

Sensitivity to line-of-sight in tolerant versus despotic macaques (*Macaca sylvanus* and *Macaca mulatta*)

Rosemary Bettle^{1*} & Alexandra G Rosati^{1,2}

¹Department of Psychology

²Department of Anthropology

University of Michigan

Ann Arbor, MI 48109

*rbettle@umich.edu

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 repertoires 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 responsiveness 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 $\pm$ 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 $\pm$ 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 1a). 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.

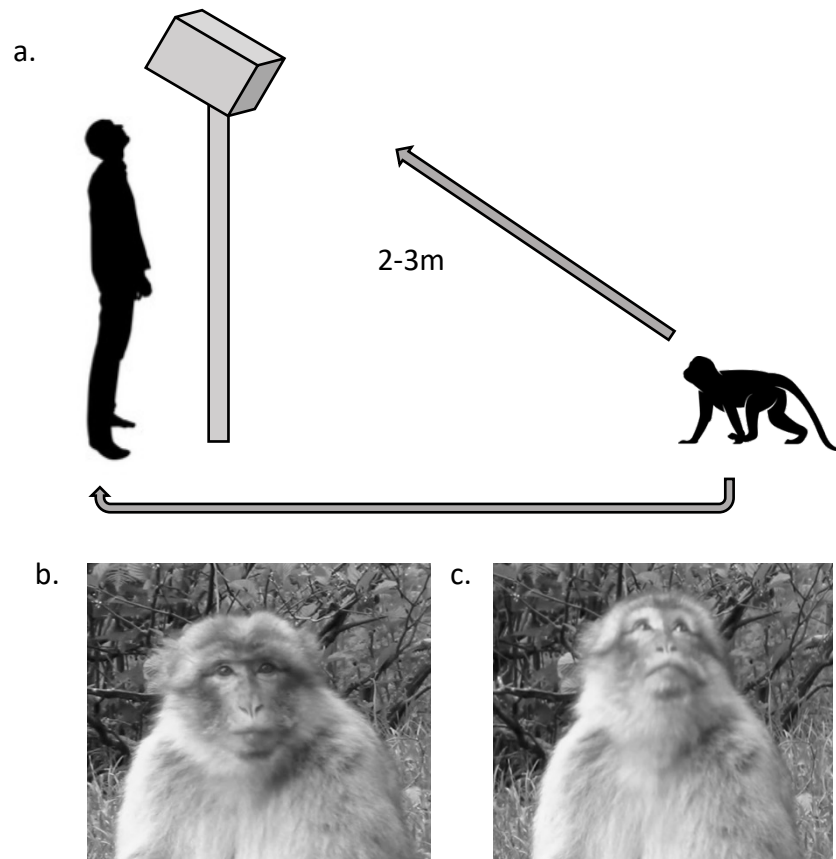


Figure 1: Methods (a) Diagram of setup. While monkeys could see the actor's target of attention from their starting position in the *no barrier* condition, they had to reorient by approaching the apparatus to do so in the *barrier* condition depicted here. (b) Video still of a Barbary macaque looking at the demonstrator at the start of a trial. (c) Video still of a Barbary macaque looking upwards to produce a gaze-following response.

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 1c 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.

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.

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* $\times$ *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* $\times$ *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 $1.59 \pm SE = 0.29s$ 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 $1.57s \pm 0.26s$, 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 2a and 2b). 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 1); 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.

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: $\chi^2 = 0.65$, $df = 1$, $p > 0.19$; AIC = 178.8 compared to 177.5 in base model), a *condition X age* interaction (LRT: $\chi^2 = 0.99$, $df = 2$, $p > 0.28$; 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 ($\chi^2 = 1.21$, $df = 4$, $p = 0.6$; AIC = 178.5 compared to 170.2 in base model). It also did not improve fit for total number of looks ($\chi^2 = 0.68$, $df = 3$, $p > 0.87$; 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).

Predictor	Estimate	SE	z-value	p-value
Sex (reference: 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 1: 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.

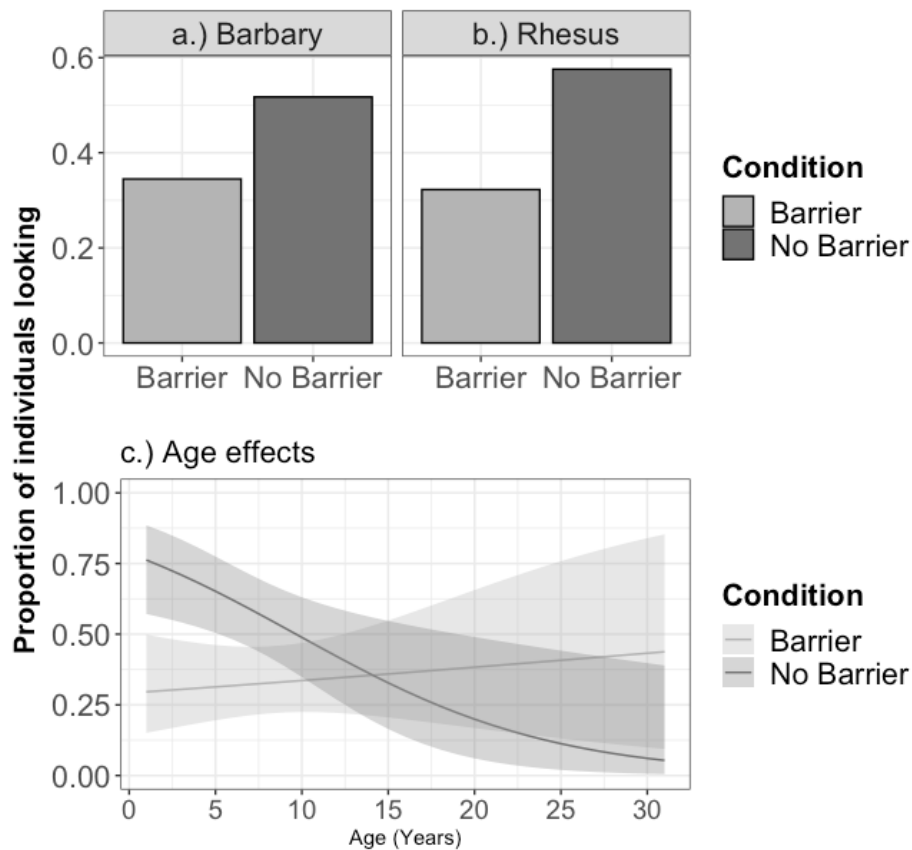


Figure 2: Gaze following responses across species. (a) Proportion of Barbary macaques who looked upwards during the look phase, across conditions. (b) Proportion of rhesus macaques who looked upwards during the look phase, across conditions. (c) Age trends by condition, collapsing across species. Ribbons represent 95% CI.

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: $\chi^2 = 7.11$, $df=1$, $p = 0.008$; AIC = 57.3 compared to 62.2 in base model). In particular, rhesus macaques approached the apparatus more often than Barbary macaques (see Fig 3). 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 (reference: barrier)	-0.001	0.766	-0.001	0.999
Species (reference: Barbary)	2.369	1.104	2.146	0.032*

Table 2: 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.

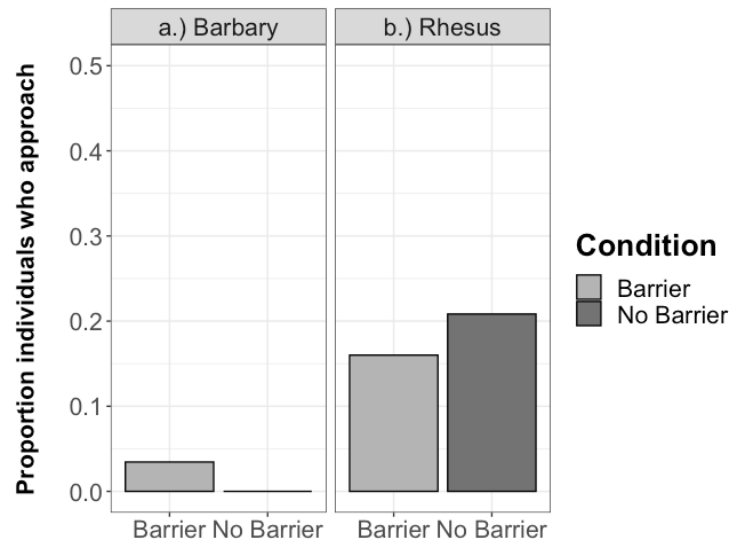


Figure 3: Approaches across species. Proportion of (a) Barbary macaques and (b) rhesus macaques who approached the apparatus across conditions.

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.

Acknowledgements

We thank Alyssa Arre, Megan Cole and Francesca De Petrillo for assistance with data collection and coding, and CSCAR at the University of Michigan for statistical advice. At Trentham Monkey Forest, we thank Matt Lovatt, Anna Smith, Diane Floyd, and all the staff for supporting our work. At the Cayo Santiago Field Station, we thank Angelina Ruiz Lambides, Nahiri Rivera Barreto, Giselle Caraballo-Cruz, and Bianca Giura. Cayo Santiago is supported by a National Center for Research Resources grant CM-5-P40RR003640-13 and NIH grant 5P40OD012217. This research was supported by a Rackham research grant to RB, a Sloan Foundation Fellowship (FG-2019-12054) and a National Science Foundation grant (1944881) to AGR.

References

- Almeling, L., Hammerschmidt, K., Sennhenn-Reulen, H., Freund, A. M., & Fischer, J. (2016). Motivational shifts in aging monkeys and the origins of social selectivity. *Current Biology*, 26(13), 1744–1749.
- Anderson, J. R., Montant, M., & Schmitt, D. (1996). Rhesus monkeys fail to use gaze direction as an experimenter-given cue in an object-choice task. *Behavioural Processes*, 37(1), 47–55.
- Anderson, J. R., Sallaberry, P., & Barbier, H. (1995). Use of experimenter-given cues during object-choice tasks by capuchin monkeys. *Animal Behaviour*, 49(1), 201–208.
- Arre, A. M., Stumph, E., & Santos, L. R. (2021). Macaque species with varying social tolerance show no differences in understanding what other agents perceive. *Animal Cognition*, 1–12.
- Baayen, R. H., & Milin, P. (2010). Analyzing Reaction Times. *International Journal of Psychological Research*, 3(2), 12–28.
- Bettle, R., & Rosati, A. G. (2019). Flexible gaze-following in rhesus monkeys. *Animal Cognition*, 22(5), 673–686.
- Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H., & White, J.-S. S. (2009). Generalized linear mixed models: A practical guide for ecology and evolution. *Trends in Ecology & Evolution*, 24(3), 127–135.
<https://doi.org/10.1016/j.tree.2008.10.008>
- Bottiroli, S., Cavallini, E., Ceccato, I., Vecchi, T., & Lecce, S. (2016). Theory of Mind in aging: Comparing cognitive and affective components in the faux pas test. *Archives of Gerontology and Geriatrics*, 62, 152–162.

- Boyd, R., & Richerson, P. J. (2009). Culture and the evolution of human cooperation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364(1533), 3281–3288.
- Bräuer, J., Call, J., & Tomasello, M. (2005). All Great Ape Species Follow Gaze to Distant Locations and Around Barriers. *Journal of Comparative Psychology*, 119(2), 145–154. <https://doi.org/10.1037/0735-7036.119.2.145>
- Bray, J., Krupenye, C., & Hare, B. (2014). Ring-tailed lemurs (*Lemur catta*) exploit information about what others can see but not what they can hear. *Animal Cognition*, 17(3), 735–744.
- Burkart, J. M., Hrdy, S. B., & Schaik, C. P. V. (2009). Cooperative breeding and human cognitive evolution. *Evolutionary Anthropology: Issues, News, and Reviews*, 18(5), 175–186. <https://doi.org/10.1002/evan.20222>
- Burkart, Judith Maria, & Heschl, A. (2007). Understanding visual access in common marmosets, *Callithrix jacchus*: Perspective taking or behaviour reading? *Animal Behaviour*, 73(3), 457–469.
- Butterworth, G., & Jarrett, N. (1991). What minds have in common is space: Spatial mechanisms serving joint visual attention in infancy. *British Journal of Developmental Psychology*, 9(1), 55–72. <https://doi.org/10.1111/j.2044-835X.1991.tb00862>.
- Byrne, R. W., & Corp, N. (2004). Neocortex size predicts deception rate in primates. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 271(1549), 1693–1699.
- Byrne, R. W., & Whiten, A. (1990). *Machiavellian intelligence: Social expertise and the evolution of intellect in monkeys, apes, and humans*.
- Call, J., Agnetta, B., & Tomasello, M. (2000). Cues that chimpanzees do and do not use to find hidden objects. *Animal cognition*, 3(1), 23–34.
- Call, J., Hare, B. A., & Tomasello, M. (1998). Chimpanzee gaze following in an object-choice task. *Animal cognition*, 1(2), 89–99.
- Cheney, D., Seyfarth, R., & Smuts, B. (1986). Social relationships and social cognition in nonhuman primates. *Science*, 234(4782), 1361–1366. <https://doi.org/10.1126/science.3538419>
- Costes-Thiré, M., Levé, M., Uhlrich, P., De Marco, A., & Thierry, B. (2015). Lack of evidence that Tonkean macaques understand what others can hear. *Animal Cognition*, 18(1), 251–258.
- Costes-Thiré, M., Levé, M., Uhlrich, P., Pasquaretta, C., De Marco, A., & Thierry, B. (2015). Evidence that monkeys (*Macaca tonkeana* and *Sapajus apella*) read moves, but no evidence that they read goals. *Journal of Comparative Psychology*, 129(3), 304.
- Csibra, G., & Gergely, G. (2009). Natural pedagogy. *Trends in Cognitive Sciences*, 13(4), 148–153.
- Csibra, G., & Gergely, G. (2011). Natural pedagogy as evolutionary adaptation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366(1567), 1149–1157.
- De Waal, F. B. M. (1982). *Chimpanzee politics: Power and sex among apes*. Harper & Row.
- Deaner, R. O., & Platt, M. L. (2003). Reflexive social attention in monkeys and humans. *Current Biology*, 13(18), 1609–1613.
- Drayton, L. A., & Santos, L. R. (2017). Do rhesus macaques, *Macaca mulatta*, understand what others know when gaze following? *Animal Behaviour*, 134, 193–199.
- Drea, C. M., & Carter, A. N. (2009). Cooperative problem solving in a social carnivore. *Animal Behaviour*, 78(4), 967–977.

- Dunbar, R. I. M. (1998). The social brain hypothesis. *Evolutionary Anthropology: Issues, News, and Reviews*, 6(5), 178–190.
- Ferrari, P. F., Kohler, E., Fogassi, L., & Gallese, V. (2000). The ability to follow eye gaze and its emergence during development in macaque monkeys. *Proceedings of the National Academy of Sciences*, 97(25), 13997–14002.
- Flom, R., Lee, K., & Muir, D. (2017). *Gaze-following: Its development and significance*. Psychology Press.
- Flombaum, J. I., & Santos, L. R. (2005). Rhesus monkeys attribute perceptions to others. *Current Biology*, 15(5), 447–452.
- Friesen, C. K., & Kingstone, A. (1998). The eyes have it! Reflexive orienting is triggered by nonpredictive gaze. *Psychonomic Bulletin & Review*, 5(3), 490–495.
- Fröhlich, M., Kuchenbuch, P., Müller, G., Fruth, B., Furuichi, T., Wittig, R. M., & Pika, S. (2016). Unpeeling the layers of language: Bonobos and chimpanzees engage in cooperative turn-taking sequences. *Scientific Reports*, 6(1), 1–14.
- Girard-Buttoz, C., Surbeck, M., Samuni, L., Tkaczynski, P., Boesch, C., Fruth, B., Wittig, R. M., Hohmann, G., & Crockford, C. (2020). Information transfer efficiency differs in wild chimpanzees and bonobos, but not social cognition. *Proceedings of the Royal Society B*, 287(1929), 20200523.
- Goossens, B. M., Dekleva, M., Reader, S. M., Sterck, E. H., & Bolhuis, J. J. (2008). Gaze following in monkeys is modulated by observed facial expressions. *Animal Behaviour*, 75(5), 1673–1681.
- Grueneisen, S., Duguid, S., Saur, H., & Tomasello, M. (2017). Children, chimpanzees, and bonobos adjust the visibility of their actions for cooperators and competitors. *Scientific Reports*, 7(1), 1–10.
- Hare, B. (2001). Can competitive paradigms increase the validity of experiments on primate social cognition? *Animal Cognition*, 4(3–4), 269–280.
- Hare, B. (2017). Survival of the Friendliest: Homo sapiens Evolved via Selection for Prosociality. *Annual Review of Psychology*, 68(1), 155–186.
<https://doi.org/10.1146/annurev-psych-010416-044201>
- Hare, B., Addessi, E., Call, J., Tomasello, M., & Visalberghi, E. (2003). Do capuchin monkeys, *Cebus apella*, know what conspecifics do and do not see? *Animal Behaviour*, 65(1), 131–142.
- Hare, B., Brown, M., Williamson, C., & Tomasello, M. (2002). The domestication of social cognition in dogs. *Science*, 298(5598), 1634–1636.
- Hare, B., Call, J., Agnetta, B., & Tomasello, M. (2000). Chimpanzees know what conspecifics do and do not see. *Animal Behaviour*, 59(4), 771–785.
- Hare, B., Call, J., & Tomasello, M. (2001). Do chimpanzees know what conspecifics know? *Animal Behaviour*, 61(1), 139–151.
- Hare, B., Melis, A. P., Woods, V., Hastings, S., & Wrangham, R. (2007). Tolerance allows bonobos to outperform chimpanzees on a cooperative task. *Current Biology*, 17(7), 619–623.
- Hare, B., Plyusnina, I., Ignacio, N., Schepina, O., Stepika, A., Wrangham, R., & Trut, L. (2005). Social cognitive evolution in captive foxes is a correlated by-product of experimental domestication. *Current Biology*, 15(3), 226–230.
- Hare, B., & Tomasello, M. (2004). Chimpanzees are more skilful in competitive than in cooperative cognitive tasks. *Animal Behaviour*, 68(3), 571–581.

- Hare, B., & Tomasello, M. (2005). Human-like social skills in dogs? *Trends in Cognitive Sciences*, 9(9), 439–444.
- Henrich, N., & Henrich, J. P. (2007). *Why humans cooperate: A cultural and evolutionary explanation*. Oxford University Press.
- Herrmann, E., Hare, B., Call, J., & Tomasello, M. (2010). Differences in the cognitive skills of bonobos and chimpanzees. *PloS One*, 5(8), e12438.
- Herrmann, E., & Tomasello, M. (2006). Apes' and children's understanding of cooperative and competitive motives in a communicative situation. *Developmental Science*, 9(5), 518–529.
- Horschler, D. J., Santos, L. R., & MacLean, E. L. (2019). Do non-human primates really represent others' ignorance? A test of the awareness relations hypothesis. *Cognition*, 190, 72–80.
- Humphrey, N. K. (1976). The social function of intellect. In *Growing points in ethology* (pp. 303–317). Cambridge University Press.
- Itakura, S., & Tanaka, M. (1998). Use of experimenter-given cues during object-choice tasks by chimpanzees (*Pan troglodytes*), an orangutan (*Pongo pygmaeus*), and human infants (*Homo sapiens*). *Journal of Comparative Psychology*, 112(2), 119.
- Jolly, A. (1966). Lemur Social Behavior and Primate Intelligence. *Science*, 153(3735), 501–506. <https://doi.org/10.1126/science.153.3735.501>
- Joly, M., Micheletta, J., De Marco, A., Langermans, J. A., Sterck, E. H., & Waller, B. M. (2017). Comparing physical and social cognitive skills in macaque species with different degrees of social tolerance. *Proceedings of the Royal Society B: Biological Sciences*, 284(1862), 20162738.
- Kaigaishi, Y., Nakamichi, M., & Yamada, K. (2019). High but not low tolerance populations of Japanese macaques solve a novel cooperative task. *Primates*, 60(5), 421–430.
- Kaminski, J., Call, J., & Tomasello, M. (2008). Chimpanzees know what others know, but not what they believe. *Cognition*, 109(2), 224–234.
- Kaminski, J., & Nitzschner, M. (2013). Do dogs get the point? A review of dog–human communication ability. *Learning and Motivation*, 44(4), 294–302.
- Kano, F., & Call, J. (2014a). Cross-species variation in gaze following and conspecific preference among great apes, human infants and adults. *Animal Behaviour*, 91, 137–150.
- Kano, F., & Call, J. (2014b). Great apes generate goal-based action predictions: An eye-tracking study. *Psychological Science*, 25(9), 1691–1698.
- Kano, F., Hirata, S., & Call, J. (2015). Social Attention in the Two Species of Pan: Bonobos Make More Eye Contact than Chimpanzees. *PLOS ONE*, 10(6), e0129684. <https://doi.org/10.1371/journal.pone.0129684>
- Krupenye, C., Kano, F., Hirata, S., Call, J., & Tomasello, M. (2016). Great apes anticipate that other individuals will act according to false beliefs. *Science*, 354(6308), 110–114.
- Kummer, H. (1982). Social knowledge in free-ranging primates. In *Animal mind—Human mind* (pp. 113–130). Springer.
- Lenth, R., Singmann, H., Love, J., Buerkner, P., & Herve, M. (2018). Emmeans: Estimated marginal means, aka least-squares means. *R Package Version*, 1(1), 3.
- Lo, S., & Andrews, S. (2015). To transform or not to transform: Using generalized linear mixed models to analyse reaction time data. *Frontiers in Psychology*, 6. <https://doi.org/10.3389/fpsyg.2015.01171>

- Lyons, D. E., & Santos, L. R. (2006). Ecology, domain specificity, and the origins of theory of mind: Is competition the catalyst? *Philosophy Compass*, 1(5), 481–492.
- MacLean, E. L., & Hare, B. (2012). Bonobos and chimpanzees infer the target of another's attention. *Animal Behaviour*, 83(2), 345–353.
<https://doi.org/10.1016/j.anbehav.2011.10.026>
- MacLean, E. L., Matthews, L. J., Hare, B. A., Nunn, C. L., Anderson, R. C., Aureli, F., Brannon, E. M., Call, J., Drea, C. M., & Emery, N. J. (2012). How does cognition evolve? Phylogenetic comparative psychology. *Animal Cognition*, 15(2), 223–238.
- Martcorena, D. C. W., Ruiz, A. M., Mukerji, C., Goddu, A., & Santos, L. R. (2011). Monkeys represent others' knowledge but not their beliefs. *Developmental Science*, 14(6), 1406–1416. <https://doi.org/10.1111/j.1467-7687.2011.01085.x>
- Martin, A., & Santos, L. R. (2014). The origins of belief representation: Monkeys fail to automatically represent others' beliefs. *Cognition*, 130(3), 300–308.
<https://doi.org/10.1016/j.cognition.2013.11.016>
- Massen, J. J., Ritter, C., & Bugnyar, T. (2015). Tolerance and reward equity predict cooperation in ravens (*Corvus corax*). *Scientific Reports*, 5, 15021.
- Melis, A. P., Hare, B., & Tomasello, M. (2006). Engineering cooperation in chimpanzees: Tolerance constraints on cooperation. *Animal Behaviour*, 72(2), 275–286.
- Micheletta, J., & Waller, B. M. (2012). Friendship affects gaze following in a tolerant species of macaque, *Macaca nigra*. *Animal Behaviour*, 83(2), 459–467.
- Moran, J. M. (2013). Lifespan development: The effects of typical aging on theory of mind. *Behavioural Brain Research*, 237, 32–40.
- Okamoto-Barth, S., Call, J., & Tomasello, M. (2007). Great Apes' Understanding of Other Individuals' Line of Sight. *Psychological Science*, 18(5), 462–468.
<https://doi.org/10.1111/j.1467-9280.2007.01922.x>
- Povinelli, D. J., Bierschwale, D. T., & Cech, C. G. (1999). Comprehension of seeing as a referential act in young children, but not juvenile chimpanzees. *British Journal of Developmental Psychology*, 17(1), 37–60.
- R Core Team. (2020). *R: A language and environment for statistical computing*. <https://www.R-project.org/>
- Richard, A. F., Goldstein, S. J., & Dewar, R. E. (1989). Weed macaques: The evolutionary implications of macaque feeding ecology. *International Journal of Primatology*, 10(6), 569–594.
- Rosati, A. G., Arre, A. M., Platt, M. L., & Santos, L. R. (2016). Rhesus monkeys show human-like changes in gaze following across the lifespan. *Proceedings of the Royal Society B: Biological Sciences*, 283(1830), 20160376.
- Rosati, A. G., & Hare, B. (2009). Looking past the model species: Diversity in gaze-following skills across primates. *Current Opinion in Neurobiology*, 19(1), 45–51.
<https://doi.org/10.1016/j.conb.2009.03.002>
- Rosati, Alexandra, Muller, M., Wrangham, R., & Pilbeam, D. (2017). Chimpanzee cognition and the roots of the human mind. *Chimpanzees and Human Evolution*, 703–745.
- Rosati, Alexandra, & Santos, L. (2017). Tolerant Barbary macaques maintain juvenile levels of social attention in old age, but despotic rhesus macaques do not. *Animal Behaviour*, 130, 199–207.
- Ruiz, A., Gómez, J. C., Roeder, J. J., & Byrne, R. W. (2009). Gaze following and gaze priming in lemurs. *Animal Cognition*, 12(3), 427–434.

- Sandel, A. A., MacLean, E. L., & Hare, B. (2011). Evidence from four lemur species that ringtailed lemur social cognition converges with that of haplorhine primates. *Animal Behaviour*, 81(5), 925–931.
- Santos, L. R., Nissen, A. G., & Ferrugia, J. A. (2006). Rhesus monkeys, *Macaca mulatta*, know what others can and cannot hear. *Animal Behaviour*, 71(5), 1175–1181.
- Seed, A. M., Clayton, N. S., & Emery, N. J. (2008). Cooperative problem solving in rooks (*Corvus frugilegus*). *Proceedings of the Royal Society B: Biological Sciences*, 275(1641), 1421–1429.
- Senju, A., & Johnson, M. H. (2009). The eye contact effect: Mechanisms and development. *Trends in Cognitive Sciences*, 13(3), 127–134.
- Shepherd, S. V. (2010). Following Gaze: Gaze-Following Behavior as a Window into Social Cognition. *Frontiers in Integrative Neuroscience*, 4. <https://doi.org/10.3389/fnint.2010.00005>
- Shepherd, S. V., Deaner, R. O., & Platt, M. L. (2006). Social status gates social attention in monkeys. *Current Biology*, 16(4), R119–R120.
- Siposova, B., Tomasello, M., & Carpenter, M. (2018). Communicative eye contact signals a commitment to cooperate for young children. *Cognition*, 179, 192–201.
- Suchak, M., Eppley, T. M., Campbell, M. W., & de Waal, F. B. (2014). Ape duos and trios: Spontaneous cooperation with free partner choice in chimpanzees. *PeerJ*, 2, e417.
- Teufel, C., Gutmann, A., Pirow, R., & Fischer, J. (2010). Facial expressions modulate the ontogenetic trajectory of gaze-following among monkeys. *Developmental Science*, 13(6), 913–922.
- Thierry, B. (2000). Management patterns across macaque species. *Natural Conflict Resolution*, 106.
- Thierry, B. (2007). Unity in diversity: Lessons from macaque societies. *Evolutionary Anthropology: Issues, News, and Reviews: Issues, News, and Reviews*, 16(6), 224–238.
- Thomsen, C. E. (1974). Eye contact by non-human primates toward a human observer. *Animal Behaviour*, 22(1), 144–149.
- Tomasello, M., Call, J., & Gluckman, A. (1997). Comprehension of novel communicative signs by apes and human children. *Child development*, 1067–1080.
- Tomasello, M., & Carpenter, M. (2007). Shared intentionality. *Developmental Science*, 10(1), 121–125.
- Tomasello, M., Carpenter, M., Call, J., Behne, T., & Moll, H. (2005). Understanding and sharing intentions: The origins of cultural cognition. *Behavioral and Brain Sciences*, 28(5), 675–691.
- Tomasello, M., Hare, B., & Fogleman, T. (2001). The ontogeny of gaze following in chimpanzees, *Pan troglodytes*, and rhesus macaques, *Macaca mulatta*. *Animal Behaviour*, 61(2), 335–343. <https://doi.org/10.1006/anbe.2000.1598>
- Tomasello, M., Hare, B., Lehmann, H., & Call, J. (2007). Reliance on head versus eyes in the gaze following of great apes and human infants: The cooperative eye hypothesis. *Journal of Human Evolution*, 52(3), 314–320.
- Topál, J., Gergely, G., Erdőhegyi, Á., Csibra, G., & Miklósi, Á. (2009). Differential sensitivity to human communication in dogs, wolves, and human infants. *Science*, 325(5945), 1269–1272.

- Werdenich, D., & Huber, L. (2002). Social factors determine cooperation in marmosets. *Animal Behaviour*, 64(5), 771–781.
- Whiten, A., & Byrne, W. (1988). Tactical deception in primates. *Behavioral and Brain Sciences*, 11(2), 233–244.