10s frame-by-frame. Following prior work (Bettle & Rosati, 2019; Rosati et al., 2016; Rosati & Santos, 2017), we coded (1) whether the monkey looked up towards the sky or not, from their initial starting position, using changes in the monkey's head and/or eye direction to judge whether the monkey looked upwards; (2) The total duration of looking up, in seconds; (3) latency to look up, in seconds; and (4) the number of discrete looks up, as a count response. There was high reliability for these measures (looking up: *Cohen's Kappa* = 0.95; duration of looking: $r_p = 0.99$; latency to look: $r_p = 0.99$; number of looks: $r_s = 0.93$).

To code the approach responses, our key measure of reorientation, the coders identified the start of the approach phase (when the timer beeped) and coded the next minute of footage. As it was not possible to directly assess looks into the barrier in this naturalistic context, we coded approaches within an arm's distance of the apparatus as a proxy that could be scored in a comparable way across conditions. We thus coded (1) whether the monkey approached within an arm's distance of the apparatus (binomial response); and (2) the latency to approach within an arm's distance of the apparatus, in seconds. The reliability coder had high reliability with the primary coder for these measures (approach: *Kappa* = 1.0; latency to approach: $r_p = 0.95$).

Statistical analyses

We analyzed the data in R v4.0.3 (R Core Team, 2020). Our two primary measures, propensity to look upwards and approaches, were both binomial responses, so we utilized logistic regressions implemented with the glm function. Initial inspection of the total looking time (in seconds) and latency to approach (in seconds) measures indicated that both showed right skew, so we used generalized linear models with an inverse-gaussian distribution (e.g., to analyze data that would be normalized by a log-transformation) in accordance with recommendations for skewed reaction time data (Baayen & Milin, 2010; Lo & Andrews, 2015). Finally, to analyze the number of looks (a count measure) we used Poisson regressions. For numerical data (e.g., total looking time and latency to look), we checked the data distribution and presence of outliers, and examined the distribution of residuals in models to further check model assumptions. This indicated that the use of the inverse gaussian models was appropriate. For the primary (binomial) measures, we examined binned residuals, which also looked appropriate. Finally, to compare model fit, we used likelihood ratio tests (Bolker et al., 2009), and also report Akaike information criterion (AIC) comparisons of the models; here, lower AIC values indicate better model fit.

Data availability

Data will be made available on Dryad Digital Repository upon publication.

Results

Within-species comparisons

We first examined the results from the Barbary macaques alone. Overall, 52% of individuals in the *no barrier* condition looked upwards, while 34% did so in the *barrier* condition. Only one individual ever approached (in the *barrier* condition). To analyze propensity to look, we first created a base model that accounted for the subject's *sex* and *age* (as a continuous predictor), and then added *condition* (barrier or no barrier), which did not significantly improve model fit ($\chi 2 = 1.84$, $df = 1$, $p > 0.17$; AIC = 84.7 compared to 84.5 in base model). We then included the interaction between *condition X age*, as age has been shown to impact gaze following responses in macaques (Rosati et al 2016; Rosati & Santos, 2017). This trended to improve fit (LRT: $\chi 2 = 5.22$, df = 2, p = 0.074; AIC= 83.3); post hoc comparisons using the *emtrends* function (Lenth et al., 2018) found a trend that older monkeys' responses to the no-barrier condition declined, such that they did not as clearly distinguish the conditions as younger monkeys (p =

0.08). Upon inclusion of this interaction, condition was a significant predictor of looking responses (*condition* estimate = 2.17, SE = 0.99, z-value = 2.19, p = 0.03) such that monkeys looked up more in the no-barrier condition. This final model including the *condition X age* interaction was also the best-fitting model according to AIC values. Overall, this indicates that Barbary macaques were sensitive to condition, but had declining flexibility in their responses with age.

Next, we examined whether condition impacted the dynamics of looking in those situations when Barbary macaques did look up. On average, Barbary macaques looked up for 1.59 ± SE = 0.29s when they produced a response, and the duration of looking did not vary across condition ($\chi 2 = 0.07$, $df = 1$, $p > 0.68$; AIC = 73.0 compared to 71.2 in base model). Their average latency to look on these trials where they did so was 1.57s ± 0.26s, and this also did not vary by condition ($\chi 2 = 0.09$, $df = 1$, $p > 0.68$; AIC = 72.4 compared to 70.6 in base model). Finally, Barbary macaques showed an average of 1.4 ± 0.11 looks upward per trial (in trials where they did look up), which also did not vary by condition ($\chi 2 = 0.0002$, $df = 1$, $p > 0.98$; AIC = 66.9 compared to 64.9 in base model). Overall, this indicates that when the monkeys did look up, the dynamics of their looking responses were similar across both conditions.

We then implemented the same series of models to analyze the rhesus data in the same way. Overall, 32% of rhesus macaques looked upwards in the *barrier* condition, while 58% looked upwards in the *no barrier* condition. Including *condition* significantly improved model fit (LRT: $\chi 2 = 4.31$, $df = 1$, $p = 0.04$; AIC = 86.2 compared to 88.2 in base model). Inclusion of the *age X condition* interaction did not further improve model fit compared to the second model (LRT: $\chi 2 = 1.37$, $df = 1$, $p > 0.24$; AIC = 87.2). Similar to the Barbary macaques, when the rhesus did look up there was no difference across conditions in the dynamics of their response for duration of looking responses ($\chi 2 = 0.17$, $df = 1$, $p > 0.45$; AIC = 109.3 compared to 107.7 in base model); latency to look ($\chi 2 = 0.53$, *df* = 1, *p* > 0.20; AIC = 104.7 compared to 103.5 in base model); or number of looks ($\chi 2 = 0.0006$, *df* = 1, *p* = 0.98; AIC = 81.9 compared to 79.9 in base model). In contrast to the Barbary, nine rhesus macaques approached overall (4 in the *barrier* condition and 5 in the *no barrier* condition). However, including condition did not significantly improve model fit (LRT: $\chi 2 = 0.19$, *df* = 1, *p* > 0.66; AIC = 47.5 compared to 45.3 in base model), indicating that rhesus monkeys were equally likely to approach regardless of condition.

Comparison across species

We then directly compared the results from the Barbary and rhesus macaques using the same basic analysis approach. Including *condition* significantly improved model fit compared to a base model accounting for subject's *age* and *sex* ($\chi 2 = 6.02$, df = 1, p = 0.01; AIC = 166.0 compared to 169.8 in base model): more monkeys overall looked upwards in the *no barrier* condition (see Fig 6a and 6b). In the third model, we included the *condition X age* interaction, given that age was an important shaper of responses, which further improved model fit compared to the second model (LRT: $\chi 2 = 5.35$, df = 1, p = 0.021; AIC = 162.8); posthoc comparisons found that monkeys overall showed declines in responses to the *no barrier* condition relative to the *barrier* condition, such that older monkeys were less sensitive to condition (p = 0.02). In the fourth model, we added in the *species X condition* interaction, which did not further improve model fit with no effect of species on performance (LRT: $\chi 2 = 0.04$, df = 2, p > 0.98; AIC = 167.2: see Table 4); that is, both species showed a similar pattern of both overall looking, and flexible modulation of looking responses across conditions. Finally, we added the three-way *age X species X condition* interaction, but this did not further improve model fit (LRT: $\chi 2 = 1.17$, df = 2, p > 0.55, AIC = 170.7): the impact of age on these responses was similar in both species. Overall, this suggests that both the tolerant Barbary and the despotic rhesus monkeys had similar propensities to follow gaze as well as similar flexibility in their modulation of this response.

Predictor	**Estimate**	**SE**	**z-value**	**p-value**
Sex (refence: female)	0.563	0.410	1.373	0.170
Age (as covariate)	0.020	0.044	0.444	0.657
Condition (reference: Barrier)	2.170	0.849	2.555	0.011*
Species (reference: Barbary)	-0.090	0.556	-0.162	0.871
Age X Condition	-0.155	0.070	-2.229	0.026*
Species X Condition	0.036	0.787	0.046	0.963

Table 4: Comparisons of gaze following responses across species. A base model included sex and age as predictors; subsequent models included interactions between condition, age, and species. Table shows the fourth model to report the lack of effects of species; the best-fit model was the third model that included an interaction between age and condition, but not species. Reference levels for predictors indicated in table.

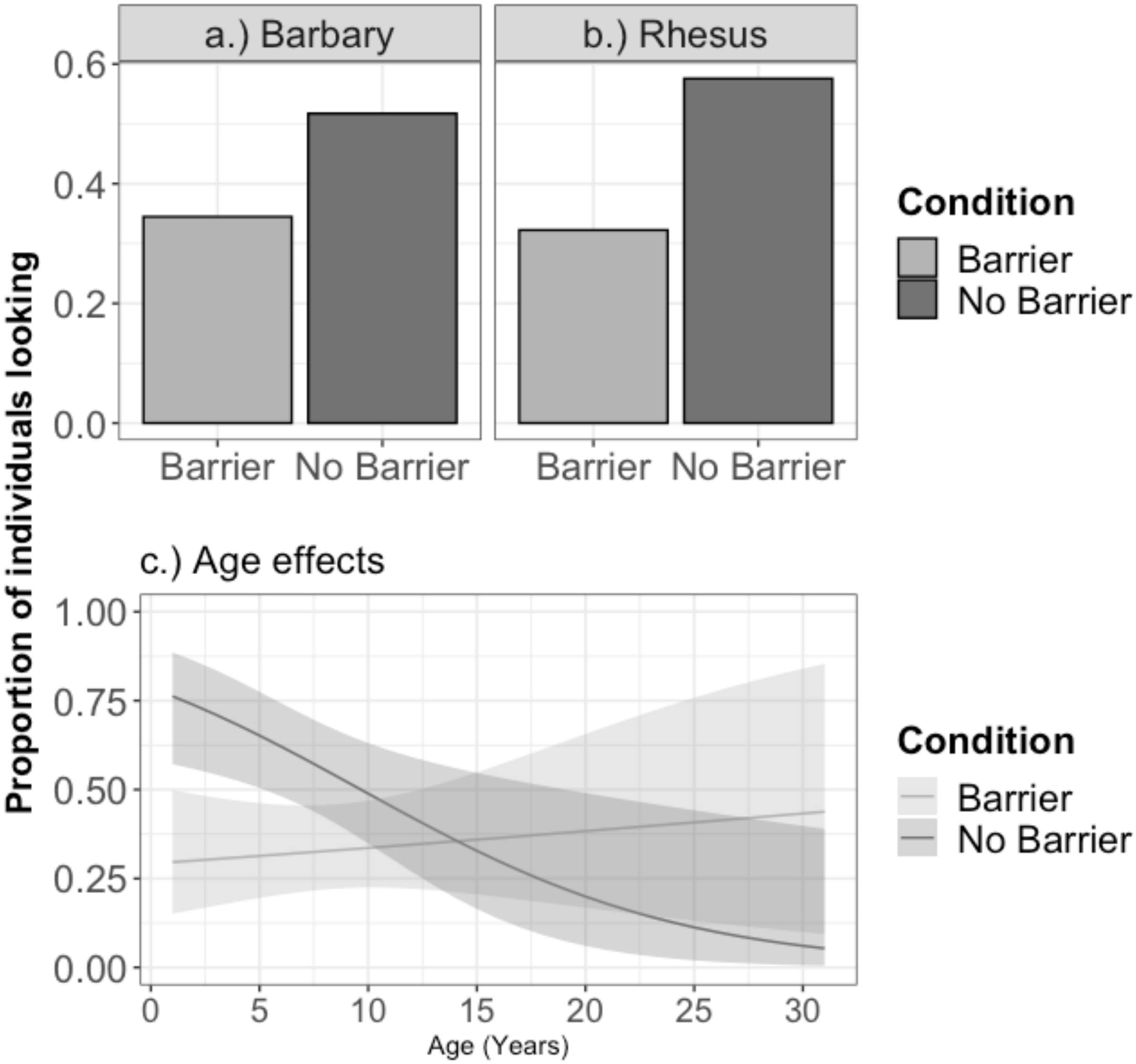

Figure 6: Gaze following responses across species. (a) Proportion of Barbary macaques who looked upwards during the look phase, across conditions. (b) Proportion of rhesus macaques who looked upwards during the look phase, across conditions. (c) Age trends by condition, collapsing across species. Ribbons represent 95% CI.

As with the comparisons within-species, we further compared the dynamics of looking in those trials where the monkeys did look. For total duration of looking, neither inclusion of *condition* (LRT: $\chi2 = 0.65$, *df* = 1, $p > 0.19$; AIC = 178.8 compared to 177.5 in base model), a *condition X age* interaction (LRT: $\chi2 = 0.99$, *df* = 2, $p > 0.28$; AIC = 180.7), nor a *species X condition* interaction ($\chi^2 = 1.40$, *df* =4, $p > 0.50$; AIC = 185.3) improved model fit compared to the base model, as in the analyses of the individual species. We found similar results when we analyzed latency to look and the number of looks. In particular, for latency to look, inclusion of the *condition X species* interaction as a predictor did not improve model fit look ($\chi2 = 1.21$, $df = 4$, $p = 0.6$; AIC = 178.5 compared to 170.2 in base model). It also did not improve fit for total number of looks ($\chi2 = 0.68$, $df = 3$, $p > 0.87$; AIC = 149.1 compared to 142.1 in base model). Overall, this indicates that the dynamics of looking were also similar across these species when they produced looking responses, according with prior comparisons of their gaze-following characteristics (Rosati & Santos, 2017).

We finally compared the species' overall likelihood to approach towards the apparatus, our measure of reorientation. Here, our base model included *age, sex* and *condition*, and we then added species into the test model. The base model indicated that younger individuals were significantly more likely to approach, and inclusion of species significantly improved model fit (LRT: $\chi2 = 7.11$, $df=1$, $p = 0.008$; AIC = 57.3 compared to 62.2 in base model). In particular, rhesus macaques approached the apparatus more often than Barbary macaques (see Fig 7). Since only one Barbary macaque ever approached, we did not conduct additional comparisons looking at the impact of species or age by condition. Overall, this indicates that rhesus were much more likely to investigate the apparatus overall than were Barbary macaques.

Predictor	**Estimate**	**Std. Error**	**z value**	**P value**
Age (as covariate)	-0.205	0.117	-1.749	0.080
Sex (reference: female)	-1.182	0.816	-1.448	0.148
Condition (refence: barrier)	-0.001	0.766	-0.001	0.999
Species (reference: Barbary)	2.369	1.104	2.146	0.032*

Table 5: Comparisons of propensity to approach across species. A base model included sex, age, and condition as predictors; the test models then included species. The best-fit model included species. Reference levels for predictors indicated in table.

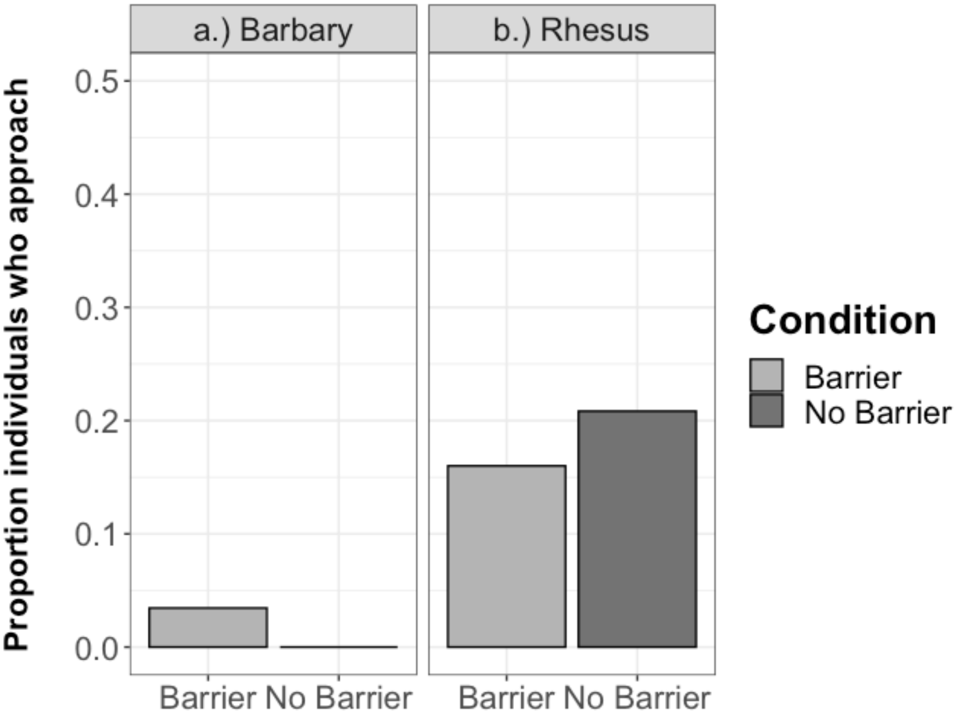

Figure 7: Approaches across species. Proportion of (a) Barbary macaques and (b) rhesus macaques who approached the apparatus across conditions.

Discussion

Despite different levels of social tolerance, Barbary and rhesus macaques showed similar patterns of gaze following. First, both species showed similar overall responsiveness to gaze cues in this context. Second, both species demonstrated similarly flexible gaze-following responses that accounted for the other individual's line-of-sight: monkeys looked up more often in the *no barrier* condition, where doing so allowed them to look at what the demonstrator was looking at, relative to the *barrier* condition where her line-of-sight was blocked. This effect of condition on looking responses also decreased with age, indicating that older monkeys produced less flexible gaze-following responses in both species. However, we did observe a species difference with regards to the motivation to reorient by approaching the apparatus: while Barbary macaques approached at a very low rate, rhesus macaques approached more often—but did so regardless of the demonstrator's looking behavior. Importantly, both of these populations are highly habituated to humans, and experience the presence of human observers from early in life, suggesting generally similar experiences with humans over ontogeny. Overall, our results suggest that a flexible understanding of others' gaze direction is present both within socially tolerant and despotic primate species. However, neither species are especially motivated to reorient to observe what others look at in this situation, although rhesus macaques may be more curious about novel items in general.

While different proposals have highlighted that either the degree of social tolerance (Burkart et al., 2009; Hare, 2017) or competition (Byrne & Whiten, 1990; De Waal, 1982; Hare, 2001; Lyons & Santos, 2006) can promote the evolution of sophisticated social cognition, our results align with a more nuanced emerging pattern concerning how specific skills that are favored in different contexts. For example, both Barbary and rhesus macaques can flexibly control their gaze-following responses, according with the finding that both more competitive chimpanzees and more tolerant bonobos perform similarly in tasks assessing their ability to follow gaze around barriers (Bräuer et al., 2005; Okamoto-Barth et al., 2007). This finding also adds to growing evidence that macaques of differing tolerance levels show similarly sophisticated social cognitive abilities. In particular, rhesus and Barbary macaques performed similarly in a task assessing their understanding of what other agents perceive (Arre et al., 2021), and macaques of varying tolerance levels showed similar results in a battery that included understanding other's intentions, responding to the demonstrator's attentional state, and gaze following (Joly et al., 2017). Consequently, one possibility is that these particular social cognitive abilities are broadly useful across competitive and tolerant contexts. For example, a sophisticated understanding of others' gaze is useful to detect the true location of biologically relevant stimuli—such as food and mates—that others are attending to (Rosati & Hare, 2009; Shepherd, 2010), regardless of social system.

We also found that older monkeys of both species were less likely to differentiate between condition with regards to their looking behavior. That is, with increasing age monkeys were less likely to look upwards in the *no barrier* condition relative to the *barrier* condition, unlike younger monkeys who more clearly differentiated these contexts. In direct comparisons we found similar trajectories in this pattern during aging in both species, although prior work indicates that Barbary macaques maintain higher levels of gaze-following into old age compared to rhesus macaques when faced with a simpler gaze following paradigm (Rosati et al., 2016; Rosati & Santos, 2017). Taken together, this suggests that while social tolerance can promote the maintenance of high levels of general social attention into old age (see also: Almeling et al., 2016), age-related declines in more sophisticated responses may occur regardless of social system. That is, older monkeys struggle to flexibly integrate contextual information (such as the presence of a barrier) into their gaze-following response, similar to the decline observed in human theory of mind abilities (Bottiroli et al., 2016; Moran, 2013). An important goal for future research is to examine whether this pattern holds up for other social cognitive abilities, and to characterize the specific cognitive abilities that may decline versus be preserved across different social contexts.

We also hypothesized that Barbary macaques would follow the demonstrator's gaze more frequently than the rhesus macaques, matching the pattern observed in more tolerant bonobos versus chimpanzees (Herrmann et al., 2010; Kano & Call, 2014a), and in line with the theoretical proposal that the ability to produce and respond to social cues is more likely to result in a mutual benefit within a tolerant social system (Hare, 2017; Tomasello et al., 2007). However, we did not find support for this idea, as both rhesus and Barbary macaques showed a similar propensity to look up in the task. One possible explanation for our results in relation to prior work is that a tolerant social style is a necessary but insufficient factor for enhanced gaze-following responses. For example, in humans, more elaborate social cognition has been proposed to result from the impact of both increased tolerance and high levels of self-control (Hare, 2017). Such a combination of skills may be necessary to reap selective benefits from enhanced gaze-following, for example because they include cognitive abilities that permit effective cooperation, yet macaques may not possess these other scaffolding skills. In line with this, humans (as well as bonobos to some extent), utilize gaze information for complex behaviors– including cooperation and cultural learning in humans (Csibra & Gergely, 2009, 2011; Siposova et al., 2018), and turn-taking exchanges in bonobos (Fröhlich et al., 2016). In contrast there is not such evidence that gaze-following feeds into these higher level social behaviors in macaques.

An alternative idea is that while both rhesus and Barbary macaques may be similarly sensitive to gaze direction, there are different reasons for this sensitivity: despotic species may primarily use these skills to out-compete others, but tolerant species to affiliate. In line with this, there is strong evidence that macaques respond differently to cues of rank or friendship according to social tolerance: while rhesus macaques gaze-follow differentially according to rank (Shepherd et al., 2006), Barbary macaques do not (Teufel et al., 2010). Similarly, crested macaques (*Macaca nigra*), another tolerant species, respond more quickly to gaze cues from conspecific friends versus non-friends (Micheletta & Waller, 2012), while competitive long-tailed macaques (*Macaca fascicularis*), are more responsive to gaze cues when a human actor exhibits a submissive facial expression versus an affiliative expression (Goossens et al., 2008). As the current study utilized a neutral context without any clear cues signaling either competition or cooperation (e.g., Bettle & Rosati 2019), an important next step is then testing how these species differ in responses to gaze cues that are explicitly cooperative versus competitive in nature. A related question is how relationships with different social actors may impact responses across species, such as gaze following responses to conspecifics who have close social bonds. This kind of work will further elucidate how gaze-following responses are actually used by these species across different social contexts and thus provide a complimentary test of hypotheses about the evolution of social intelligence.

While the Barbary and rhesus macaques showed similar gaze-following responses, they differed in their approach behavior. The rhesus macaques approached the apparatus at a higher overall rate than the Barbary macaques: only one Barbary macaque approached, compared to nine rhesus macaques. In this situation, the rhesus macaques appeared to be more motivated than the Barbary macaques to investigate the apparatus. One possibility is that this motivation to investigate the apparatus reflects enhanced selection for curiosity in rhesus relative to Barbary macaques, as has been proposed given their status as a ‘weed species’ that has persisted through dependence upon human resources (Richard et al., 1989). Yet it is important to note that rhesus do preferentially re-orient and approach specifically in such a barrier condition when the target of the actor’s attention is on the ground, rather than upwards (see also; Bettle & Rosati, 2019). That is, rhesus are capable of flexibly reorienting. As such, an important question is whether Barbary macaques also preferentially reorient in a different context like this.

In sum, we found that both tolerant Barbary macaques and despotic rhesus macaques show similar patterns of gaze-following in terms of overall responsivity to gaze cues, flexibility of their gaze behavior, and a decline in this flexibility with increasing age. These results suggest that having a sophisticated understanding of others' gaze, and being responsive to others' gaze cues, is advantageous in both despotic and tolerant social groups. Overall, this highlights how species with different social tolerance levels can evolve broadly similar cognitive capacities in some social domains, despite theoretical proposals that social tolerance is a key driver of social cognitive evolution. Thus, future work will need to take a more nuanced approach to disentangling precisely which social skills vary across different kinds of social systems and social organizations, versus which may be broadly advantageous across multiple contexts. Teasing apart when and why tolerance shapes particular cognitive abilities is crucial to understand the evolutionary history of intelligent behavior.

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Chapter 4: The Evolutionary Origins of Natural Pedagogy: Rhesus Monkeys Show Sustained Attention Following Nonsocial Cues [2]

Abstract

The natural pedagogy hypothesis proposes that human infants preferentially attend to communicative signals from others, facilitating rapid cultural learning. In this view, sensitivity to such signals are a uniquely human adaptation and as such nonhuman animals should not produce or utilize these communicative signals. We test these evolutionary predictions by examining sensitivity to communicative cues in 206 rhesus monkeys (*Macaca mulatta*) using an expectancy looking time task modeled on prior work with infants. Monkeys observed a human actor who either made eye contact and vocalized to the monkey (*social cue*), or waved a fruit in front of her face and produced a tapping sound (*nonsocial cue*). The actor then either looked at an object (*referential look*) or looked towards empty space (*look away*). We found that, unlike human infants in analogous situations, rhesus monkeys looked longer at events following nonsocial cues, regardless of the demonstrator's subsequent looking behavior. Moreover, younger and older monkeys showed similar patterns of responses across development. These results provide support for the natural pedagogy hypothesis, while also highlighting evolutionary changes in human sensitivity to communicative signals.

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[2] This research was previously published in *Developmental Science* (Bettle & Rosati, 2021).

Introduction

One of the biggest challenges faced by any developing organism is to learn about the world around it. Social information provided by others can facilitate such learning, and human infants are highly sensitive to social cues that can help them acquire this information (Baldwin, 1993; Flom et al., 2017; Meltzoff et al., 2009; Tomasello, 2009). An influential hypothesis proposes that human infants are uniquely receptive to 'ostensive' social communicative cues, like directed gaze or infant-directed speech, which denote that information is being intentionally communicated (Csibra, 2010; Csibra & Gergely, 2009; Gergely & Csibra, 2006). While children can also learn new information even when it is not intentionally conveyed (Gredebäck et al., 2018; Schmidt et al., 2011), this proposal argues that communicative cues may enable especially efficacious social learning if infants preferentially attend to and interpret these communicative acts appropriately (Csibra, 2010; Gergely & Csibra, 2006; Moore, 2016; Sperber & Wilson, 1986). A key claim of the natural pedagogy hypothesis is that humans are uniquely adapted to produce and interpret these 'ostensive' cues which signal that important information is being conveyed, and thus facilitate cultural learning (Csibra, 2010; Csibra & Gergely, 2009; Gergely & Csibra, 2006). Here we test a key prediction of this proposal by examining whether rhesus monkeys are similarly sensitive to social communicative cues.

Empirical evidence testing this proposal indicates that human infants do attend to and interpret communicative signals in a way that facilitates social learning. First, infants *preferentially attend* to cues such as eye contact or infant-directed speech, looking more at faces with direct gaze than averted gaze, and preferring infant-directed speech (Cooper & Aslin, 1990; Farroni et al., 2002). Second, infants expect these signals to be followed by *referential information.* For example, infants are more likely to follow an experimenter's gaze following ostensive cues, compared to attention-grabbing but nonsocial cues (Senju & Csibra, 2008). These signals appear to help the infants selectively attend to the referent (e.g., target object) that the adult is looking at. Similarly, in expectancy violation looking-time paradigms, infants look longer when an experimenter gives an ostensive cue and then fails to look at an object, compared to when the adult does look to an object (Csibra & Volein, 2008)—that is, they seem to expect that ostensive cues will be referential. Finally, infants infer that ostensive cues precede *generalizable information*, rather than applying only to the 'here-and-now' or to a particular person's preferences. For example, infants preferentially encode kind-relevant properties about an object following ostensive cues (Yoon et al., 2008, Topál et al., 2008). These results support the claim that ostensive cues can enable cultural learning in humans—knowledge that should be generalizable across different people and contexts within a shared culture.

The natural pedagogy hypothesis specifically predicts that these patterns of social cue production and use are unique to humans, facilitating the novel patterns of cultural behavior seen in our species (Csibra & Gergely, 2009; Csibra & Gergely, 2011). In line with this, there is little evidence that animals *produce* these communicative signals. Nonhuman primates do have complex forms of vocal and gestural communication, some of which has been proposed reflect intentional communication (Byrne et al., 2017; Tomasello & Call, 2019; but see Fischer & Price, 2017). However, there is currently no clear evidence that non-human primate communication involves ostensive signals which specifically denotes the signaler's intent to communicate to the receiver, a crucial component of human-like communication (Csibra & Gergely, 2011; Grice, 1989). For example, while some animals may engage in behaviors that meet a functional, evolutionary definition of teaching focused on whether information is conveyed at a cost to the actor (Musgrave et al., 2016; Thornton & McAuliffe, 2006; Thornton & Raihani, 2008), there is no evidence that 'teachers' produce intentional communicative signals to facilitate learning.

However, some nonhumans may be *sensitive* to such cues, a potential precursor to human-like natural pedagogy. For example, dogs attend to eye contact and name-calling (Kaminski et al., 2012), and preferentially gaze follow to the referent object after the production of these cues (Téglás et al., 2012). More generally, domesticated animals are fairly successful at following a human demonstrator's social cues, such as directed gaze or pointing (Bräuer et al., 2006; Hare et al., 2002; Hare et al., 2005; Hare & Tomasello, 2005; Kaminski et al., 2005). One explanation for these findings is that the process of dog domestication selected for cognitive abilities, such as interpreting human social cues, that facilitated living amongst humans (Hare, 2007, 2017; Hare & Tomasello, 2005). An important question is then whether nonhuman primates are sensitive to ostensive signals, given that primates are our closest evolutionary relatives. To date, only one study has tested the natural pedagogy hypothesis in primates (Kano et al., 2018). Chimpanzees, bonobos, and orangutans watched as a human demonstrator gave an ostensive cue or a nonsocial cue and then looked towards one of two objects, following methods used previously with infants (Senju & Csibra, 2008). In fact, apes did not preferentially follow the demonstrator's gaze to the cue object following the ostensive signals, although chimpanzees showed greater attention towards both objects following these signals. Thus, chimpanzees might attend to these cues, but fail to utilize gaze information to identify the intended referent. Notably, this study tested mostly adults, whereas the natural pedagogy hypothesis proposes that cue sensitivity is especially important for young individuals who must rapidly absorb social knowledge (Csibra, 2010; Csibra & Gergely, 2009; Gergely & Csibra, 2006). As such, a comparative developmental perspective is critical to testing this hypothesis (Goméz et al., 2005; Matsuzawa et al., 2007; Rosati et al., 2014).

In the current work, we therefore examined sensitivity to social communicative cues in rhesus monkeys varying in age from juvenility to adulthood. Rhesus monkeys do not exhibit human-like culture, but have many similarities to humans in their social cognition, and therefore can provide an important test of whether humans have a unique sensitivity to these cues. For example, rhesus monkeys and humans exhibit similarities in gaze sensitivity. Like humans, macaque newborns engage in long bouts of mutual gaze and facial gesture imitation with their mother (Dettmer et al., 2016; Ferrari et al., 2009; Simpson et al., 2016). Rhesus also robustly follow others' gaze (Emery et al., 1997; Rosati & Santos, 2017; Tomasello et al., 2001), with developmental trajectories mirroring those in humans (Rosati et al., 2016; Tomasello et al., 2001). Macaques also have a rich vocal and gestural communication system comprising different vocalizations and expressions including screams in agonistic contexts (Gouzoules et al., 1984; Maestripieri & Wallen, 1997), affiliative lip-smacking (Ferrari et al., 2009; Morrill et al., 2012; Simpson et al., 2013), and grunts or threats (Partan et al., 2002; Maestripieri & Wallen, 1997).

Here, we tested a large sample (n = 206) of semi-free-ranging rhesus monkeys on a new expectancy looking-time paradigm integrating components of previous infant studies (Csibra & Volein, 2008; Senju & Csibra, 2008). In a between-subjects design, monkeys watched a demonstrator give either an ostensive signal (*social cue condition;* the demonstrator made directed eye contact and vocalized), or observed a salient but nonsocial cue (*nonsocial cue condition;* a fruit moved in front of the demonstrator's face concurrent with a mechanical knocking sound). Immediately following this cue, monkeys observed the demonstrator either look towards a location where an object was revealed (*look to object outcome*), or in the opposite direction to empty space (*look away outcome*). We tested if monkeys (1) preferentially watch events following social communicative cues; (2) expect communicative cues to be followed by referential actions; and (3) exhibit exacerbated sensitivity to such cues as juveniles. We predicted that if monkeys were sensitive to ostensive signals, they would show longer looking times following the social cue, especially when the demonstrator then produced the unexpected non-referential looking behavior. In contrast, the natural pedagogy hypothesis predicts that nonhumans will not prioritize such cues. Second, we predicted that if such signals facilitate social learning in monkeys, then juveniles should demonstrate enhanced sensitivity. In contrast, the natural pedagogy hypothesis predicts that this early sensitivity is a human-specific adaption, in which case older monkeys may show greater skillfulness than younger ones through learning to preferentially attend to such social cues through direct experience with humans over their lifetime.

Methods

Subjects

We tested 206 rhesus monkeys (51 or 52 per condition; 115 males and 91 females; 1.8 to 23.6 years old) at the Cayo Santiago Field Station (see Rawlins & Kessler, 1986). We tested 99 adults and 107 juveniles, age balanced across conditions. This free-ranging population is well-habituated to humans, as behavioral observations and cognitive tasks are regularly conducted with this population. Individuals can be identified through tattoos and ear notches. This population has successfully been tested in a number of looking-time paradigms testing different aspects of social cognition (Marticorena et al., 2011; Martin & Santos, 2014; Rosati et al., 2018).

Procedure and apparatus

Monkeys were randomly assigned to one of four conditions in a 2x2 design manipulating whether the monkey saw a *social* or *nonsocial cue*, and whether the demonstrator subsequently *looked to object* or *looked away* from an object during the test trial. Monkeys saw a white stage (backdrop: 76cm x 51cm; base: 76cm x 15cm) with a front screen (76cm x 51cm) that could be raised and lowered (see Figure 8). At the front were two smaller purple occluders (10cm x 10cm) which could also be lowered to reveal an object (a plastic orange). A track in the stage (63 cm long) allowed the experimenter to manipulate the orange out of the monkey's view. Such fruit stimuli are highly interesting to the monkeys (De Petrillo & Rosati, 2019; Hughes & Santos, 2012; Marticorena et al., 2011; Martin & Santos, 2014)

Experimenter 1 (E1; the actor) first identified a calmly-sitting monkey, then placed the apparatus approximately 2m away and knelt behind it. Experimenter 2 (E2; the cameraperson) knelt beside to film the monkey's looking responses. Both wore baseball caps to cover their eyes with the brim when necessary (see Figure 8). All monkeys first saw a *habituation trial* (identical across trials). E1 lowered the front screen then watched the fruit as it traveled behind each of the small occluders (see Figure 8). Once the fruit returned to the center, E1 called 'now' and looked down, and the monkey's looking was video-recorded for 10s. This habitation trial thus familiarized the monkey to the basic setup and the fact that the orange could move. After 10s, E2 called 'stop' and E1 raised the front occluder.

Next, the monkey observed the production of a cue followed by a test trial. In the *cue production phase*, the monkey either saw a *social cue* or a *nonsocial cue* (see Figure 8b). In the social cue, E1 made eye contact with the monkey and called out 'monkey, monkey!'. In the nonsocial cue, an apple popped up from behind the stage and moved in front of E1's face concurrent with a tapping sound. Importantly, the stage obscured E1's hands and arms such that the *nonsocial cues* were not visibly produced by E1: E1could manipulate this apple out of the monkey's sight behind the stage, and the tapping sound was produced by surreptitiously knocking the back of the apparatus. This lasted approximately 3s; then the apple was removed. Next, E1 lowered the purple occluders to reveal the orange (the right side; see Figure 8c). Concurrent with this, she said "now" and either looked towards the orange (*look to object*) or towards empty space (*look away*) in the *test trial*. The monkey's looking time was again recorded for 10s. Cue and trial outcome condition assignment was random, using a pre-designated list carried by E2; E1 was not told the condition until the trial started. The monkey never received any food reward in the task.

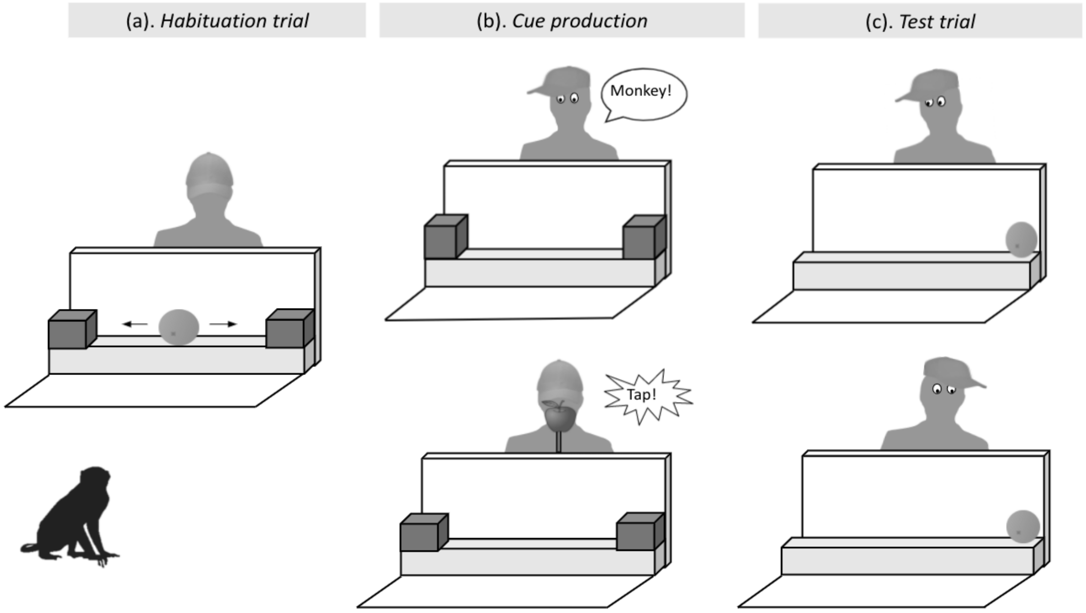

Figure 8: Setup and experimental procedure. In the (a) habituation trial, the occluder dropped to reveal an orange that moved back-and-forth behind both small purple occluders, before stopping in the center; E1 moved her head to follow the fruit's movements and said 'left box, right box' as the orange moved behind each occluder. She then called 'now' and looked down (obscuring her eyes with the cap) to initiate the trial. In the (b) cue production phase, monkeys either saw a demonstrator make eye contact and vocalize in the social cue condition, or saw an apple move in front of her face and heard a tapping sound in the nonsocial cue condition. E1 manipulated the stick and made the sound by tapping on the back of the apparatus, but this was not visible to the monkey because the stage obscured her hands and arms. The apple dropped behind the back of the apparatus at the end of this period. In the (c) test trial, monkeys saw both small purple occluders fall as the demonstrator either looked toward the revealed location of the orange (look to object), or looked toward empty space (look away)

Exclusions

In this free-ranging population, monkeys were sometimes approached but failed to complete the study (did not produce scorable responses). Reasons for exclusion included: disinterest and leaving the testing area (n=54); interference by other monkeys (n=16); approaching too close (n=8); poor video quality (n=5), or experimenter or equipment error (n=11). This rate of aborted sessions (n=94) is similar to other looking time tasks in this population (Marticorena et al., 2011; Martin & Santos, 2014). If a monkey was tested more than once (e.g., because they were only individually identified after the test: n=24), we only coded and analyzed their first session.

Video coding and reliability

Two coders blind to trial type and condition independently scored both trials from the final subjects. Each trial was clipped from longer video sessions and assigned a random trial ID to remove condition information. The coders examined these video clips frame-by-frame using MPEG Streamclip to assess total looking time per trial out of 10s. There was high reliability between the two coders ($r_p = 0.92$).

Statistical analyses

We analyzed the data in R v3.4.1 (R Development Core Team, 2019). Our primary analysis examined duration of looking across habituation and test trials using linear mixed models implemented with the *lmer* function in the package lme4 (Bates et al. 2015). In some analyses we further examined a difference score for each individual (Test looking time – Habituation looking time), which has commonly been used in looking time research with infants (Spelke et al., 1992). To analyze these scores, we implemented linear regressions using the *lm* function. We compared model fit using likelihood ratio tests (Bolker et al., 2009). We accounted for sex in all models as prior work suggests that male and female rhesus monkeys can show different responses to social information (Rosati et al., 2016; Rosati & Santos 2017; Simpson et al., 2016). To examine age-related changes in responses, we compared age cohorts based on life history transitions, with juvenile less than 5 years of age (the onset of sexual maturity), and adults over age 5 (Bercovitch et al. 2003; Rosati et al. 2016; Rawlins & Kessler 1986). We also performed additional checks using age in as a continuous predictor.

Data availability

Data is available on Dryad Digital Repository.

Results

We first examined monkeys' looking times to the habituation versus test trial across conditions. On average, monkeys looked mean = 4.73 ± SE = 0.20s in the habituation trial, but showed different patterns of looking to the test trial (see Figure 9). In particular, they looked relatively longer in test trials compared to habituation trials following nonsocial cues regardless of the actor's subsequent looking behavior (*look to object outcome:* 6.09±0.32s; paired samples t-test comparing habituation to test: t_{50}=3.21, p=0.002; 95% CI of the mean difference = [0.43, 1.89]; *look away outcome*: 5.84±0.35s, t_{51}=4.76, p<0.0001, 95% CI = [1.05, 2.57]). However, they did not differ in their looking to test trials compared to habituation trials following social cues (*look to object outcome:* 5.58±0.40s; t_{50}= 1.83, p=0.07, n.s., 95% CI = [-0.09, 1.84]; *look away outcome:*

5.24±0.38s, t_{51} =-0.06, p = 0.95, n.s., 95% CI = [-0.93, 0.88]). Thus, monkeys exhibited more sustained attention to the test events following the nonsocial cue.

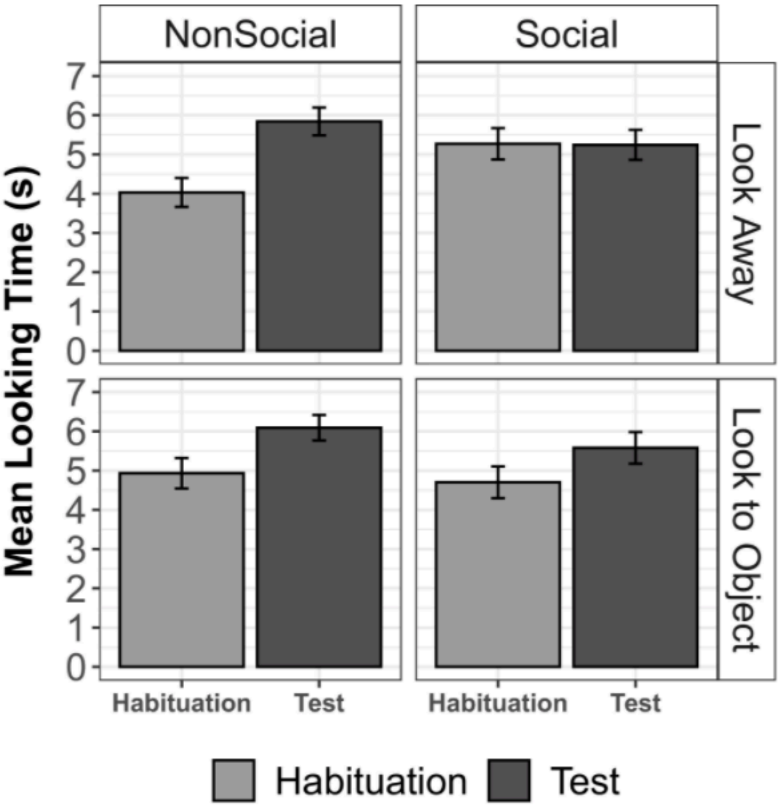

Figure 9: Looking responses across habituation and test trials depending on cue and looking outcome. After an initial habituation trial (identical for all conditions), monkeys experienced either a social cue or nonsocial cue, and then observed an actor either look to an object (referential look) or look away in the test trial. Looking times show duration of looking in seconds out of a possible total 10s; error bars indicate SE.

To compare responses across conditions, we used linear mixed models accounting for *subject identity* (as a random effect); *sex; age cohort;* and *trial type* (habituation versus test trial). In the second model, we added the interaction between *trial type* and *cue type* (social versus nonsocial) and to test whether monkeys attended differentially to test depending on cue. This improved model fit [LRT: 2 =6.38, df=2, p=0.04]: monkeys looked longer following nonsocial but not social cues. This confirms that monkeys exhibited more sustained looking after nonsocial cues. In the third model, we additionally added the interaction between *trial type* and *test trial outcome* (look to object or look away), which did not further improve fit [LRT: 2 =0.65, df=2, p=0.72, n.s.]: monkeys did not modulate their looking according to whether the look was referential. Finally, inclusion of the three-way interaction between *trial type*, *social cue,* and *test trial outcome* also did not improve model fit [LRT: 2 =7.13, df=4, p=0.13, n.s.]. Thus, the full model showed that monkeys looked longer following non-social cues, but did not adjust looking based on the actor's subsequent looking behavior. In the final model males also looked overall longer than females and juveniles longer than adults, similar to prior results (De Petrillo & Rosati, 2019; Hughes & Santos, 2012). Finally, we ran a similar analysis where we examined test trial responses while controlling for each individual's habituation looking time, and also found that monkeys looked longer following nonsocial cues.

We next examined monkeys' difference scores (Test – Habituation Looking) to parse age-related change in patterns of relative looking across condition. Both younger and older monkeys had more positive scores following nonsocial cues (*juveniles:* 1.27±0.38s; *adults*: 1.72±0.36s; see Figure 10) compared to social cues (*juveniles:* 0.08±0.46s; *adults:* 0.80±0.47s). To analyze this, we first created a base linear model that included each subject's *cohort* and *sex*. We then added *cue type*, which improved model fit [LRT: 2=6.46, df=1, p=0.01]: monkeys show more relative looking following nonsocial cues. Next, we added *test trial outcome,* which did not improve model fit [LRT: 2=0.13, df=1, p=0.72, n.s.]. Finally, in the full model, we included a 3-way interaction between *age cohort*, *cue type*, and *test trial outcome* to test whether differential responses to social cues and referential looking varied over development. This also did not improve model fit [LRT: 2 = 5.81, df = 5, p=0.33, n.s.]. That is, while younger monkeys did look longer overall at events (as indicated by the prior analyses of looking duration), they did not show a differential pattern of relative looking across conditions compared to older monkeys. Additional checks using age in years as a continuous predictor found largely similar results.

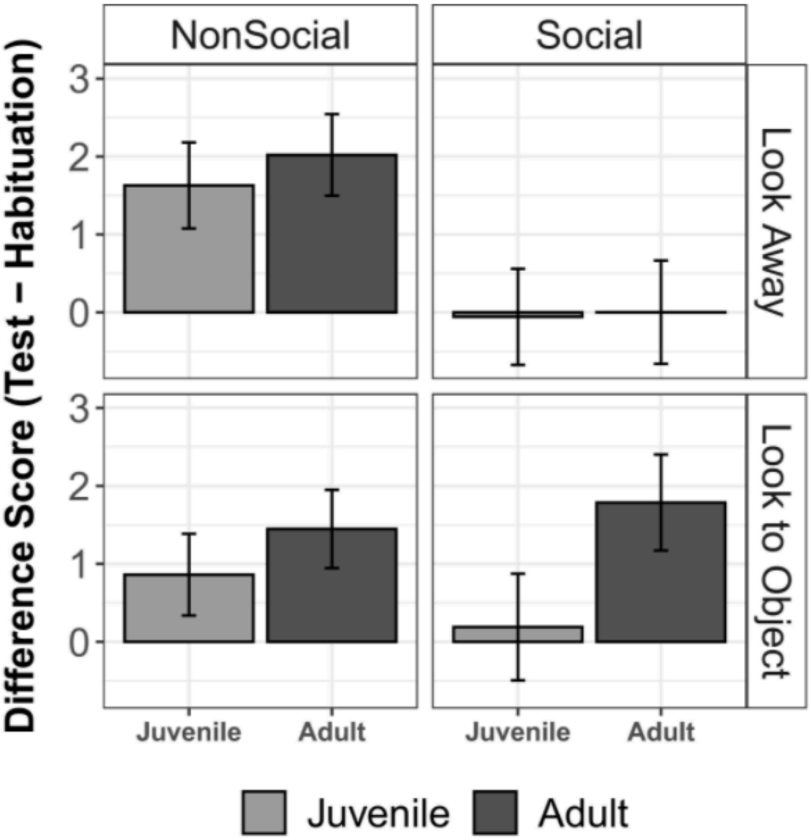

Figure 10: Relative patterns of looking over development. Both younger and older monkeys showed similar increases in looking to the test events following nonsocial cues as indexed by more positive looking time difference scores (Test Looking – Habituation Looking). In contrast, both age groups showed lower difference scores following social cues. Error bars indicate SE

Discussion

We tested comparative predictions from the natural pedagogy hypothesis by assessing how rhesus monkeys respond to communicative social signals and interpret subsequent looking behaviors by an actor. We found three key results. First, rhesus monkeys showed more sustained attention to events after non-social cues compared to social, communicative cues. Second, monkeys did not differentiate between a referential look to an object and a look to empty space—

even though the referential cues signaled the location of a food item, an ecologically important type of information for primates. Finally, we compared these responses across the lifespan in the first comparative developmental study of primate responses to ostensive cues, and found no evidence that monkeys show lifespan changes in their sensitivity to these signals.

These results indicate that monkeys exhibit important differences in responsivity to social cues compared to human infants. First, monkeys attend more to events following nonsocial cues, whereas human infants are more likely to follow an adult's gaze following social cues specifically (Senju & Csibra, 2008), and generally find social communicative signals extremely salient (e.g., Baron-Cohen, 1997; Flom et al., 2017; Grossmann et al., 2008; Hood et al., 1998). Second, monkeys looked longer after non-social cues regardless of whether the actor produced a referential look. In contrast, human infants are surprised when the adult gives a social cue and fails to subsequently look towards an object (Wu & Kirkham, 2010; Csibra & Volein, 2008). These differences suggest that monkeys are not sensitive to the communicative function of gaze the way humans are, even though they are responsive to shifts in a human's or a conspecific's gaze direction (Bettle & Rosati, 2019; Emery et al., 1997; Flombaum & Santos, 2005; Rosati et al., 2016; Rosati & Santos, 2017; Tomasello et al., 2001). Overall, these findings provide a new line of support for the natural pedagogy hypothesis, which argues that sensitivity to ostensive cues is unique to humans (Csibra, 2010; Csibra & Gergely, 2009; Gergely & Csibra, 2006). This further suggests that while some domesticates, like dogs, might be sensitive to such human communicative cues, this sensitivity may have evolved independently in response to the domestication process (Hare et al., 2002; Topál et al., 2009).

In the current work, we also examined whether younger monkeys show greater sensitivity to social cues than older monkeys. The natural pedagogy hypothesis highlights that ostensive signals are especially important for learning in infancy (Csibra, 2010; Csibra & Gergely, 2009; Gergely & Csibra, 2006), yet to date no work has tested whether juvenile animals are specifically responsive to these cues. Despite our large sample of both juvenile and adult monkeys, we did not find evidence for developmental change in responses to social cues. While younger monkeys exhibited longer looking times to various kinds of stimuli in general, as in prior work (De Petrillo & Rosati, 2019; Hughes & Santos, 2012; Rosati et al., 2018), they did not show different pattern of relative looking across conditions compared to adults. This suggests than juvenile monkeys do not prioritize ostensive cues the way human infants do (Csibra, 2010; Csibra & Gergely, 2009; Gergely & Csibra, 2006). Moreover, the lack of lifespan developmental change also suggests that older monkeys did not learn to utilize the human-produced social cues through direct experience that such cues may predict that a human is looking at something interesting.

One possibility is that monkeys might be sensitive to other kinds of individuals, such as conspecifics, given that we used a human demonstrator in order to tightly control the actor's actions in the experiment. However, there are several reasons that this cannot explain our results. First, macaques follow the gaze of humans and conspecifics at similar rates, suggesting that human-produced gaze cues are interesting and relevant to them (Rosati & Santos, 2016, 2017; Tomasello et al., 2001). Indeed, a variety of results indicate that macaques utilize sophisticated social cognitive processes in their interactions with humans, and most evidence for these abilities in nonhumans comes from studies involving human actors (Bettle & Rosati, 2019; Drayton & Santos, 2017; Flombaum & Santos, 2005; Marticorena et al., 2011; Martin & Santos, 2014; Santos et al., 2006). It is also possible that macaques might be more sensitive to other kinds of social cues than those used here. While the monkeys showed similar looking responses following the directed eye contact and vocalization cues as they did in the habituation trial without such cues, suggesting that they did not actively look away from the human social signals, other species-specific signals may be more relevant to them. For example, macaques use affiliative signals such as lip-smacking (Morrill et al., 2012; Simpson et al., 2013) and vocalizations such as grunts and girneys (Partan et al., 2002), which may be similar in function to directed gaze and infant-direct speech in humans.

Relatedly, nonhuman primates might selectively respond to communicative cues produced by specific individuals that they have a close, tolerant relationship with. For example, mother-infant monkey dyads engage in reciprocal lip-smacking and mutual gaze (Ferrari et al., 2009), which may serve to establish a mutual intent to communicate. In addition, chimpanzees are more sensitive to social cues from a human caregiver with whom they have a close relationship (Kano et al., 2018). In that way, social tolerance may promote communication between individuals who would otherwise avoid or even antagonise the other. A critical next step is therefore to examine whether more tolerant primate species exhibit enhanced sensitivity to social communicative cues, such as Barbary macaques (Almeling et al., 2016; Rosati & Santos, 2017; Teufel et al., 2010; Thierry, 2000). In humans, higher levels of social tolerance has been proposed to facilitate new forms of cooperation and communications (Hare, 2017; Hare & Tomasello, 2005), so examining how more socially tolerant species response to these signals is important for assessing the natural pedagogy hypothesis as well.

In conclusion, our work shows that monkeys across the lifespan preferentially attended to events following nonsocial cues compared to social communicative signals, and did not exhibit referential expectations that a look to an object will follow these cues. This supports the proposal that sensitivity to social signals may facilitate a novel cultural learning function in humans (Csibra & Gergely, 2009; Gergely & Csibra, 2006; Kaplan et al., 2003). Human children are unique in terms of the volume of culturally-specific and cognitively opaque information they need to learn, which means that the information human children must absorb is difficult to learn via other learning processes that are more widely shared across species. This human-specific ability to intentionally transmit complex cultural knowledge may also be impossible without the extensive cooperation present in humans (Tennie et al., 2009). Our results therefore highlight the evolutionary changes in social cognition that may have occurred to support our species' shift towards increasing dependence upon cultural learning.

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Chapter 5: Cognitive Predictors of Social Behavior in Barbary Macaques

Abstract

Primates lead complex social lives, and this complexity is thought to drive the evolution of primate intelligence. In particular, the social intelligence hypothesis posits that primate sociality selected for cognitive skills which allow individuals to respond adaptively to others' behavior. However, whether social intelligence actually impacts naturalistic social behavior is currently unknown, despite the critical importance of this evidence to evaluating the social intelligence hypothesis. Moreover, the link between specific features of cognition and social behavior remain unclear, as different proposals have argued that social intelligence can affect social behavior through several distinct pathways including (1) tracking relationships with multiple social partners, (2) forming of strong affiliative bonds or other prosocial behavior, or (3) facilitating more sophisticated competition with conspecifics. To test the relationship between cognition and natural social behavior, we experimentally assessed individual variation in social cognition across 40 free-ranging Barbary macaques using a test battery. We then observed each individual's natural social behavior, allowing us to examine how intelligence predicts social behavior. The combination of experimental measures of cognition and naturalistic observations of social behavior provides new insights into how complex social intelligence evolves across species.

Introduction

Why are primates intelligent? The dominant explanation for the evolution of cognition in primates is that the nature of primate sociality has selected for increased intelligence (Dunbar, 1998; Humphrey, 1976; Jolly, 1966; Whiten & Byrne, 1988). The basic idea is that primate social lives are sufficiently complex that they require more sophisticated cognitive skills to track social relationships, and to deal with a shifting social landscape. While there are several variations on this proposal, they all hold in common the idea that skillfully interacting with other individuals presents an intellectual challenge to an individual—and that this exerts a selective pressure. The social intelligence hypothesis has been hugely influential in understanding the evolution of cognition across species, including in humans (Hare, 2017).

However, the social intelligence hypothesis has proved difficult to empirically test. Some of the most well-known evidence for this hypothesis comes from a specific formulation of this idea called the 'social brain hypothesis', which specifically proposes that more socially-complex species will have larger brains. Tests of this idea take the form of correlations between social complexity, typically indexed by social group size and brain size across taxa. Currently, many different taxonomic groups have been examined for these associations, including primates (Barton, 1996; Dunbar, 1998; Dunbar & Shultz, 2007), carnivores (Dunbar & Bever, 1998), and cetaceans (Marino, 1996). Yet as brain size is an indirect proxy for intelligence, this approach may not reflect specific cognitive abilities (Healy & Rowe, 2007; Holekamp, 2007). In addition, subsequent analyses of brain size have also found support for the alternative hypothesis that ecological complexity, rather than social complexity, better predicts brain size (DeCasien et al., 2017).

Another approach to understanding the relationship between cognition and sociality has come from studies that contrast cognitive abilities across species with different social structures.

In particular, many species living in complex groups, such as large multi-male multi-female societies with dominance hierarchies, have demonstrated high levels of aptitude in social cognitive tasks. For example, species including chimpanzees, capuchins, rhesus macaques and ring-tailed lemurs live in relatively large complex groups, and these species appear to be fairly successful at attributing goals to others (Kano & Call, 2014; Uller & Nichols, 2000), taking other's perspectives (Flombaum & Santos, 2005; Hare et al., 2000; Sandel et al., 2011), and attributing knowledge to others (Hare et al., 2001; Kaminski et al., 2008; Marticorena et al., 2011). In contrast, species that live in smaller or less complex groups, such as pair-bonded mongoose lemurs and marmosets, or ruffed lemurs and black lemurs living in small family groups, have struggled in similar paradigms (Burkart & Heschl, 2007; Sandel et al., 2011). While it is important to note that chimpanzees, rhesus macaques and capuchins have been especially well-tested (ManyPrimates et al, 2019), this pattern is suggestive of a relationship between social system and social cognitive skill ability. However, these tasks have not tested whether variation in cognitive abilities is actually linked to real-life social behavior, a key prediction of the social intelligence hypothesis.

A final approach to examining the social intelligence hypothesis has examined how primate sociality is linked to fitness in wild primate populations, to assess selection on social behavior. Many primates form close social bonds (Langergraber et al., 2009; Mitani, 2009; Silk et al., 2006a, 2006b), and recent evidence shows that social bonds are associated with greater fitness. For example, female baboons with closer social bonds experience higher offspring survival and longevity (Silk et al., 2009, 2010). In chimpanzee males, social bonds have been linked to increased fitness through several pathways: individuals who form strong bonds with the alpha male have greater siring success, and individuals who have a larger number of social connections overall also have greater siring success (Feldblum et al., 2021). Within Barbary macaques specifically, affiliation has been linked to fitness through forming larger huddles against the cold (Campbell et al., 2018; McFarland & Majolo, 2013): Barbary macaques with a larger number of huddling partners have better thermoregulation during cold weather events, which improves survival rates across both sexes during harsh winters. At the same time, the number of different aggressive partners also predicts survival probability in Barbary macaques—which the authors suggest may be because it stabilizes the affiliative social relationships that promote fitness-relevant behaviors such as huddling (Lehmann et al., 2016). Overall, these findings are congruent with the social intelligence hypothesis, but crucially these social behaviors—while plausibly related to cognitive skills—are not direct measures of cognition. Thus it is unknown whether the individuals with greater social intelligence actually have stronger social bonds, or display particular patterns of aggression.

Another challenge to testing the social intelligence hypothesis is that the behavioral function of social intelligence is currently underspecified in this theory. That is, different versions of this proposal (all under the umbrella of the social intelligence hypothesis) have emphasized different potential functions of social intelligence. One core hypothesis is that social intelligence allows an individual to keep track of and engage in an increasing number of social relationships (Dunbar, 1998). Support for this hypothesis includes the correlation between brain size and group size across primates (Barton, 1996; Dunbar, 1998), as well as within human comparisons that have indicated a positive relationship between an individual's grey matter density in social cognition brain regions and social network size (Kanai et al., 2012). Yet other proposals have specifically emphasized the Machiavellian function of cognitive abilities (Whiten & Byrne, 1988). Evidence for this view includes the positive relationship between species' brain size and the presence of deceptive interactions (Byrne & Corp, 2004), as well patterns of complex competition and deception in primates (Chapais, 1995; De Waal, 1992; Hirata, 2006). Finally, some recent views have instead emphasized how social cognitive abilities can shape the quality of social relationships, such as in establishing and maintaining positive relations or other forms of prosocial behavior (Cheney et al., 1986; Hare, 2017). Forming such bonds may require the ability to recognize that another individual has a cooperative intent and to maintain positive relations (for example via grooming, social support and other prosocial behaviors; Mitani, 2009). While these potential functions for social intelligence are not mutually exclusive, no research has directly compared them: an integrative approach that utilizes both experimental tests (to directly assess cognitive mechanisms) and observational approaches is crucial to test between these hypotheses.

In this study, we therefore tested how individual variation in social intelligence predicts natural behavior in free-ranging, naturally-living Barbary macaques where experimental manipulations are possible. Barbary macaques exhibit a variety of sophisticated social cognitive skills, including individual recognition (Schell et al., 2011), flexible use of communicative gestures (Hesler & Fischer, 2007; Joly et al., 2017), gaze following (Rosati & Santos, 2017; Teufel et al), and knowledge attribution (Arre et al., 2021). With regards to their social behavior, Barbary macaques are a tolerant macaque species, with a relatively relaxed dominance hierarchy (Thierry, 2007). Social competence is likely crucial to biological fitness in Barbary macaques, because this species lives in complex multimale multifemale groups and displays high rates of both affiliative and aggressive behavior (Thierry, 2007). Social bonds in Barbary macaques have also been specifically linked to fitness-relevant behaviors such as coalition formation (Berghänel et al., 2011; Carne et al., 2011) and social huddling (McFarland & Majolo, 2013). We thus examined how social cognition predicts social behavior in this species. To do so, we designed a primate social cognition test battery consisting of three well-validated experimental tasks: gaze following, goal attribution, and knowledge attribution. In particular, we measured each individual’s propensity to follow gaze (using methods from Rosati et al., 2016; Rosati & Santos, 2017), their ability to attribute goals to an agent (using methods from Woodward, 1998), and their ability to attribute knowledge to an agent (using methods from Arre et al., 2021). Each monkey also completed a motivational control, to serve as an independent metric of each individual’s interest in novel people and experimental stimuli.

In addition to this experimental battery to characterize individual variation in cognition, we observed the same animals’ social interactions in their natural social groups in a series of focal follows to assess key aspects of their sociability (how many individuals they sat in proximity to, and interacted with), competitive abilities (patterns of aggression) and affiliation (patterns of grooming as a key metric of social behavior). This approach—combining both experimental assessments and focal follows—was possible because this unique population is highly habituated to human experimenters, but also free-ranges in a natural context. We then used this data to test the relationship between social cognition and behavior. In particular, we aimed to disentangle three key hypotheses about this relationship: (1) does social intelligence enable interaction with a larger number of individuals; (2) does social intelligence facilitate strong social bonds; and (3) does social intelligence facilitate competitive behavior? Given that Barbary macaques are socially tolerant and display comparatively low rates of aggression (Thierry, 2007), and that social bonds have been linked to fitness-relevant affiliative behaviors such as huddling in this species (Campbell et al., 2018; McFarland & Majolo, 2013), we predicted that social intelligence would best predict metrics of affiliation.

Methods

Subjects

Our sample comprised 40 adult male Barbary macaques (ranging in age from 4.1 years to 23.1 years), living at Trentham Monkey Forest in the UK. We tested monkeys from two social groups: 19 monkeys from the 'French' group, and 21 monkeys from the 'German' social group. The macaques are free to range through a 60-acre forested area, and are well-habituated to humans. In particular, they are accustomed to staff members who provision the monkeys, to researchers, and to the presence of tourists on defined paths that run around the forest. Each macaque could be identified, by means of particular facial and body features—such as particular patterns on freckles on their face. Accordingly, the macaques have this site have previously successfully participated in both cognitive (Arre et al., 2021; Rosati & Santos, 2017) and behavioral studies (Berthier & Semple, 2018; Carne et al., 2011; Edwards et al., 2013; Gustison et al., 2012; Maijer & Semple, 2016; Whitehouse et al., 2016; Wiper & Semple, 2007).

Methods overview

In a pre-registered study, each macaque underwent a social cognitive test battery assessing core cognitive skills: gaze following, goal attribution, knowledge attribution, and a motivational control. These tasks were temporally 'interwoven' with the behavioral focal follows (described below), such that monkeys would typically complete one or two focal follows in between each cognitive task, but monkeys never experienced a cognitive task and a focal follow on the same day. The sequence of tasks was consistent across all individuals, who completed them in the same order: gaze-following, knowledge attribution, goal attribution, and finally the motivational control.

Each social task included key test and control conditions, allowing us to extract a measure of relative performance. As the goal of this battery was to index individual variation across individuals using well-validated tasks, rather than demonstrate the existence of these skills per se, the sequence of trial types for each task was kept consistent (rather than counterbalanced) across individuals. This was to avoid potential order effect confounds that might impact patterns of individual variation.

Gaze-following task procedure

The first cognition task that each monkey completed was gaze-following, which tested whether monkeys would look up to co-orient with a demonstrator. The task consisted of a sequence of test trials (where the actor looked up) and control trials (where the actor looked down, as a baseline measure of how often the monkey looked upwards). While the monkey was sitting calmly, the experimenters approached the monkey to within 1-2m. Following methods from (Rosati & Santos, 2017), Experimenter 1 (E1) then attracted the monkey's attention, by calling 'monkey' and snapping her fingers close to her eyes (see Fig 11). When she had attracted the monkey's attention, she began each trial by looking in the relevant direction while simultaneously saying 'now', to mark the start of the trial. Experimenter 2 (E2) acted as the cameraperson, and stood 2-3m behind E1 (further away from the monkey than E1) in order to film the monkey's face. After ten seconds, E2 called 'stop' to end the trial. Monkeys were always tested in the vicinity of a tree, so that E1 could feasibly be looking at something above. However we did not test when there was a monkey overhead, in order to avoid possible visual or auditory confounds.

Monkeys completed one test followed by one control trial, then experienced a pause of two minutes before proceeding with the second identical set of trials; this pause was introduced to reduce habituation effects on the macaques' gaze-following responses given that monkeys tend to habituate over sequential repeated trials (e.g., Rosati et al 2016). During this two minute trial, E1 and E2 stayed still, or followed the macaque from a distance, if the macaque moved areas during this two minute period. Subjects had to complete at least the first test and control trial for this data to be included in the battery; subjects who did not initially complete the second set of test and control trials (for example, because they moved into an area that was impossible to follow them into, during the two minute pause) underwent the second set of trials separately at a later date when they were located for testing. Individuals who did not complete the first two trials repeated the entire session on a later day as described below.

Figure 11: Gaze-following procedure. (a) The demonstrator catches the monkey's attention prior to each trial. (b) In test trials, the demonstrator looks directly upwards while the monkey attends. (c) In control trials, the demonstrator looks directly downwards while the monkey attends.

Knowledge attribution task procedure

Our method was modelled after similar prior work with macaques (Arre et al., 2021; Marticorena et al., 2011), and tested whether monkeys could infer that seeing leads to knowing using a looking time methodology. Monkeys observed a fruit moving between two boxes on a stage, and an actor who also watched the moving fruit. The actor then reached into different boxes, after seeing it move in a way that was either consistent or inconsistent with their knowledge of the fruit's location.

First, the two experimenters approached the monkey while they were sitting calmly, and knelt 1-3m away. E1 placed the apparatus just in front of herself, and the cameraperson (E2) knelt behind E1 to film their responses. Each session comprised two familiarization trials, followed by two test trials (see Fig 12), again in the same fixed order for all monkeys. The familiarization trials were designed to acquaint the monkeys with the events that they would see within each test trial, while the two key test trials then captured the monkey's responses towards either the unexpected outcome (first test trial) or an unexpected outcome (second test trial). Each trial was conducted in quick succession after resetting the experimental apparatus and recapturing the monkey's attention if needed.

Similarly to prior work (Arre et al., 2021; Marticorena et al., 2011), the knowledge attribution apparatus consisted of a white stage measuring 64cm long, and was 20cm deep. On this stage there was a track cut lengthways. allowing a lemon (that was propped on top of an L-shaped dowel rod) to be surreptitiously moved across the stage from behind the apparatus such that it appeared to move independently (not due to the experimenter's manipulations). On the left-hand side of the stage was a purple box, measuring 17cm by 17cm. A green box of equal size was on the right-hand side of the stage. As in prior work, both boxes were open on the side that faced the track, such that the lemon moved into either box, but covered with leaves on that side so that the lemon could not be directly seen once it moved into the box. The backboard to the stage was 46cm high, reaching approximately chest height of E1 when she knelt behind it. We also added an occluder measuring 64cm by 46cm to the front of the stage, which could be raised (using fishing line) to hide the stage from the monkey's view

At the start of each trial, E1 would capture the monkey's attention by calling 'monkey, monkey' and lower the flap to reveal the stage to the monkey. Following prior work (Arre et al., 2021), the first familiarization trial introduced that the actor could reach into the boxes on the stage, so monkeys saw E1 reach into the purple box that was on the left-hand side (from the monkey's perspective; see Fig 12). This was the location she later reached into in the test trials as well. She said "now" when initially producing the reach and then held this position for ten seconds, while the monkey's looking response was filmed by E1. E2 said 'stop' at the end of the 10 secs period, at which point E1 raised the occluder. While the stage was hidden from the monkey, she surreptitiously moved the lemon to the center of the stage in preparation for the second trial. The second familiarization trial introduced the presence of the fruit stimuli, so here monkeys saw the lemon in the center of the stage, as E1 looked down towards it. E1 said "now" when lowering the occluder to reveal the fruit, and held this position for ten seconds, while the monkey's looking responses were again filmed by E1. E2 again called 'stop' at the end of the ten secs period.

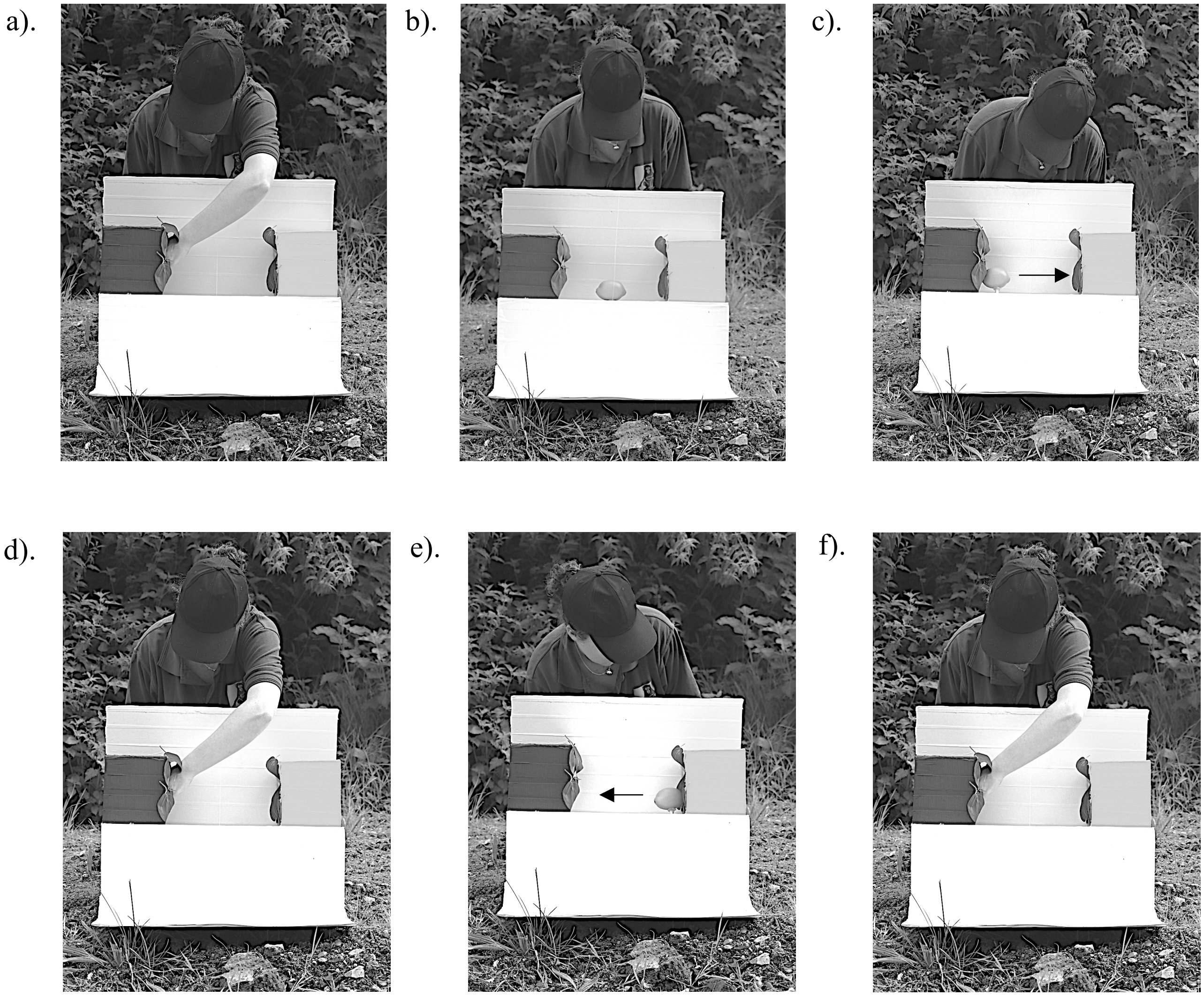

Figure 12: Knowledge attribution procedure. (a) During the first familiarization trial, the demonstrator holds a pose where she reaches into the left-hand box. (b) During the second familiarization trial, the lemon is visible in the center of the stage. (c) The lemon moves from the left box into the right box, as the demonstrator watches and follows the lemon's movement with her head direction. (d) During the Unexpected trial, the demonstrator reaches into the left box—even though she just saw the lemon go into the right box. (e) The lemon then moves from the right box into the left box, as the demonstrator watches and follows the lemon's movement with her head direction. (f) During the Expected trial, the demonstrator reaches into the right box—where she saw the lemon go.

Monkeys then proceeded to the two test trials, which were the key trials for this study. In the first test trial indexing responses to unexpected outcomes, monkeys watched as the occluder dropped to reveal an empty stage. The monkeys then saw the lemon emerge from the left box, and move across the stage into the right box, while E1 closely watched the lemon's movement, e.g. her head orientation tracked the lemon's movement. Once the lemon reached the right box, E1 reached into the left box, which is an unexpected outcome given that she saw the lemon go into into the other location. As E1 reached into the left box, she called 'now' to the mark the start of the trial. She then held still for ten secs, as the monkey's looking time response was filmed. E2 called 'stop' at the end of this 10 secs period. In the second test trial indexing responses to expected outcomes, the procedure was largely similar except that here the actor ultimately reached to the box where she saw the fruit go. In particular, the lemon emerged from the right box, and moved across the stage into the left box, and then here E1 reached into the left box (e.g., consistent with her knowledge) Monkeys needed to complete all 4 trials within the same session, for the session to be included. Individuals who did not complete all four trials repeated the entire session on a later day as described below.

Goal attribution task procedure

This task was based on similar prior work with human infants (Woodward, 1998), using looking time methods to test whether monkeys can attribute goals to a demonstrator. In particular, monkeys here saw an actor who either reached for a 'preferred' object (consistent with their goal) or reached in the same location as they had in the past (an action inconsistent with their established goal). Similar to the procedure for knowledge attribution, the two experimenters approached the monkey while they were sitting calmly, and knelt 1-3m away. E1 placed the apparatus just in front of herself, and the cameraperson (E2) knelt behind E1. Each session comprised two sets of trials each involving different pairs of objects (the unexpected set and the expected set), and here in each set monkeys experienced a habituation and test trial for each set. The familiarization trials in this study were designed to expose the monkeys to the particular objects used on that trial set as well as demonstrate E1's intention to reach a particular object. The test trials then captured the monkey's responses towards unexpected versus expected outcomes. As in the other cognitive tasks, every monkey followed the same sequence of trials (unexpected followed by expected), and each trial followed in succession after the time it took to reset the stage and recapture the monkey's attention.

The apparatus in this study consisted of a black stage that measured 59cm long, and was 17cm deep. The backboard measured 62cm high, reaching approximately shoulder height of E1 when she knelt behind it. The backboard had a concealed flap, that measured 44cm by 26cm; the flap could be opened from behind the apparatus to move the objects or switch the objects that were on the stage between trials without the monkey seeing this occur. The two sets of trials involved two distinct objects of different colors and shapes (but approximately the same size), in order to reduce potential carryover effects between the two sets of trials. The first pair consisted of a blue sandcastle (the preferred object, as described below), measuring 12 by 14cm, and a green bowling pin, measuring 8cm by 20cm. The second pair consisted of a mini American football (the preferred object), measuring 16cm by 8cm, and a mini traffic cone, measuring 10cm by 12cm.

The first trial in each set was a familiarization trial that established the experimenter's preferences for that pair of objects. Here, monkeys saw E1 reach repeatedly towards one of two objects (always the one on the left-hand side of the stage, from the monkey's perspective). E1 reached but failed to grasp the sandcastle three times, as if it were just out of her reach: the purpose of this was to demonstrate to the monkey her goal of reaching the object. She then reached out and successfully touched the left object on her fourth attempt (without actually moving it; see Fig 13), and said 'now' as she touched the object to mark the start of the trial. She held this position for 10 secs, as the monkey's looking response was filmed. After this 10 secs period was complete, E2 said 'stop' to end the trial. In the subsequent test trials, monkeys watched as the occluder dropped to reveal that the two objects had switched positions. In the unexpected test trial (the first of the two sets), E1 then reached in the same location and thus touched a new object; as in the habituation trials, she called 'now' to mark the start of the trial when she touched the object. In contrast in the expected test trials, she produced a reach to a new location but towards the same object she had reached for in the habituation trial (e.g., the objects now on the right side). Thus, these two test trials captured whether monkeys expected the actor to reach in line with her goals, or just produce superficially-similar behaviors regardless of her goals. Monkeys needed to complete all 4 trials within the same session, for the session to be included. Individuals who did not complete all four trials repeated the entire session on a later day as described below.

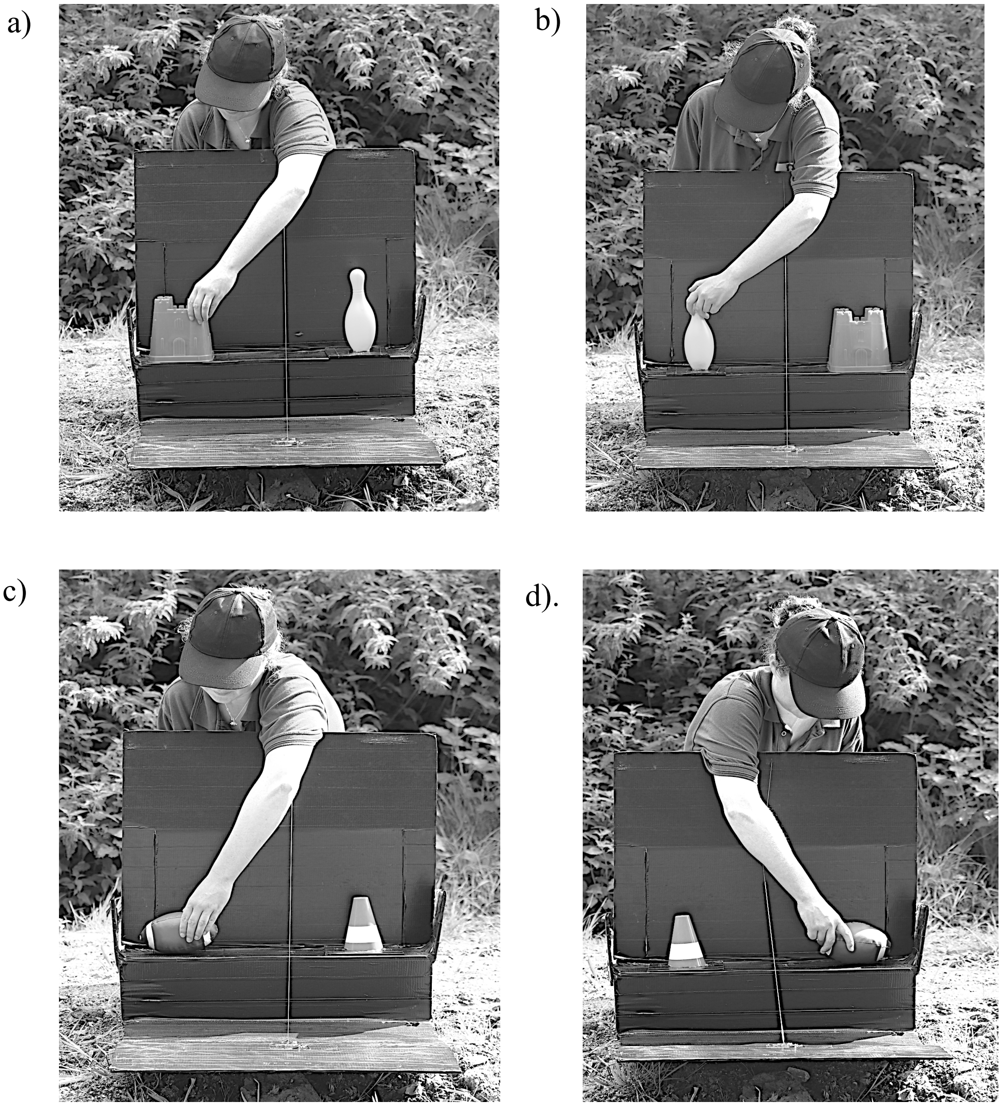

Figure 13: Goal attribution procedure. (a) During the first familiarization trial, the demonstrator reaches for the sandcastle. (b) During the Unexpected test trial, the location of the sandcastle and bowling pin have switched. The demonstrator reaches for the bowling pin, in the location she previously reached for the sandcastle—despite showing her preference for the sandcastle in the familiarization trial. (c) During the second familiarization trial, the demonstrator reaches for the football. (d) During the Expected trial, the location of the football and mini traffic cone have switched. The demonstrator reaches for the football, in its new location—matching her preference from the familiarization trial.

Motivational control task procedure

This task assessed each monkey's motivation to approach novel objects, and served as a control to account for any individual variation in the general experimental setups we used in the social tasks, specifically their interest in food, objects, and people. Here, E1 and E2 identified a monkey who was sitting calmly. While E2 stood a couple of meters behind E1, E1 approached the monkey to within 3-4m. E1 then captured the monkey's attention by saying 'monkey, monkey' and showed the monkey the mini apple. E1 then placed the small box upon the ground, and pretended to put the mini apple into the box (in reality, she hid it in the palm of her hand). This aspect of the setup aimed to assess motivation for a fruit reward. She then stood up, and placed the toy truck 1m behind the box, further away from the monkey (see Fig 14); this assessed interest in objects. She then walked away to where E2 was standing. E2 timed 30 secs from when the truck was placed upon the ground, and the monkey's response was filmed. E2 called 'stop' once this period was complete. We examined both approaches to the food and subsequent approaches to the toy.

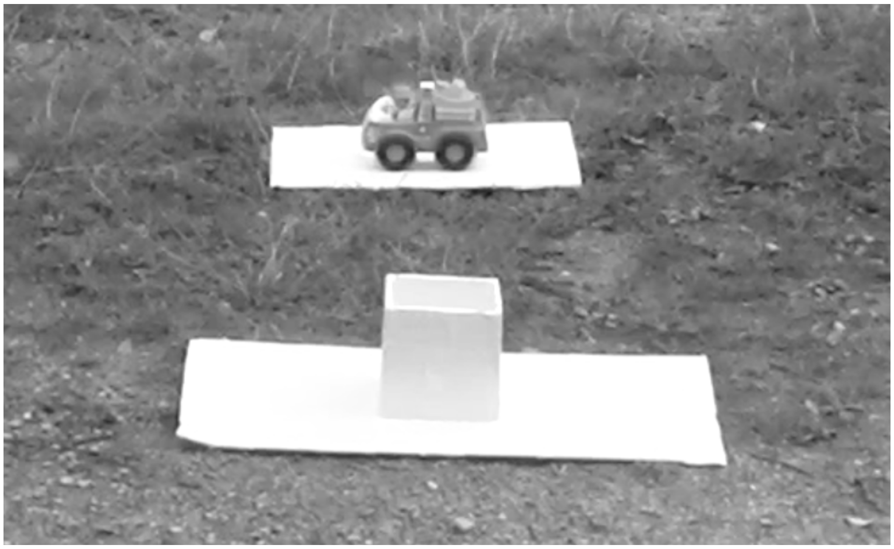

Figure 14: Motivational assessment. Monkeys were presented with a white box, that the demonstrator mimed dropping a small apple into. Behind the box was a toy truck.

Exclusions and repeated sessions

During cognitive testing, monkeys would occasionally fail to produce scorable responses: for instance they would be displaced by another monkey, or failed to attend to the testing procedure. On these occasions, we repeated the cognitive task, typically after a 2 day 'break'. During video coding, we also excluded any monkeys who failed to attend during habituation or test trials (i.e. who never looked at the stage) for the social tasks. This occurred for 4 monkeys in the knowledge task, 2 monkeys in the goals task, and 1 monkey in the gaze-following task: these monkeys were excluded specifically for the analyses for that particular cognitive task, and from the analyses that examined overall performance across all cognitive tasks. We did not have any exclusions for the motivation task.

Video coding and reliability

Two coders who were blind to trial type and condition then independently scored each trial, for each cognitive task. Each trial was clipped from the longer video session, and for tasks with multiple trials they were assigned a random trial ID to blind coders to condition information. The coders then examined these video clips frame-by-frame using Filmora. For the gaze task, two coders then assessed whether the monkey's gaze behavior (e.g., whether the monkey ever gazed upwards, following the same methods described for gaze coding in Chapters 2 and 3). For the knowledge and goal attribution tasks, the coders assessed the monkey's looking time behavior; how long the monkey looked towards the apparatus (following the same methods described in Chapter 4). For the motivational control task, the coders assessed whether the monkey approached within an arm's length of either the food box or the object, whether they touched the box or the object, and their latency to do so.

Behavioral methods

We collected focal observation data from the same monkeys, concurrently with the collection of the cognitive data. The goal of this data collection was to assess each monkeys' patterns of natural social behavior: specifically, their patterns of sociability, affiliation and aggression. Each individual was focaled on 8 occasions; focals lasted 15-30 minutes for a total of 146 hrs of data in total, with a mean of 3.65 +/- SD = 0.06 hours of focal observational data per animal. Focal follows were abandoned if we lost sight of the focal for more than two consecutive 2 min scans, and data was only included if we collected at least half of the planned focal follow (aka 15 minutes of a 30 minute follow). During focal follows, we collected continuous data concerning all social behaviors (such as grooming, huddling, and aggression) directed towards the focal, or from the focal. Every 2 minutes, we also collected scan data concerning that individual's activity, as well as the other individuals within 2m proximity, touching proximity, and whether anyone was huddling with the focal. We also accounted for several other potential sources of variation in the focals' behavior in collecting the data. For example, focals were distributed to capture behavior at different times of day (ensuring that every focal subject was observed at least once within each timeslot from 9-11am, 11-1pm and 1-3pm, and was never observed more than three times within the same timeslot). We also recorded the presence of staff provisioning the group, the presence of tourists, and the location of the focal in the park.

Behavioral metrics

From these data, we calculated metrics for each individual corresponding to different proposed functions of social intelligence. To test the hypothesis that socially intelligent individuals use these abilities for overall sociability or gregariousness, such as the ability to engage with a larger number of individuals overall, we first calculated the *average number of individuals* that were within 2m proximity to each focal during scans. We also calculated the *average number of individuals that the focal interacted* with per minute of observational time (by engaging with them via grooming, or via other forms of affiliative behavior such as huddling, or by engaging in aggression with them). To count as 'interacting' in this second metric, they had to actively engage in aggression, grooming or another forms of affiliation with another individual: merely sitting in proximity did not count. Both of these metrics were aimed at capturing the number of social partners that the focal individual would need to track in their social group.

To test the hypothesis that socially intelligent individuals use these abilities to enable aggressive behaviors, we first calculated the *rate that each individual aggressed others*, by totaling the number of aggressive events from the focal (threats, chases and attacks) and dividing this by the hours that the focal was observed (e.g., 3.67 hours for 220 minutes of follow time). We additionally assessed *the number of different individuals that each focal aggressed*, per hour of focal follow time. These metrics aimed at capturing competitive ability in the monkeys. We also calculated the *rate that each individual received aggression*, using a similar method. Note that this is a distinct behavioral pattern than giving aggression, and much work with primates suggests that higher-status individuals may specifically give more aggression but that lower-status individuals receive more aggression (Deag et al., 1977). As such, the social competencies needed to decide whether to aggress others, versus avoid aggression from others, may be distinct.

To test the hypothesis that socially intelligent individuals use these abilities to enable affiliative behaviors, we then calculated the *rate that each individual groomed others*, by totaling the amount of time spent grooming others and dividing this by the number of minutes that the focal was followed. We additionally assessed *the number of different individuals that each focal* *engaged in grooming with*, per hour of focal time. These metrics aimed at capturing affiliative tendencies in the monkeys. We also calculated the rate that the focal was groomed by others, using a similar method. Note that this is a distinct behavioral pattern than giving grooming, and much work with primates suggests that higher-status individuals may specifically receive more grooming (Sonnweber et al., 2015). As such, the social competencies needed to decide whether to groom others, versus those that may make an individual an attractive grooming partner, may be distinct.

Finally, as dominance status can pattern many aspects of primate behavior, we calculated dominance rank for each individual to control for this in subsequent analyses. Dominance rank based upon the direction and outcome of submissive interactions, using Modified David's Score. We then assigned every individual a Low, Medium or High categorical rank depending on this score.

Statistical analyses

We analysed the data in R v4.0.3 (R Development Core Team, 2019) following our pre-registered analysis plan. We first conducted a set of preliminary analyses examining the cognitive data and behavioral data separately. For the cognitive data, we first examined performance in each task in turn, to assess whether monkeys' responses at the group level aligned with our expectations from prior studies. For example, we tested whether monkeys preferentially looked upwards (in the gaze-following task) or looked longer at unexpected outcomes (in the knowledge and goal attribution tasks). To do this, we implemented models using the glmer or lmer function from the lme4 package, and compared model fit using likelihood ratio tests (Bolker et al., 2009). In our base models, we accounted for age, rank (as low, medium or high, based on Modified David's Score), group membership, and subject's *identity* as a random affect. Following this, we also assessed for relationships between our cognitive measures. For the behavioral data, we ran a series of correlation tests to assess the relationships between our different behavioral measures.

To test different versions of the social intelligence hypotheses, we then examined whether the inclusion of our cognitive metrics (assessing gaze-following, knowledge attribution and goal attribution, as well as a composite score that combined performance across all three measures) improved the fit of linear models examining patterns of natural behavior. These linear models were implemented with the lm function, and the model fit was compared using likelihood ratio tests (Bolker et al., 2009). In our base models, we accounted for age, rank (as low, medium or high, based on Modified David's Score), group membership, and motivational score– all of which we predicted would affect behavior or cognitive performance, based on prior work (Berthier & Semple, 2018; Carne et al., 2011; Rosati & Santos, 2017). The motivational score was a binomial Y/N measure, assessing whether the monkey approached the box during the motivational assessment: 50% of monkeys approached the box overall (where the demonstrator mimed dropping a fake apple). We did not include approaches to the truck, since only 2 monkeys ever approached the truck.

To index individual variation in performance from each cognitive task for these analyses, we used a difference score to capture each monkey's performance. In the gaze-following task, this difference score measured how many trials the individual looked upwards for, in test trials relative to control trials. Here, more positive scores indicate that individuals tended to follow the experimenter's gaze, whereas negative scores indicate that the monkey more frequently looked upwards during control trials. These control trials measured each monkey's baseline level of upwards looks, as the demonstrator looked downwards during these trials. In the knowledge attribution task, this difference score was calculated as the individual's looking time in the *unexpected* test trial minus their looking time in the *expected* trial, to index relative looking towards the unexpected outcome; here more positive scores indicate more relative looking to the surprising event (as expected if monkeys attribute knowledge to the actor), whereas more negative scores indicate that monkeys did not attribute knowledge in this way. In the goal attribution task, we used a slightly different score as the *unexpected* and *expected* trials each involved different objects that the monkeys showed different interest towards, in terms of relative looking. We therefore calculated the looking time difference score as the *unexpected test* looking time – *unexpected habituation* looking time, minus the *expected test* looking time – *expected habituation* looking time. Similarly to the knowledge task, here more positive scores indicate more relative looking towards the unexpected outcome (as expected if monkeys attribute goals to the actor), but this score also accounts for differential looking overall to the different sets of objects.

Finally, we also calculated a composite cognition performance score integrating performance across all three tasks. Here, monkeys received a '1' for each task where their difference score was positive for that task. In the gaze-following task, this would reflect that they looked upwards more frequently in the test trials relative to the control trials, and in both looking time tasks (knowledge attribution and goal attribution) this would reflect that they looked longer in the *unexpected* trials relative to the *expected* trials. This composite cognitive score therefore varied from 0 to 3 for each individual monkey.

Data availability

Data will be made available on Dryad Digital Repository upon publication.

Results

Cognitive performance

We first examined the monkey's responses in the gaze-following task. On average, monkeys looked up in 44.87% ± SE = 0.057 of the test trials, where the demonstrator looked upwards. Monkeys looked up in 21.79% ± 0.047 of the control trials, where the demonstrator looked downwards. To test whether more monkeys looked upwards more often within the test trials as predicted, we implemented a base model which included *age*, *social group* (French or German) and *rank* (high, medium, or low), as well as a random affect for subject's *identity*. In the test model, we then added *trial type* (test or control), which significantly improved model fit [LRT: $\chi2 = 9.91$, df = 1, p = 0.0016]; monkeys were more likely to look upwards during the test trials (see Fig 15a). There was also a good distribution of individual variation in performance; the average difference score was 0.46 ± 0.13, with difference scores in the task ranging from -1 to 2 across individuals (see Fig 15b).

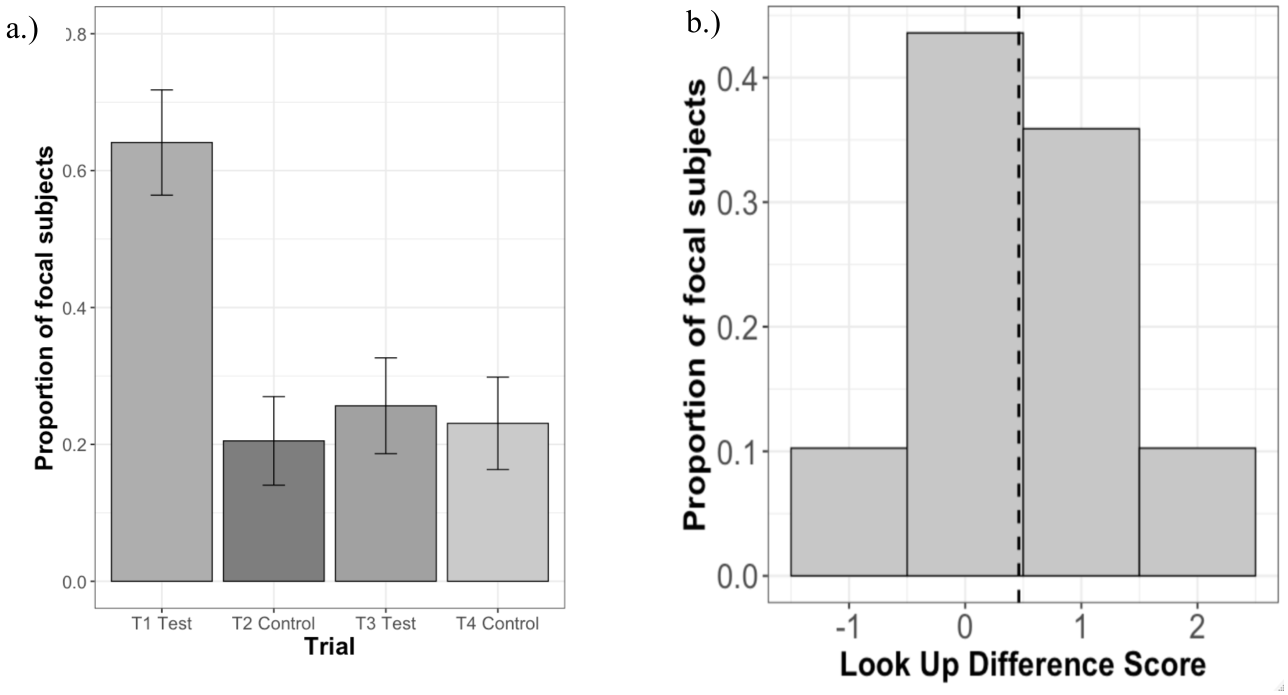

Figure 15: Gaze following task responses. (a) The proportion of monkeys who looked upwards across each trial. (b) The distribution of look up difference scores across monkeys (look up responses in test trials – look up responses in baseline trials, with the look up responses as a binary variable.) Dashed line indicates group mean of the difference score.

We next examined the monkey's looking times in the knowledge attribution task. On average, monkeys looked 4.34 secs ± SE = 0.44 in the first habituation trial, 4.30 ± 0.43 in the second habituation trial, 3.95 secs ± 0.46 in the *unexpected test trial*, but only 3.28 secs ± 0.43 secs in the *expected test trial*. We then assessed patterns of looking in the test trials, the key trials for this task. Our base model included *age, group* and *rank,* the *mean habituation looking time* (average looking time across both habituation trials*)*, and *identity*. In the test model, we then included *trial type* (e*xpected* or *unexpected* test trial*)*. This trended towards improving model fit [LRT: $\chi2$ = 3.43, df = 1, p = 0.064]; monkeys tended towards looking longer in the *unexpected* condition overall (see Fig 16a). In addition, there was a good distribution of individual variation in performance: the average difference score was 0.67 secs ± 0.34, and individual's differences scores ranged from -4 to 7.73 (see Figure 16b).

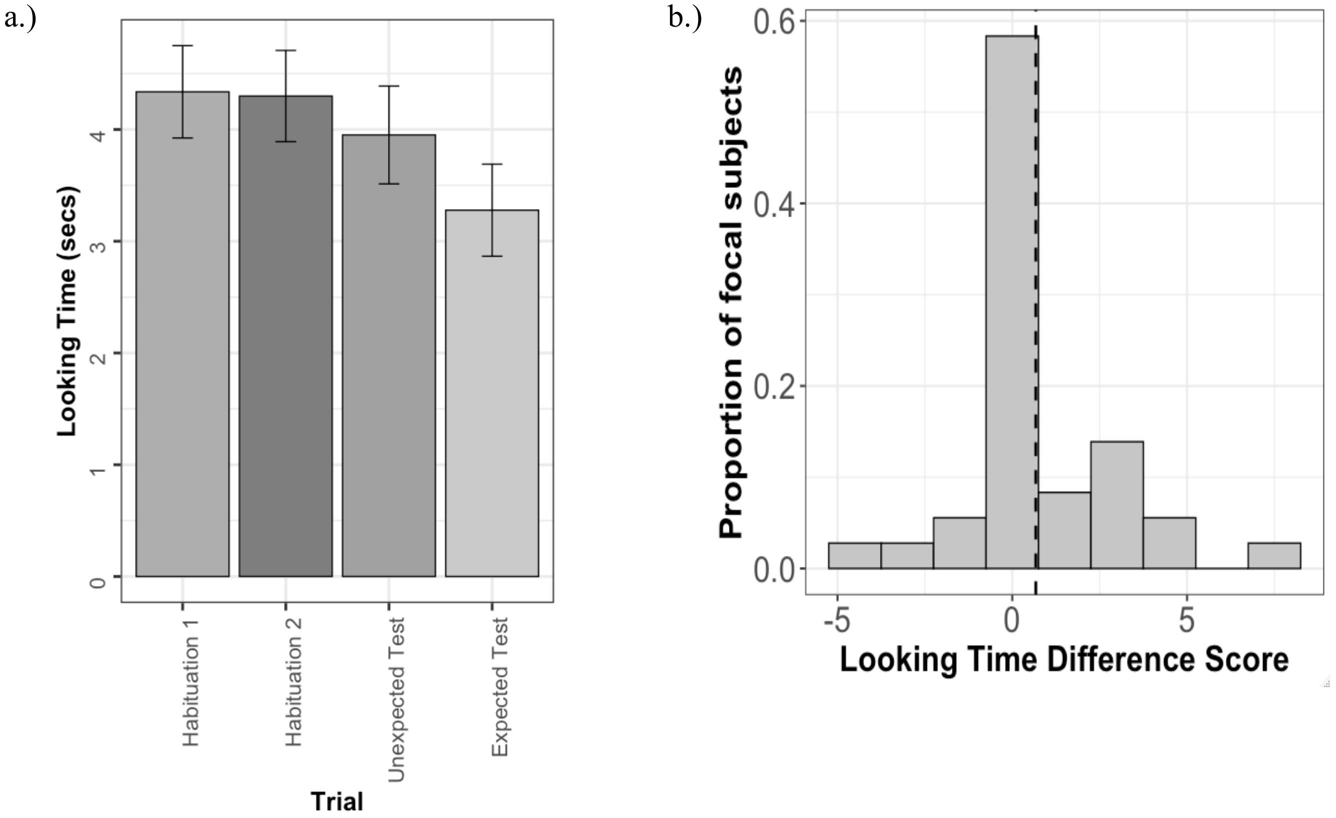

Figure 16: Responses to the knowledge attribution task. (a) Looking time across each trial. (b) Distribution of looking time difference scores (looking time in *Unexpected* trial – looking time in *Expected* trial) for the knowledge attribution task, across monkeys. Dashed line indicates group mean.

We next examined each monkey's looking times in the Goal attribution task. On average, monkeys looked for 2.31 secs ± SE = 0.24 in the *first habituation trial* (where monkeys saw the first set of objects, used in the *unexpected* trial set), and then increased looking to 3.16 secs ± 0.44 in the *unexpected test trial*. In the *second habituation trial* (where monkeys saw the second set of objects, used for the *expected* condition) monkeys looked for 4.97 secs ± 0.43, and then decreased their looking to 2.92 secs ± 0.40 in the *expected test trial*. As the goals task (unlike the knowledge attribution task) used different sets of objects for the unexpected and expected condition, we here analyzed a difference score for each condition: (test trial looking time – habituation looking time) to account for variation in overall interest in the different sets of objects. The mean difference score in the unexpected condition was 0.85 secs ± 0.48, a positive score indicating that monkeys increased their looking to the unexpected outcome, whereas the mean difference score in the expected condition was -2.05 secs ± 0.48, a negative score indicating that subjects continued to habituate to the expected outcome. We then modelled this difference score across condition. In the base model, we included *age, group, rank*, and *identity* as in the prior analyses. In the test model, we then included condition (expected or unexpected), which improved model fit [LRT: $\chi2 = 18.42$, df = 1, p = 1.77e-05]; monkeys had a higher relative looking time scores in the *unexpected* condition (see Fig 17a). In addition, there was a good distribution of individual variation in performance: the average overall difference score was 2.90 ± 0.70, and individuals' overall differences scores ranged from -6.07 to 14.4 (see Fig 17b).

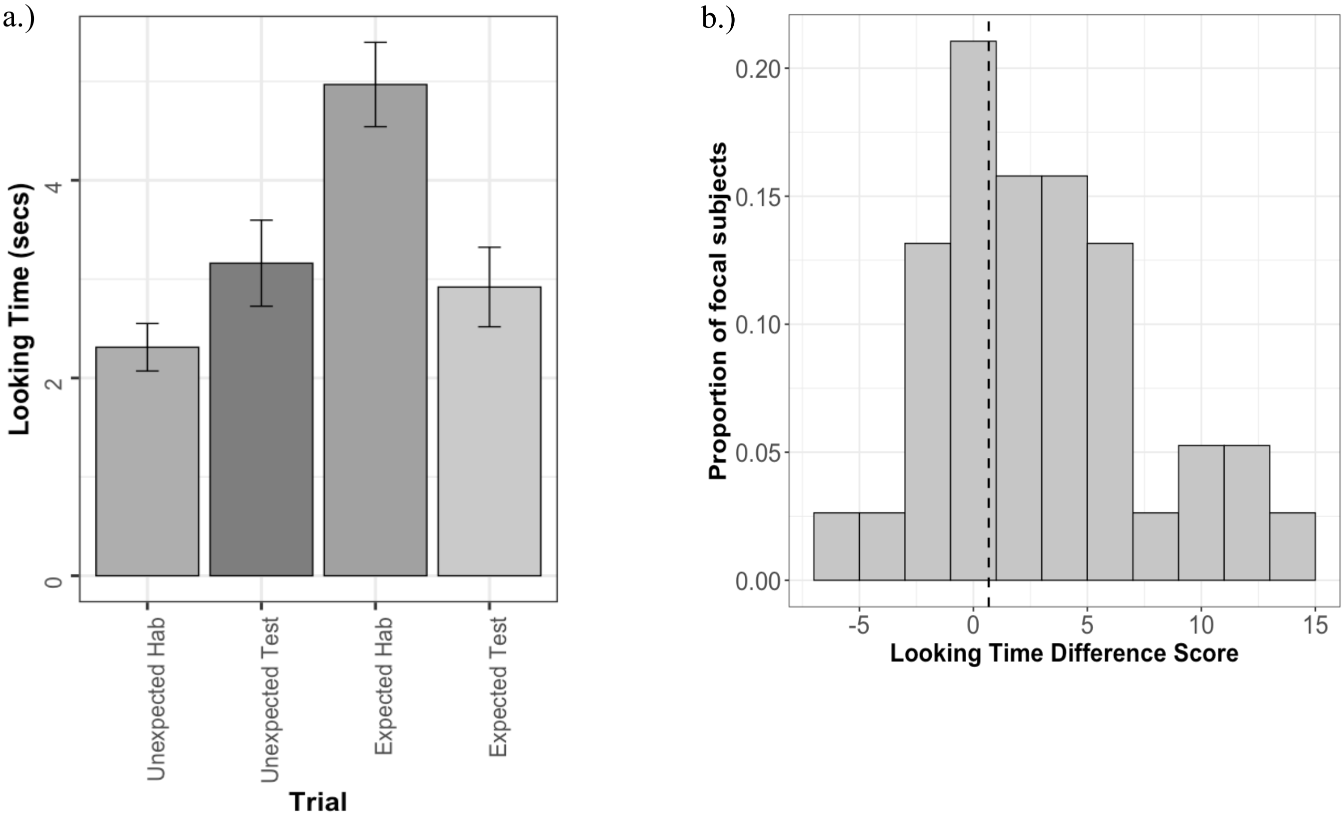

Figure 17: Looking time responses in the goal attribution task. (a) Looking times across each trial. (b) Distribution of looking time difference scores (looking time in *Unexpected* test trial – looking time in *Unexpected* habituation trial/ looking time in *Expected* test trial – looking time in *Expected* habituation trial) across monkeys.

Correlations between cognitive metrics

We ran bivariate Pearson's correlations to assess whether our cognitive measures correlated with each other. We did not find a correlation between the Gaze difference score and the Knowledge difference score [r(33) = 0.012, p = 0.94], between the Gaze difference score and the Goals difference score [r(35) = 0.23, p = 0.17], or between the Knowledge difference score and the Goals difference score [r(32) = 0.15, p = 0.41]; see Fig 18. This suggests that our cognitive tasks tested distinct cognitive abilities, since performance in each task did not predict performance in other tasks. None of our cognitive metrics correlated with age or motivational score, although age negatively correlated with motivational score [r(38) = -0.33, p = 0.035].

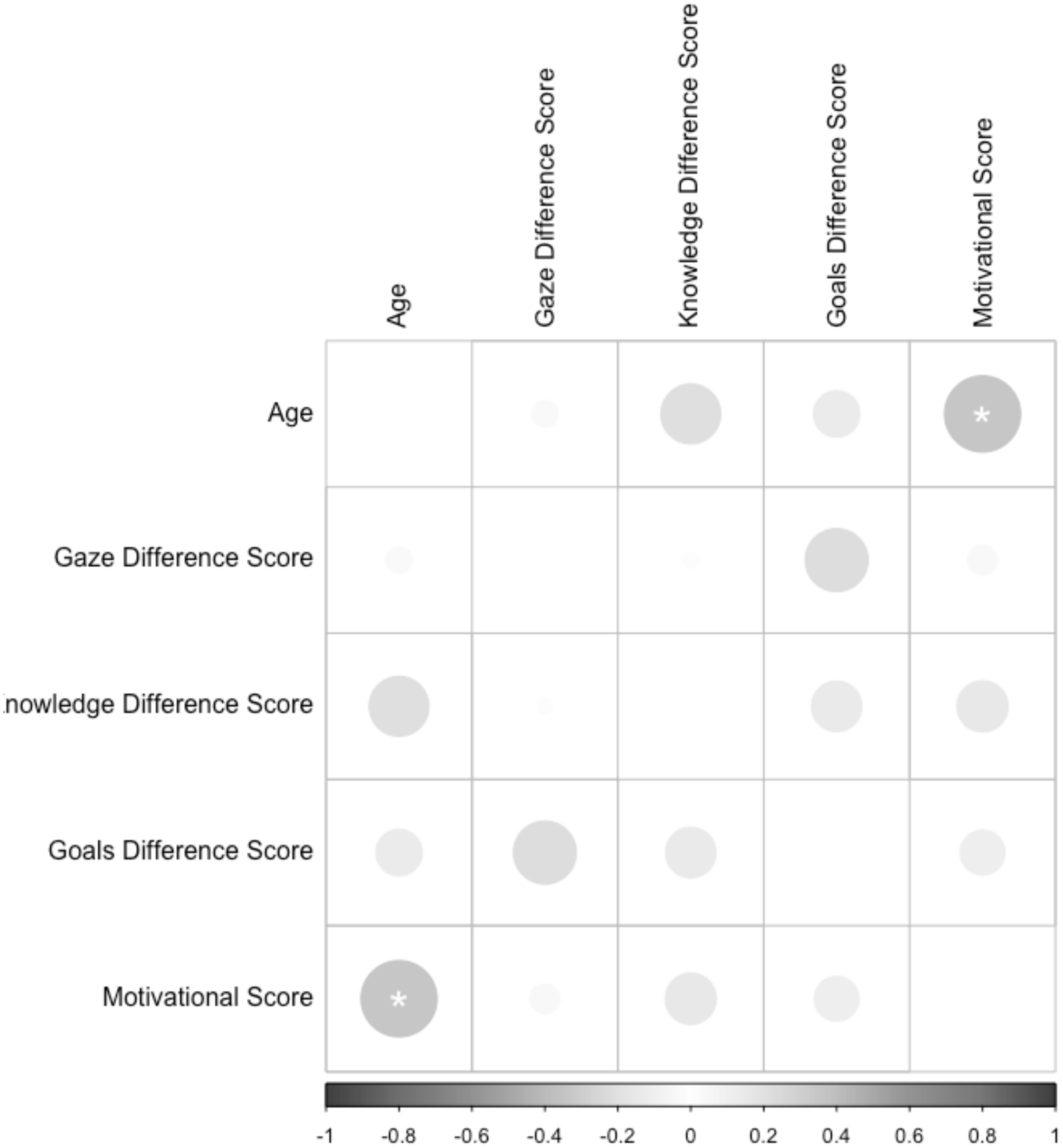

Figure 18: Correlations between different cognitive measures (Gaze difference score, Knowledge Difference Score and Goals difference score) as well as age and motivational score. Size of circle reflects strength of correlation, and star denotes significant relationship. The only significant correlation was between motivational score and Age; older monkeys had a lower motivational score.

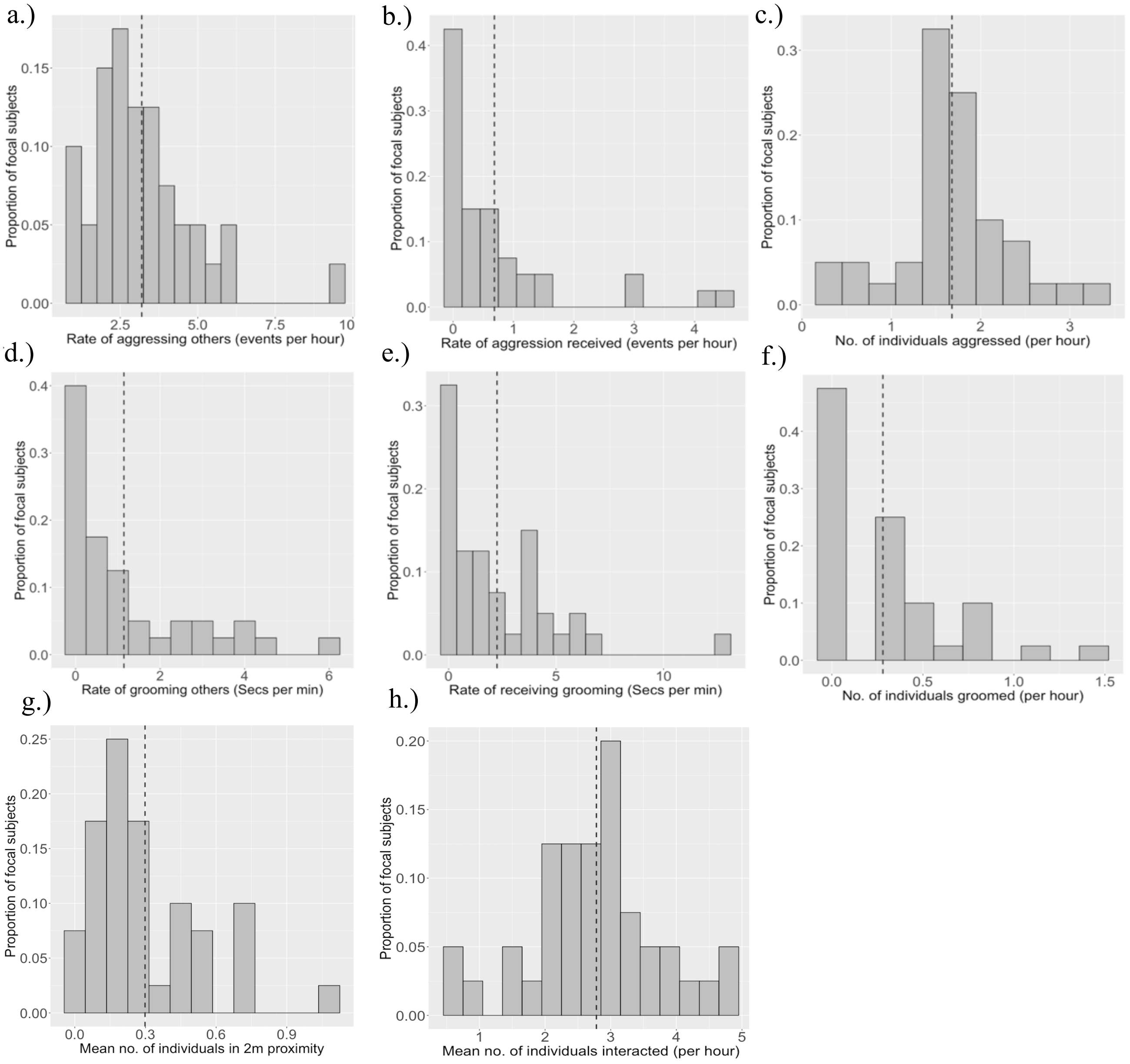

Figure 19: Distribution of behavioral metrics. Dashed line indicates group mean. (a) The rate of aggressing others. (b) The rate of receiving aggression. (c) The number of different individuals aggressed. (d) The rate of grooming others. (e) The rate of receiving grooming. (f) The number of different individuals groomed. (g) Mean number of individuals within 2m proximity during scans. (f) Mean number of individuals interacted with.

Behavioral metrics

We next examined patterns of variation in our social behavioral metrics. Over our 40 subjects, on average there were 0.30 ± SE = 0.04 monkeys in proximity to the focal per scan, which occurred every two minutes. Monkeys actively interacted with an average of 2.78 ± 0.16 individuals per hour across all focals. We then looked at the aggression data, which we calculated as the number of aggressive events per hour of focal time. Monkeys aggressed others at a rate of 3.19 ± 0.26 events per hour, and received aggression at a rate of 0.68 ± 0.18 events per hour. Monkeys aggressed an average of 1.68 ± 0.11 other monkeys per hour of focal follow time. We finally looked at patterns of affiliation. Here, the average rate of grooming others (duration of time spent grooming others in seconds, divided by total follow time in minutes) was 1.14 ± 0.24, and the average rate of time spent being groomed by others was 2.25 ± 0.43 (see Fig 19). Monkeys groomed an average of 0.28 ± 0.056 different individuals per hour of focal follow time. Additional analyses examined if these metrics varied by subject's rank or age (reported in the next section).

We then performed a series of bivariate Pearson's correlations to assess whether these behavioral measures correlated with each other. For the data on sociability, we found a correlation between the number of individuals interacted with and the mean number of individuals within 2m [r(38) = 0.53, p = 0.00038], see Fig 20, suggesting these metrics were capturing similar variation. We also found a negative correlation between age and number of individuals interacted with [r(38) = -0.35, p = 0.027], which was expected based on prior work (Rathke & Fischer, 2020): we therefore controlled for age through analyses.

There was similarly a correlation between the rate of aggressing others and the number of different individuals that the subject aggressed [r(38) = 0.81, p = 3.44e-10], see Fig 20, suggesting again that these core metrics also captured similar variation. Rate of aggressing others and the rate of being aggressed were not correlated [r(38) = 0.14, p = 0.39], which is not surprising given that individuals may avoid aggressing higher ranking monkeys– who in turn may be more likely to aggress other individuals. In line with this, the rate of aggressing others correlated with rank (as

MDS) [r(38) = 0.42, p = 0.007], and the rate of receiving aggression showed a negative correlation with rank [r(38) = -0.44, p = 0.005]. We therefore controlled for rank through all analyses.

Finally, in looking at affiliative measures there was a correlation between rate of grooming others and number of individuals groomed [r(38) = 0.68, p = 1.25e-6], suggesting that these measures captured similar variation. However, we found no correlation between the rate of giving and receiving grooming [r(38) = 0.11, p = 0.51], which is again not surprising given that grooming may be directed up the hierarchy. In line with this, we found a correlation between rank and receiving grooming [r(38) = 0.43, p = 0.006]. Overall, this suggests that our core measures of sociality, competition, and affiliation captured relevant variation in different components of social behavior.

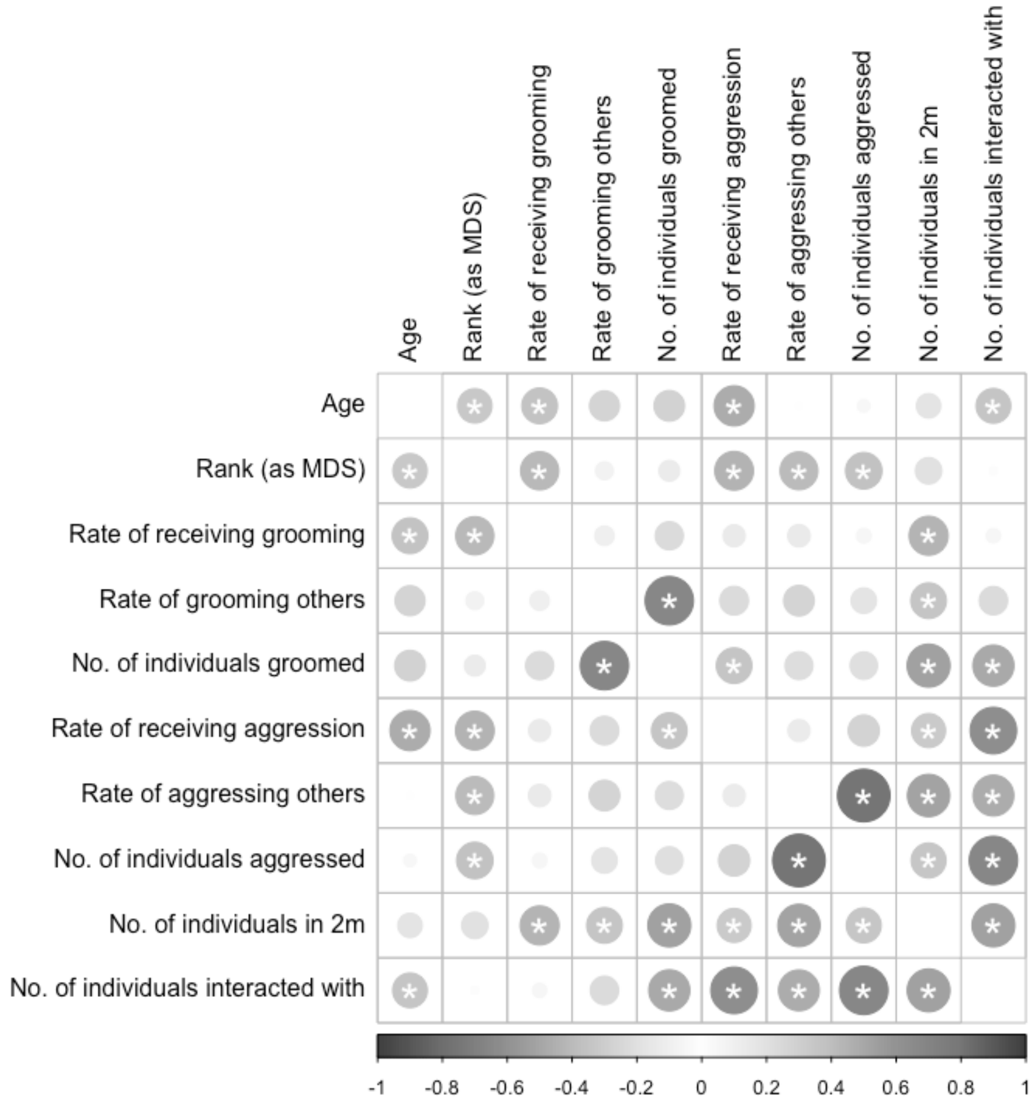

Figure 20: Correlations between different behavioral metrics. Size of circle indicates strength of correlation, and star denotes significant relationship.

Relationships between cognition and social behavior

We then examined whether individual responses were predicted by patterns of natural social behavior, performing separate analyses to assess the relationships between cognition and sociability, aggression and affiliation.

Relationships between cognition and sociability

We first assessed whether social cognitive performance predicts overall sociability. To start, we modelled the average number of individuals that the focal was within 2m proximity to. We accounted for age, rank, group and motivational score. Rank was trending towards being a significant predictor; higher ranking monkeys tended to have more individuals in proximity. Group also trended towards being a significant predictor; individuals from the German group tended to have more individuals within 2m proximity. We then added individual's *gaze score* in the second model, which trended towards improving model fit [LRT: $\chi2 = 0.18$, df = 1, p = 0.051]; individuals with a higher *gaze score* tended to have more individuals within proximity, see Fig 21 and Table 6. We then added the *knowledge score*, which did not improve model fit [LRT: $\chi2 = 0.021$, df = 1, p = 0.50]. Finally, we added the *goals score*, which improved model fit [LRT: $\chi2 = 0.29$, df = 1, p = 0.0077]; individuals with a higher Goals difference score had a higher average number of individuals within proximity, see Fig 22 and Table 7. As a final test, we examined whether adding the composite score, which integrated performance across tasks, to the base model improved fit, and it did not [LRT: $\chi2 = 0.047$, df = 1, p = 0.28]. Overall, this suggests that following others' gaze may predict this metric of sociability.

We also modelled the number of individuals that each focal interacted with using the same approach. We again included age, rank and group in the base model; age was the only significant predictor. In line with prior research, older monkeys interacted with fewer individuals (Rathke & Fischer, 2020). Inclusion of neither the *gaze score* [LRT: $\chi2 = 1.07$, df = 1, p = 0.25], the *knowledge score* [LRT: $\chi2 = 0.075$, df = 1, p = 0.76], or the *goals score* improved model fit [LRT: $\chi2 = 0.76$, df = 1, p = 0.23]. We also added the *composite score*, which did not improve model fit either [LRT:

χ2 = 0.35, df = 1, p = 0.40]. Overall, this suggests that different cognitive process may play a role in proximity to others versus direct interactions with others.

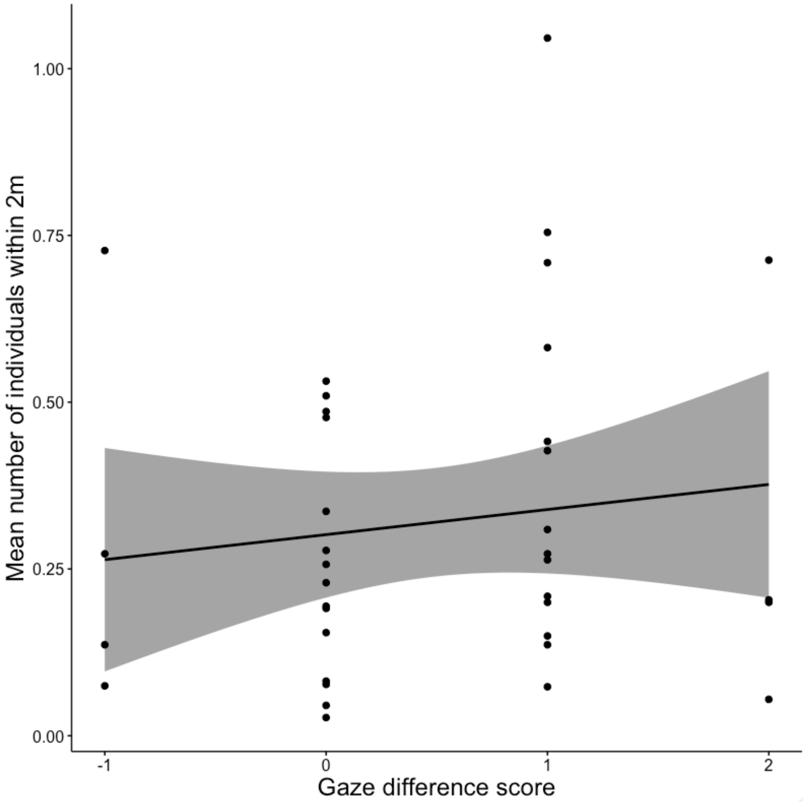

Figure 21: Relationship between gaze difference score, and the mean number of individuals within 2m proximity.

	Estimate	**Standard Error**	**t**	**P value**
Age (as covariate)	-0.013	0.008	-1.580	0.124
Medium rank (reference: low rank)	-0.035	0.091	-0.384	0.704
High rank (reference: low rank)	0.166	0.090	1.842	0.075
Group (reference: French)	0.179	0.073	2.452	0.020*
Motivational score (as covariate)	0.039	0.077	0.513	0.612
Gaze difference score	0.092	0.047	1.953	0.060

Table 6: Predictors from the model predicting the mean number of individuals within 2m proximity. This model was compared to a base model that only included age, rank, group and motivational score as predictors. Baseline reference for predictors indicated in table.

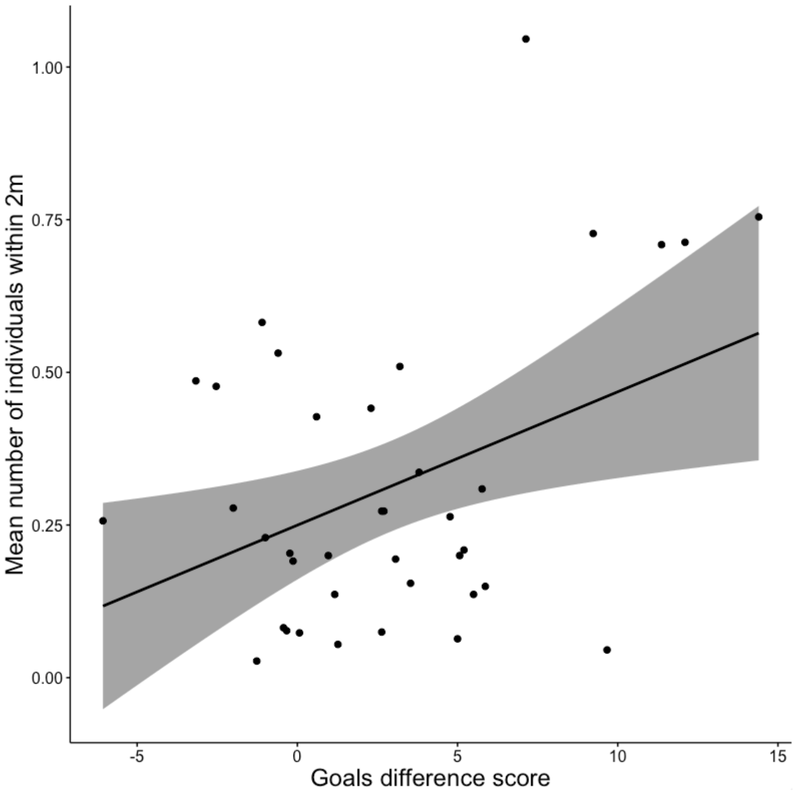

Figure 22: Relationship between goals difference score and the mean number of individuals within 2m proximity.

	Estimate	Standard Error	t value	P value
Age (as covariate)	-0.007	0.008	-0.942	0.354
Medium rank (reference: low rank)	-0.093	0.083	-1.124	0.270
High rank (reference: low rank)	0.078	0.088	0.887	0.382
Group (reference: French)	0.165	0.067	2.470	0.019
Motivational Score (as covariate)	0.064	0.071	0.908	0.371
Goals difference score	0.020	0.008	2.666	0.012*

Table 7: Predictors from the model predicting the mean number of individuals within 2m proximity. This model was compared to a base model that only included age, rank, group and motivational score as predictors. Baseline reference for predictors indicated in table.

Relationships between cognition and aggression

We took a similar approach to test the role of different social cognitive processes in competition. First, we modelled each subject's rate of aggressing other individuals. In the base model, we included the subject's age, group membership, rank and motivational score. Rank was a significant predictor in this base model: high- and medium-ranking monkeys aggressed others more than low-ranking monkeys, as expected based on past work. We then added the subject's *gaze score* [LRT: $\chi2 = 0.75$, df = 1, p = 0.58], then *knowledge score* [LRT: $\chi2 = 2.63$, df = 1, p = 0.28], neither of which improved model fit. We then added the *goals score,* which showed a trending relationship to improve model fit [LRT: $\chi2 = 6.56$, df = 1, p = 0.08]; monkeys with a higher *goals score* tended to aggress other individuals at a higher rate, see Fig 23 and Table 8. As a final test, we added the Composite score, which did not improve fit [LRT: $\chi2 = 2.30$, df = 1, p = 0.33].

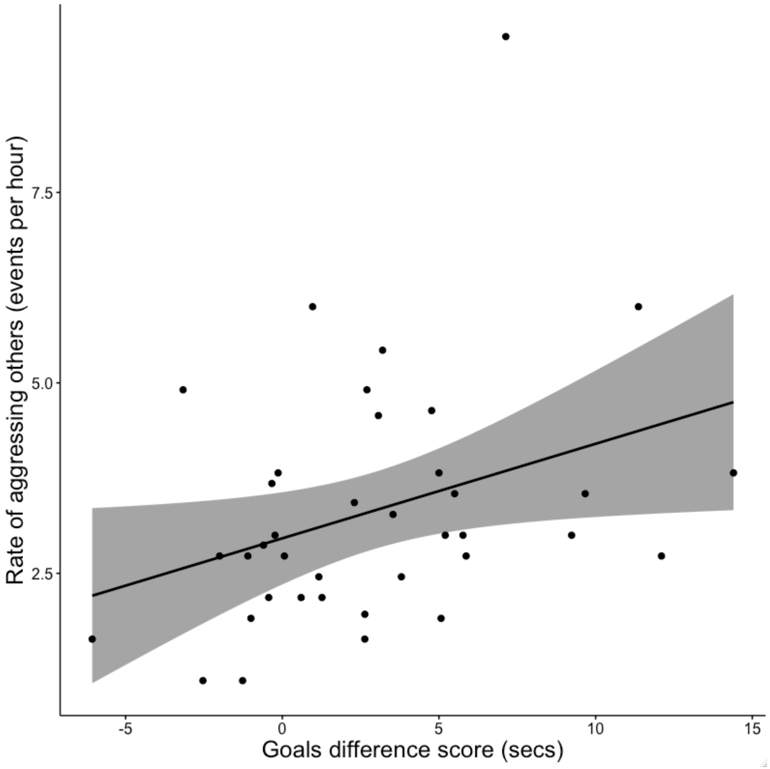

Figure 23: Relationship between the goals difference score and the rate of aggressing other individuals.

	Estimate	**Standard Error**	**t value**	**P value**
Age (as covariate)	0.016	0.056	0.282	0.780
Group (reference: French)	0.306	0.480	0.637	0.529
Motiovational Score (as covariate)	0.518	0.508	1.021	0.315
Medium rank (reference: low rank)	1.378	0.595	2.317	0.027*
High rank (reference: low rank)	1.390	0.630	2.206	0.035*
Goals difference score	0.097	0.055	1.766	0.087

Table 8: Predictors from the model predicting the rate that the focal aggressed other individuals. This model was compared to a base model that only included age, rank, group and motivational score as predictors. Baseline reference for predictors indicated in table.

Next, we modelled the number of different individuals that each subject aggressed. In the base model, we found that rank was again a significant predictor: medium- and high-ranking monkeys aggressed more individuals than did lower-ranking monkeys. Inclusion of the *gaze score* did not improve model fit [LRT: $\chi2 = 0.023$, df = 1, p = 0.80]. Similarly, neither the *knowledge score* [LRT: $\chi2 = 0.84$, df = 1, p = 0.12] or *goals score* [LRT: $\chi2 = 0.66$, df = 1, p = 0.14] improved model fit. Finally we added the *composite score,* which also failed to improve model fit [LRT: $\chi2 = 0.0029$, df = 1, p = 0.92].

Finally, we modelled each subject's rate of receiving aggression from other individuals. This is different from aggressing other individuals; while monkeys might use social intelligence to enable their abilities to successfully aggress others, it is in the best interest of each monkey to receive minimal aggression from others. In the base model, only age was a significant predictor; older monkeys received less aggression. Inclusion of neither the *gaze score* [LRT: $\chi2 = 0.05$, df = 1, p = 0.82], *knowledge score* [LRT: $\chi2 = 0.11$, df = 1, p = 0.69], nor *goals score* [LRT: $\chi2 = 1.90$, df = 1, p = 0.15] improved fit. Finally, we added the Composite score, which also failed to improve model fit [LRT: $\chi2 = 1.47$, df = 1, p = 0.12]. This suggests that the cognitive processes impacting avoidance of aggression may be different from those governing decisions to aggress others.

Relationships between cognition and affiliation

We finally assessed whether grooming was predicted by social cognitive performance. We assessed each individual’s rate of grooming others. Here, neither age, rank or group were significant predictors in the base model. Inclusion of the *gaze score* did not improve model fit [LRT: $\chi2 = 0.94$, df = 1, p = 0.53]. Similarly, the *knowledge score* [LRT: $\chi2 = 0.63$, df = 1, p = 0.60], *goals score* [LRT: $\chi2 = 0.35$, df = 1, p = 0.70] and *composite score* [LRT: $\chi2 = 0.72$, df = 1, p = 0.86] all failed to improve model fit. This suggests that these cognitive processes do not drive variation in the rate of grooming others.

We then examined the number of different individuals that each subject groomed. The base model showed that monkeys from the ‘German’ group had a higher number of grooming partners overall than those in the ‘French’ group. Inclusion of the *gaze score* [LRT: $\chi2 = 0.016$, df = 1, p = 0.70], the *knowledge score* [LRT: $\chi2 = 0.016$, df = 1, p = 0.68], *goals score* [LRT: $\chi2 = 0.0036$, df = 1, p = 0.85] and *composition score* [LRT: $\chi2 = 0.00011$, df = 1, p = 0.97] all failed to improve model fit. This suggests that these social cognitive abilities do not affect the number of different grooming partners.

We finally examined the rate of receiving grooming from others. In the base model, rank was a significant predictor; higher-ranking monkeys received more grooming, which was expected based on prior work. In addition, rates of being groomed were trending towards being higher within the German group specifically. Inclusion of the *gaze score* improved model fit [LRT: $\chi2 = 24.64$, df = 1, p = 0.02]; monkeys with a higher *gaze score* received grooming at a higher rate, see Fig 24 and Table 9. Neither inclusion of the *knowledge score* [LRT: $\chi2 = 0.38$ df = 1, p = 0.78], the *goals score* [LRT: $\chi2 = 1.00$, df = 1, p = 0.67], or the *composite score* [LRT: $\chi2 = 3.08$, df = 1, p = 0.43] improved model fit. Overall, this suggests that gaze-following has a role in promoting affiliative interactions, such as receiving grooming from others.

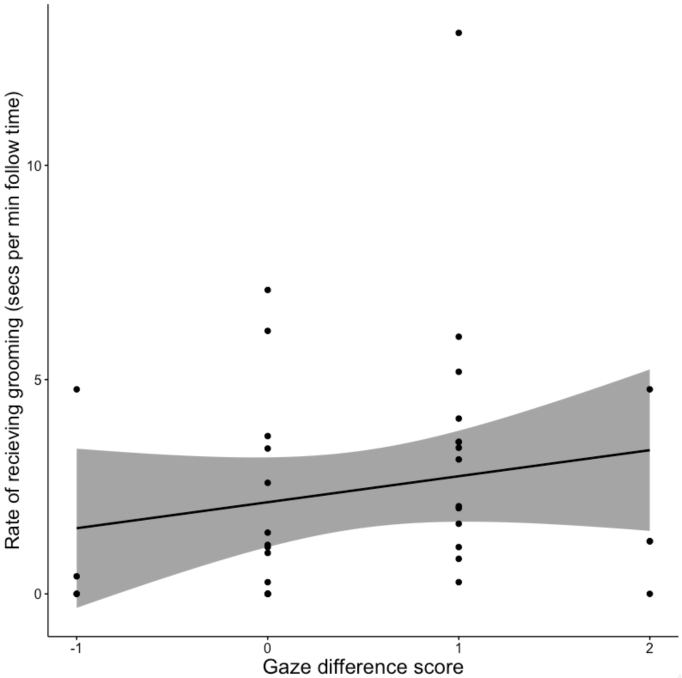

Figure 24: Relationship between gaze difference score and rate of receiving grooming.

	Estimate	**Standard Error**	**t value**	**P value**
Age (as covariate)	0.114	0.083	1.381	0.177
Group (reference: French)	1.826	0.720	2.536	0.016*
Motivational score (as covariate)	-0.359	0.757	-0.474	0.639
Medium rank (reference: low)	0.187	0.897	0.208	0.836
High rank (reference: low)	2.627	0.888	2.957	0.006*
Gaze difference score	1.067	0.463	2.302	0.028*

Table 9: Predictors from the model predicting the rate that the focal received grooming. This model was compared to a base model that only included age, rank, group and motivational score as predictors. Baseline reference for predictors indicated in table.

Discussion

We experimentally measured multiple social cognitive skills and observed real-world social behaviors in the same individuals. Our results show that social intelligence predicts several metrics of social behavior in free-ranging Barbary macaques, supporting the social intelligence hypothesis. In particular, we found that abilities to follow others' gaze were an important predictor of the rate of receiving grooming from other individuals, and showed a trending affect to predict the number of individuals that the focal was near. The ability to attribute goals predicted the number of individuals that the focal was near, but also showed a trending affect to predict the rate that the focal aggressed other individuals. Overall, this suggests that social cognition may facilitate sociable patterns of behavior in this tolerant species, and may help make the individual an attractive social partner. Given that we found some evidence that goal attribution abilities predict aggression, this ability may also further facilitate successful social competition—this relationship between cognition and aggression might be stronger in a despotic species, or for especially complex forms of aggression. Understanding how cognition predicts 'real-world' social behavior provides key insights into how these cognitive abilities evolved, and became so exaggerated in humans.

This data represents the first empirical evidence linking individual variation in social intelligence to real-world behavior in primates, providing a critical test of the social intelligence hypothesis. This proposal, broadly defined, argues that primate social complexity selected for intelligence to deal with these social challenges (Byrne & Whiten, 1990; Dunbar, 1998; Hare, 2017b; Humphrey, 1976b; Jolly, 1966b). A key assumption of this hypothesis is that social intelligence shapes patterns of social behavior, as this is the trait that selection can 'see' and therefore can act upon. In this study, we utilized well-validated measures of social cognition to demonstrate how different social cognitive abilities (gaze-following, knowledge attribution and goal attribution) impact patterns of natural social behavior in Barbary macaques, a species that lives in complex social groups and previously demonstrated social cognitive abilities such as knowledge attribution (Arre et al., 2021) and the ability to follow gaze (Rosati & Santos, 2017). Our results provide evidence that social cognition does shape patterns of natural social behavior in primates, providing a 'substrate' for selection to act upon. This works adds to prior research linking social complexity to measures of brain size (Barton, 1996; Dunbar, 1998), and to work that links the presence of sophisticated forms of aggression to brain size (Byrne & Corp, 2004), but extends this research by directly measuring the cognitive traits in question.

Which aspects of social behavior might be enabled by sophisticated social cognition, in Barbary macaques? First, we found that propensity to follow gaze predicted the rate of being groomed by others, and showed a trending affect towards predicting the number of individuals within close proximity to the focal. Consequently, this provides support for hypotheses that have linked social cognition to patterns of affiliation (Cheney et al., 1986; Hare, 2017), and to overall sociability (Dunbar, 1998). Importantly, gaze-following ability did not predict the rate that the focal groomed other individuals, but instead only predicted the rate of being groomed by other individuals. Taking the two results together, one possibility is therefore that individuals with high rates of gaze-following are especially motivated to be in proximity to others—which results in getting groomed at a high frequency, even if this individual does not otherwise engage with others at an especially high rate. A complementary possibility is that other individuals might be especially motivated to be in proximity and groom these individuals with high rates of gaze-following, for instance because they are especially attractive social partners. Our findings align with prior work that have linked gaze-following to social motivation: while the role of gaze-following in promoting natural patterns of social behavior has not previously been tested in macaques, work with humans has found that people with autism show lower rates of gaze-following, and are also less motivated to socially engage with others (Bedford et al., 2012; Leekam et al., 1998).

Second, we found that the ability to attribute goals to other individuals predicted the number of individuals within 2m proximity, and showed a trending affect to predict the rate that the focal aggressed other individuals. This therefore provides support for the hypothesis that social intelligence allows individuals to interact with a larger number of individuals (Dunbar, 1998b), and also provides some support for the hypothesis that social intelligence enables aggression (Whiten & Byrne, 1988). Regarding the finding that goal attribution ability predicts the number of individuals in proximity to the focal, one possibility is that individuals who are skilled at recognizing other's intentions are better able to recognize the competitive or affiliative intent of other individuals, enabling them to recognize when being in proximity is welcomed versus when it is not– individuals who lack this sensitivity to others' intent may instead choose to spend their time away from other individuals. Sensitivity to others' goals might also all individuals to recognize opportunities for social competition ("he wants that piece of food"), facilitating aggression.

Notably, we found stronger evidence that cognition affects patterns of sociability than patterns of aggression—although we did find a trending relationship between goal attribution ability and aggression produced from the focal. This may be due to the tolerant social system of Barbary macaques; in despotic species with high rates of severe aggression, it may be more critical to utilize social intelligence to facilitate aggression. In line with this idea, most experimental work has generally found strongest evidence for theory of mind abilities in primates, such as knowledge and goal attribution, within competitive paradigms (perspective taking: Canteloup et al., 2016; Flombaum & Santos, 2005; Santos et al., 2006. Knowledge attribution: Marticorena et al., 2011;

Martin & Santos, 2014; Overduin-de Vries et al., 2014—although see Bettle & Rosati, 2019 for evidence that rhesus macaques can utilise a sophisticated understanding of others' gaze in a neutral context). Another potential explanation for our lack of relationship between cognition and aggression is that social intelligence might specifically enable aggressive behaviors that are thought to be cognitively-taxing, such as tactical deception (the ability to deliberately mislead another individual for one's own gain; Byrne & Whiten, 1990), and the formation of aggressive coalitions (Alexander, 1989; Harcourt & de Waal, 1992). While we examined overall rates of aggression as a first attempt to address the social intelligence hypothesis, one possibility is that social intelligence specifically enables 'complex' forms of aggression. Consequently, one goal for my future work is to specifically examine patterns of coalitionary aggression using the focal data from this project, including coding from filmed focal follows.

An alternative explanation for our results is that the relationships we observed between our cognitive measures and behavioral metrics were caused by an unidentified third variable that correlates with both the cognitive measures and behavioral metrics. While it is impossible to rule out this possibility, we did aim to account for the most obvious possibilities. First, one possibility is that rank could drive differences in both cognitive tasks and social behavior. For example, the ability to do well in our cognitive tasks might requires resources or time, and monkeys who have these resources may be high ranking and thus more likely to engage in aggression. Indeed, its currently unclear how rank may affect social cognition as most studies in cognition are not able to extract specific rank metrics (Arre et al., 2021; Drayton & Santos, 2017; Marticorena et al., 2011; Martin & Santos, 2014; Rosati & Santos, 2017; Santos et al., 2006). However, we could successfully extract animal's rank from our social observations and all analyses here accounted for rank. A second possibility is that general difference in motivation and attention may drive the variation we see here. However, all of our cognitive metrics all used ‘difference scores’ to measure performance (e.g. looking time in the *Unexpected* trial – looking time in the *Expected* trial) which accounted for overall variation in looking and rather extracted patterns of *relative* looking or gazing to index success. In addition, we explicitly measured motivation and interest in the experimental stimuli in the motivational control, and our analyses included this as a covariate.

One possible limitation of this research is that we used a human demonstrator rather than a conspecific. We did so for practical reasons given that it is impossible to prompt conspecifics to engage in appropriate behaviors across tasks and conditions. Use of a human demonstrator allowed us to tightly control the demonstrator’s behavior across all individuals, in a way that would not be feasible with conspecific demonstrator. Importantly, current work indicates that macaques follow the gaze of both human and conspecific demonstrators at similar rates (Ferrari et al., 2000; Rosati & Santos, 2017; Teufel et al., 2010; Tomasello et al., 2001). Further, most work demonstrating more sophisticated social cognitive skills in macaques have also used a human demonstrator (Arre et al., 2021; Drayton & Santos, 2017; Marticorena et al., 2011; Martin & Santos, 2014; Santos et al., 2006). The fact that these experimental measures correlated with real-world patterns of social behavior with conspecifics also strongly suggests that our social cognitive tasks actually measured relevant features of social cognition, and that the subjects viewed the demonstrator as a social agent.

In sum, we found that individual variation in Barbary macaque social cognition predicted several metrics of natural social behavior. Overall, these results support the social intelligence hypothesis by demonstrating that more robust social cognition does shape some facets of social behavior. But this study also goes beyond this basic proposal to examine the specific processes by which cognition drives different specific aspects of social behavior. In particular, we found relationships between cognition and patterns of sociability and affiliation, within this tolerant species. Overall, understanding the relationship between cognition and patterns of natural behavior in primates will enable a richer understanding of how social intelligence evolves, including the social intelligence abilities that are uniquely exaggerated in humans.

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Chapter 6: The Primate Origins of Human Social Cognition[3]

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.

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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.

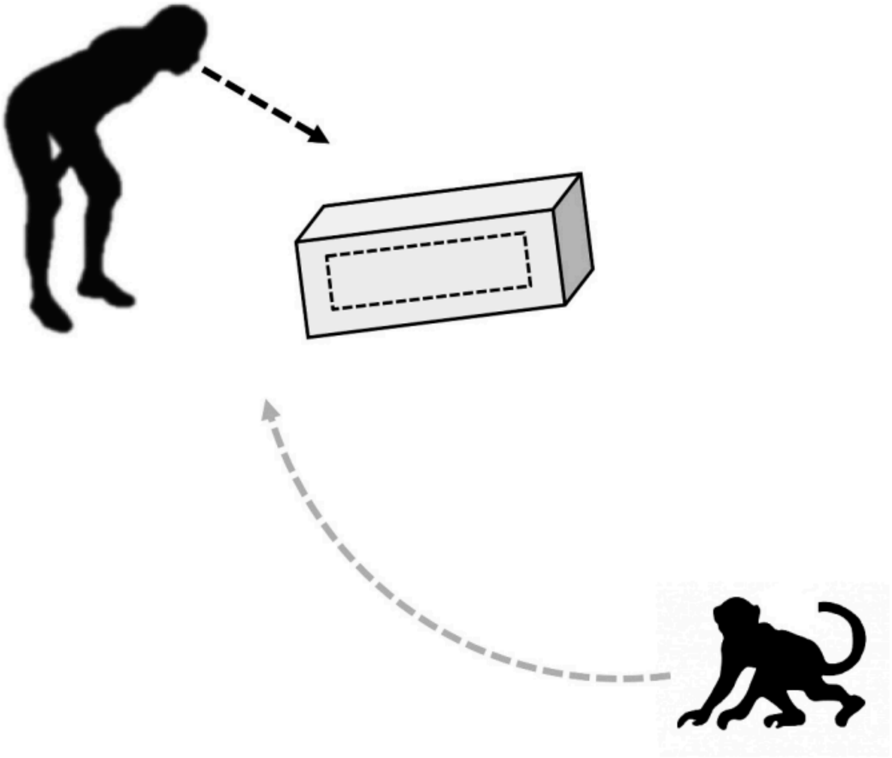

Figure 25: Testing geometric gaze-following in primates (adapted from Bettle & Rosati, 2019). The monkey watches as a human demonstrator looks towards behind a free-standing box. In the barrier condition, the monkey cannot see the target location, whereas in the no-barrier condition there is a window 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).

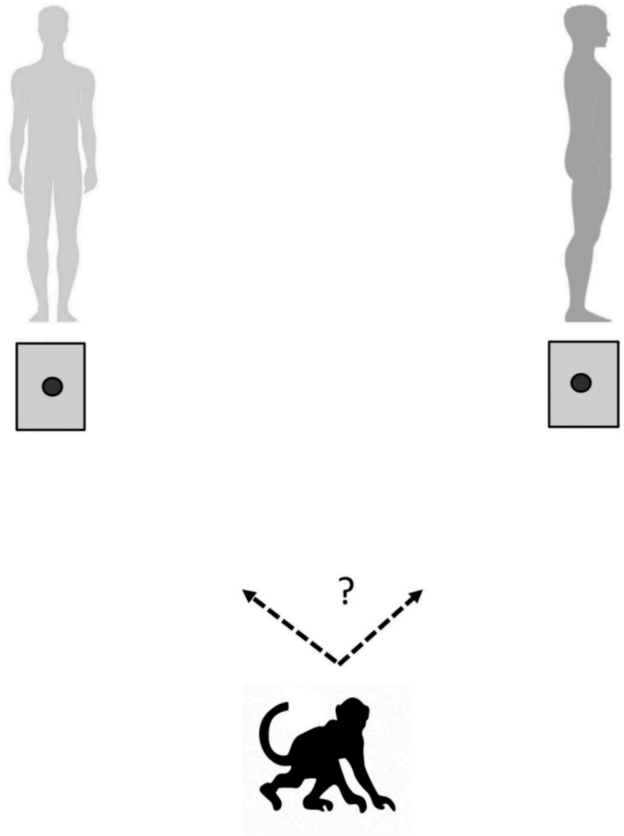

Figure 26: Testing visual perspective-taking in primates (adapted from Flombaum & Santos 2005). The monkey has the opportunity to 'steal' a contested grape from one of two human competitors. One of these competitors can see the grape in front of them as well as the monkey's approach, whereas the other 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 27). 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.

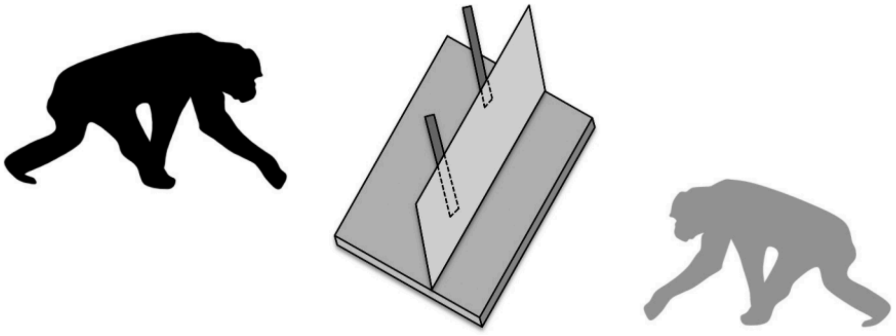

Figure 27: Testing level-2 visual perspective-taking in primates (adapted from Karg et al 2016). Here, two chimpanzees have a different perspective on the same objects (two breadsticks). While the subject chimpanzee (on the left) can see that both breadsticks are the same size, from the competitor's 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 28). In contrast, six-year-old children do account for other's false beliefs in this same situation.

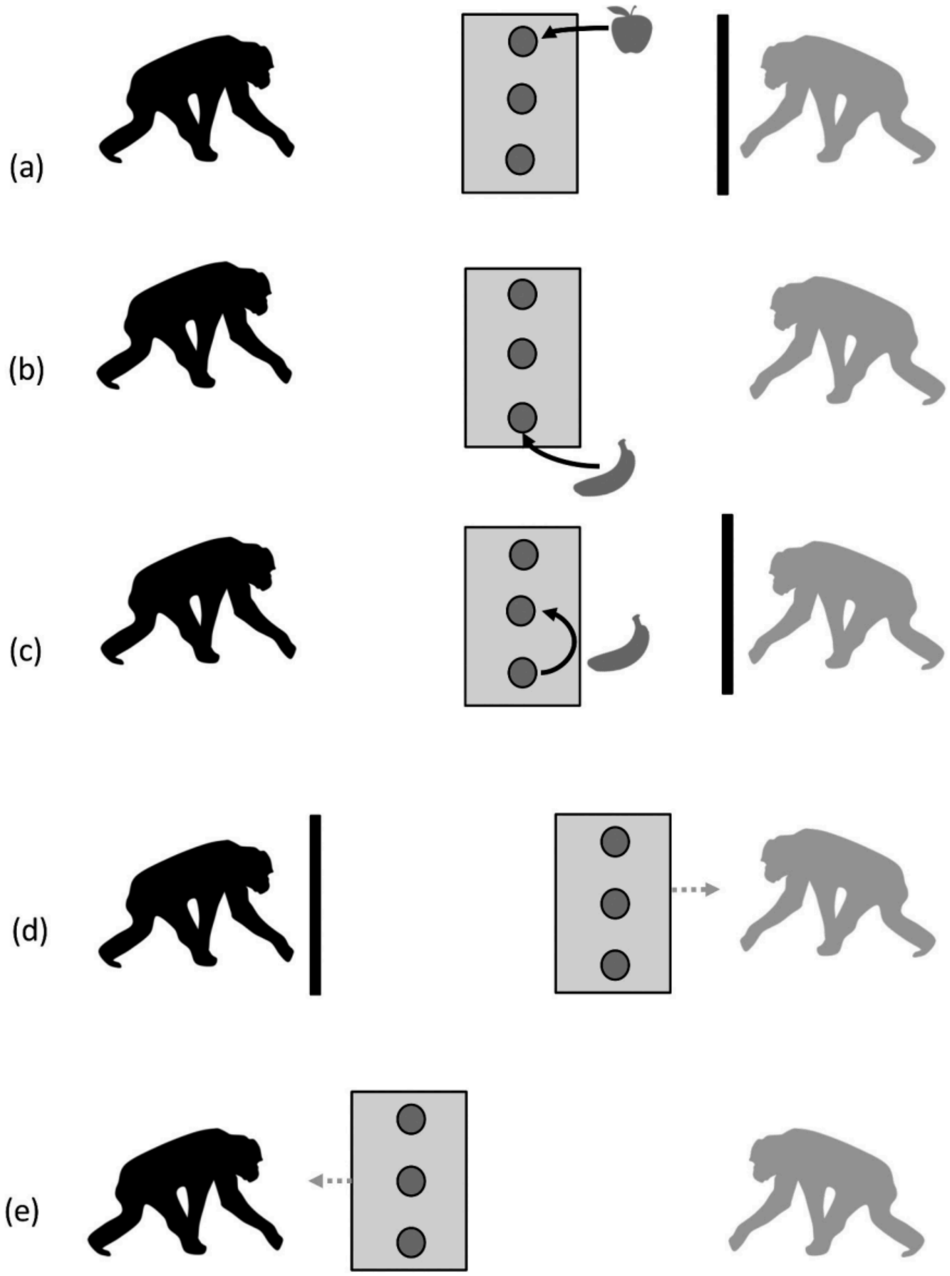

Figure 28: Testing false belief understanding in primates (adapted from Kaminski et al. 2008). Two chimpanzees play a back-and-forth game to acquire food hidden in containers. (a) The subject chimpanzee (on the left) watches as a low value food item (apple) is hidden; the competitor's view is occluded. (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 29). 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).

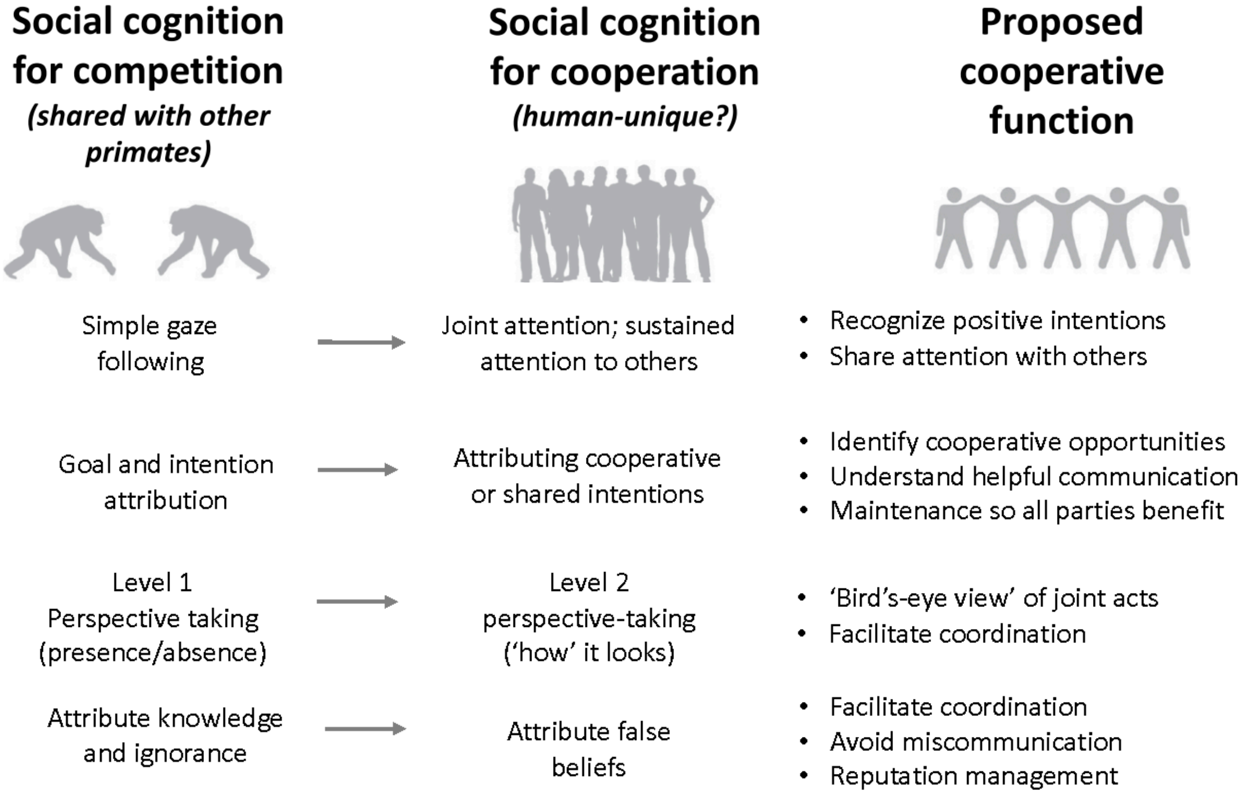

Figure 29: Evolutionary transitions from non-human to human theory of mind. Human unique-components of theory of mind are proposed to extend or elaborate on components of social cognition shared with other primate species. Whereas nonhuman primate social cognition may serve a primarily competitive function, 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 involve 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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Chapter 7: General Discussion

Summary of results

This dissertation examined the evolution of social intelligence by first testing patterns of social cognitive abilities across species that vary in social style, and second testing how individual variation in cognition predicts patterns of natural social behavior. In Chapter 2, I found that despotic rhesus macaques can account for another individual's line-of-sight during their gaze-following response. Further, rhesus macaques can utilize this sophisticated understanding of other's gaze even within a non-competitive context, in contrast to hypotheses arguing that primates show these abilities primarily within competitive contexts (Hare, 2001; Lyons & Santos, 2006). In Chapter 3, I contrasted the abilities of rhesus macaques and more tolerant Barbary macaques to account for others' line-of-sight. Despite hypotheses predicting that either more tolerant species (Cheney et al., 1986; Hare, 2017) or more despotic species (Byrne & Whiten, 1990; Hare, 2001) should show more robust social cognitive abilities, both species performed similarly in this paradigm. However, neither species was especially motivated to actually share attention with the demonstrator; both species showed low rates of approach towards the object that the demonstrator looked into, in contrast to human infants in analogous paradigms (Moll & Tomasello, 2004). In Chapter 4, I then tested rhesus macaques' sensitivity to gaze as a communicative ("ostensive") cue, which has been proposed to be an ability that facilitates efficient cultural learning in humans. I found that rhesus macaques did not pay preferential attention to events following social cues, in contrast to human infants in similar paradigms (Csibra & Gergely, 2011). Overall, this suggests that the use of gaze as a cue for communication, or to share attention more broadly, may be exaggerated in humans.

In my final empirical chapter, I then examined how individual variation in Barbary macaque social cognition predicts patterns of social behavior. Chapter 5 shows that social cognitive abilities in Barbary macaques (as measured by an experimental social cognition test battery) predict several measures of social behavior. In particular, gaze-following predicted the rate of receiving grooming, and showed a trending effect to predict the average number of individuals within proximity. Goal attribution ability predicted the number of individuals within proximity, and showed a trending affect to predict the rate of aggressing other individuals. Overall, this suggests that social cognitive abilities are utilized to enable patterns of sociability (and increase an individual's attractiveness as a grooming partner), in line with hypotheses which have focused upon the role of sociability and affiliation in driving the emergence of social intelligence (Cheney et al., 1986; Dunbar, 1998; Hare, 2017). However, social cognition may also play a role in generating aggression even within this tolerant species, in accordance with proposals that social intelligence facilitates patterns of social competition (Whiten & Byrne, 1988). Taken together, this highlights that social intelligence may evolve via facilitating both affiliative and competitive patterns of behavior. Finally, in Chapter 6 I developed a theoretical framework for understanding variation in primate versus human social cognition, arguing that while social cognition may promote competitive abilities in primates, in humans these abilities may be further extended to enable successful cooperation.

The role of social style in promoting sophisticated social cognition in macaques

These studies provide new evidence for the role of social style in shaping social cognition. Overall, these findings suggest that social cognition is flexible: sophisticated social cognitive abilities can be utilized across competitive and non-competitive contexts, and can facilitate patterns of affiliation, sociability, and aggression. This would seem to limit the effect of social style upon social intelligence—because social intelligence can facilitate patterns of behavior that are advantageous in both tolerant and despotic social environments. However, a more fine-grained approach suggests that there may be a differentiation between different social cognitive abilities. In particular, while some abilities (such as gaze-following) may flexibly facilitate different patterns of affiliative versus aggressive behavior across species of different tolerance levels, theory of mind abilities such as goal and knowledge attribution may play a greater role in enabling aggressive behavior.

In Chapter 3, I found that both rhesus and Barbary macaques display similar abilities to account for another individual's line-of-sight into their gaze-following response, in contrast to proposals that either more despotic (Byrne & Whiten, 1990) or more tolerant species (Burkart, Hrdy, & Van Schaik, 2009; Hare, 2017) should have more sophisticated social cognition. Why might these species display similar gaze-following abilities, despite difference in social tolerance? One possibility is that despotic and tolerant social styles both select for these abilities, to facilitate different patterns of behavior: in despotic species these abilities may facilitate aggression and other forms of social competition, while in tolerant species these abilities may enable affiliation. In line with this, in Chapter 5 I also found that gaze-following predicts the rate of being groomed, as well as the average number of individuals within 2m, within tolerant Barbary macaques. Furthermore, in Chapter 4 I found that despotic rhesus macaques did not demonstrate sensitivity to gaze sensitivity as a communicative cue. A crucial next step that I am addressing in ongoing work is to test how social cognition predicts natural patterns of behavior in rhesus macaques. For example, if gaze-following better predicts aggressive behavior in rhesus macaques, this would provide support for the idea that similar abilities to understand others' gaze have evolved in Barbary and rhesus macaques, even though they support different functions.

Notably, prior work has indicated that gaze sensitivity, such as the ability to account for another individual's line-of-sight, does indeed have a variety of behavioral functions. Within macaques specifically, there is strong evidence that different species utilize gaze cues in different ways according to social tolerance; eye contact tolerance appears to be higher in species with a more egalitarian structure (Harrod et al., 2020). Further, while rhesus macaques gaze-follow differentially according to rank (Shepherd et al., 2006), Barbary macaques do not (Teufel et al., 2010). Similarly, crested macaques (*Macaca nigra*), another tolerant species, respond more quickly to gaze cues from conspecific friends versus non-friends (Micheletta & Waller, 2012), while competitive long-tailed macaques (*Macaca fascicularis*), are more responsive to gaze cues when a human actor exhibits a submissive facial expression versus an affiliative expression (Goossens et al., 2008).

Second, while gaze-following abilities may facilitate both affiliative and aggressive behavior according to social tolerance, I found some evidence that theory of mind abilities such as goal attribution may more specifically enable aggression. In particular, I found that Barbary macaques' goal attribution abilities showed a trending relationship towards predicting the rate of aggressing other individuals—despite their low levels of aggression overall. Given this, one possibility is that there is an even stronger relationship between individuals' aptitude in these tasks and their rate of aggressive behavior in more despotic species like rhesus macaques who display more severe and frequent aggression. That is, there may be a relationship between knowledge attribution and aggression in this species (which we failed to find in Barbary macaques), as well as a stronger relationship between goal attribution and aggression. If this prediction is correct, it suggests that these abilities are more specifically utilized (relative to gaze sensitivity) to enable competition in primates. In line with this, note that many paradigms where primates have demonstrated theory of mind abilities have been competitive in nature, and many primate species that have succeeded in these paradigms (such as chimpanzees, rhesus macaques and ring-tailed lemurs) have more despotic social systems. Note that it is not the case the primates are necessarily 'constrained' to utilizing these abilities within competitive contexts, as I found evidence that even rhesus macaques can utilize sophisticated social cognitive processes outside of competitive contexts in Chapter 2), but rather that they may primarily be utilized in competitive contexts in primates' natural social environments, and have been selected for due to this usage.

I did not find evidence for enhanced social cognitive abilities within despotic rhesus macaques versus Barbary macaques in a direct comparison of their cognition (in Chapter 3), even though goal attribution showed a trending effect to predict aggression in Chapter 5—which occurs with a greater frequency and severity in despotic species. Given that both species showed evidence for the cognitive ability in question (accounting for others' line-of-sight during gaze-following) one possibility is that this task was not sufficient to capture differences across the species. That is, perhaps this is a fairly basic skill but there are other sophisticated social cognitive abilities that rhesus macaques do possess, but that Barbary macaques do not. Consequently, future work can aim to test species' aptitude in theory of mind abilities that seem to be especially difficult, for instance because they emerge later in humans, such as level-2 perspective-taking, and understanding other individual's preferences when they differ from one's own. This may identify differences in the cognition of these species, which will be highly informative towards a full understanding of how social style shapes cognition.

Does social cognition predict behavior?

The second goal of this thesis was to examine the function of social intelligence by examining how individual variation in social cognition predicts patterns of natural behavior. In Chapter 5, I found that gaze-following predicted the rate of receiving grooming, and showed a trending effect to predict the average number of individuals within proximity. Goal attribution ability predicted the number of individuals within proximity, and showed a trending affect to predict the rate of aggressing other individuals. This suggests that different social cognitive abilities may evolve through different selective benefits: abilities such as gaze-following may have a more sociable and affiliative role (perhaps especially in tolerant species such as Barbary macaques), while other more complex theory of mind abilities may play a stronger role in enabling aggressive behaviors, an important feature of primate lives. This nuance contrasts with hypothetical proposals of social cognitive evolution, which have not generally linked particular cognitive abilities to particular selective benefits. For example, the Machiavellian intelligence hypothesis broadly proposes that social intelligence capacities enable performance in social competition (Byrne & Whiten, 1990), and proposals that emphasize the role overall sociability (Dunbar, 1998), or of cooperation and affiliation in cognitive evolution have also not specified which cognitive mechanisms might be selected for (Cheney et al., 1986; Hare, 2017). Consequently, the results from Chapter 5 finds that all three hypotheses regarding the evolution of primate social cognition have some support: improved social cognition appears to increase sociability and affiliation, alongside rates of aggression. In this tolerant social species, we found the strongest relationships between cognition and sociability, and between cognition and receiving affiliation.

One limitation of this research is that my approach could not specifically link these differences in sociability to measures of fitness, such as reproductive success. Nonetheless, it seems very likely that the behavioral metrics measured were relevant to fitness. In Barbary macaques specifically, affiliation has been linked to fitness through forming larger huddles against the cold (Campbell et al., 2018; McFarland & Majolo, 2013): Barbary macaques with a large number of huddling partners have better thermoregulation during cold weather events, which improves survival rates across both sexes. Along similar lines, Barbary macaque males are more likely to receive coalitionary support during aggression, if they have a social bond with this individual (Young et al., 2014). While the fitness benefits of coalitionary support have not been measured in Barbary macaques, it is likely that this support reduces the chances of injury during aggression, and helps the individual move up the dominance hierarchy—which promotes mating success (Paul et al., 1993). At the same time, the number of different aggressive partners also predicts survival probability in Barbary macaques, potentially because this stabilizes the affiliative social relationships that promote fitness-relevant behaviors such as huddling (Lehmann et al., 2016). Given this, we can assume that aggression, grooming, and other social metrics do matter for ultimate outcomes in Barbary macaques. However, these links between social behavior and fitness can be indirect and complicated (Ostner & Schuelke, 2018). Thus, linking social intelligence directly to fitness would provide a full account of how social intelligence evolves.

Implications for human social cognition

The studies in this thesis also provide insights into human social cognition. As a species, humans are marked by our exceptional forms of cooperation (Bowles & Gintis, 2004; Boyd & Richerson, 2005; Henrich & Henrich, 2007; Tomasello, 2019). One proposal is that this has resulted in selection for novel cognitive traits, that support unique forms of cooperation and cultural learning. Overall, my results were broadly congruent with this idea, as I found evidence that rhesus macaques are not sensitive to the use of a gaze as a communicative cue in Chapter 4, and neither species was especially motivated to approach to look at what a demonstrator looked at in Chapter 2 or 3, unlike human infants in analogous set-ups. Overall, this suggests that macaques do not interpret gaze in the same cooperative and communicative way as humans seem to. I also failed to find evidence that knowledge or goal attribution abilities predict the rate of producing affiliative behaviors in Chapter 5 (although I did find evidence that links cognition to the rate of receiving affiliative behavior), despite testing a highly tolerant nonhuman-primate species—in contrast, evidence from humans has closely linked theory of mind abilities to patterns of affiliation and prosocial behavior.

Human cooperation is unusual in several respects. For example, we cooperate with strangers, in vast networks, and across different contexts (Burkart, Hrdy, & Van Schaik, 2009; Henrich & Henrich, 2007; Moll & Tomasello, 2007). This newer cooperative selection pressure might have been enabled via an increase in social tolerance, permitting selection to act upon newer cooperative behaviors that were impossible prior to this increase in tolerance (Hare, 2017). Alternatively, selection for cooperation may have been facilitated via our increasing dependence upon cooperatively-transmitted cultural information (Henrich, 2015), or via dependence upon forms of cooperative foraging (Tomasello et al., 2012). Overall, this cooperative selection pressure is thought to have resulted in novel cognitive abilities in humans, that facilitate increasingly sophisticated forms of cooperation. In particular, these abilities are thought to include theory of mind skills that enable cooperation, as well as abilities that promote cultural learning (Csibra & Gergely, 2011; Henrich, 2015; Moll & Tomasello, 2007; Tomasello & Carpenter, 2007).

Broadly, my results provide support for the idea that unique aspects of human social cognition might have been driven by adaptation for cooperation, even though primate cognition in general may have evolved for more competitive functions. In particular, in Chapters 2 and 3 I found evidence that both Barbary and rhesus macaques are sensitive to others' line-of-sight during gaze following. However, despite this similarity to human sensitivity to gaze, I also found that rhesus macaques were not sensitive to gaze as a communicative cue, which is congruent with the idea that gaze has taken on a new role in humans to facilitate cooperative interactions. In particular, it has been proposed that using gaze as a communicative cue underpins our especially effective social learning (Csibra & Gergely, 2011), is utilized as a cue to mark intent to cooperate (Siposova et al., 2018), and of shared attention during conversation (Wohltjen & Wheatley, 2021). Furthermore, in Chapter 3 I also found that neither Barbary nor rhesus macaques were especially motivated to actually approach in order to see what the demonstrator looked at, in contrast to human infants in analogous set-ups, who approach at a high rate (Moll & Tomasello, 2004). Overall this suggests that while nonhumans are sensitive to gaze as relevant information, they do not interpret it in the same helpful, communicative way as even infants do.

One question for future research is to examine how primates' responses to social stimuli (such as communicative cues) vary according to the relationship between the individuals. While human infants respond to cues generated by strangers, perhaps this reflects selection to succeed in a large social network. The roots of this capacity may then be present in other species, but be more constrained to responding to individuals with whom they have a close relationship. For example, mother-infant monkey dyads engage in reciprocal lip-smacking and mutual gaze (Ferrari et al., 2009), which may serve to establish a mutual intent to communicate. In addition, chimpanzees are more sensitive to social cues from a human caregiver with whom they have a close relationship (Kano et al., 2018). Testing this will provide further insight into how human-unique patterns of cooperation have shaped our cognition.

My results provided limited support for the idea that tolerance promotes sophisticated social cognition in primates. I did find evidence that cognitive abilities such as gaze-following and goal-attribution predict being in close proximity to others, and the rate of receiving grooming—which suggests that these abilities may evolve to support sociable and affiliative behaviors, and could therefore potentially evolve to become increasingly sophisticated in tolerant species with especially high rates of affiliation. However, goal-attribution also showed a trending relationship to predict the rate of aggressing other individuals; it is not the case that primate social cognition solely promotes affiliative behaviors, even within a highly tolerant primate species. Furthermore, I did not find evidence that tolerant Barbary macaques have more sophisticated social cognition than rhesus macaques. One possible explanation is that a tolerance is a necessary but insufficient factor for especially sophisticated social cognition. For example, in humans, more elaborate social cognition has been proposed to result from the impact of both increased tolerance and high levels of self-control (Hare, 2017). Such a combination of skills may be necessary to reap selective benefits from enhanced social cognition, for example because they include cognitive abilities that permit effective cooperation, yet macaques may not possess these other scaffolding skills.

Finally, in Chapter 5 I further found that social intelligence abilities such as goal attribution show a trending relationship towards predicting the rate of aggression—even within highly tolerant

Barbary macaques. While social intelligence did also predict the rate of receiving affiliation, it did not predict the rate of actually producing affiliative behaviors. This means that cognition might affect the attractiveness of the individual in question as a social partner, rather than making them actually more affiliative. In contrast, analogous studies linking children's social intelligence abilities to their social behavior has frequently found that theory of mind ability shows a negative relationship to aggression (Capage & Watson, 2001), and predicts measures of peer acceptance (Slaughter et al., 2002). If a similar study to Chapter 5 was carried out in humans, I predict that theory of mind ability would be strongly linked to patterns of affiliation. In line with hypotheses arguing that humans have experienced a unique selective pressure to engage in successful cooperation, this suggests that theory of mind has been 'coopted' for more cooperative use in the human lineage. Taken together, this suggests that (1) social intelligence may be promoted by its effects upon multiple types of social behavior (such as overall sociability versus aggression), that (2) different forms of social cognition (such as gaze-following versus theory of mind abilities such as goal attribution and knowledge attribution) may nonetheless facilitate different patterns of social cognition and that (3) these abilities may facilitate especially affiliative and prosocial behaviors in humans, relative to other primates.

General conclusions

Social cognition is a key component of what makes us human: we are intensely social primates, that engage in novel behaviors such as extensive cooperation, teaching and intentional communication. By studying these abilities in other primate species, it is possible to identify the evolutionary pressures that promote the evolution of these key social cognitive abilities—and hence to understand why we are the way that we are, on an ultimate level. Together, this work provides novel insights into how social intelligence evolves in primates. Specifically, these results suggest that social cognitive abilities overall are relatively flexible across contexts, and can predict patterns of sociability, affiliation, and aggression—although these abilities may preferentially predict patterns of sociability and affiliation, within species with a tolerant social style. However, specific social cognitive abilities under the umbrella of 'social intelligence' may promote different patterns of social behavior. In particular, while gaze may promote a wide range of social behaviors according to the social style of the species in question, abilities such as knowledge and goal attribution may play a greater role in social competition. Lastly, human social cognition appears especially rich compared to other primate species—for example, we are skilled at attributing false beliefs to other individuals, and at imaging how things appear from another person's perspective. These social cognitive abilities exhibited by humans that go beyond those seen in other primates may critically facilitate patterns of cooperation and culture, that are not seen in other species. Overall, humans appear unique in the way that we have 'coopted' our primate social cognitive skills for cooperative and cultural endeavors.

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