



Macaque species with varying social tolerance show no differences in understanding what other agents perceive

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Abstract

A growing body of work demonstrates that a species' socioecology can impact its cognitive abilities. Indeed, even closely related species with different socioecological pressures often show different patterns of cognitive performance on the same task. Here, we explore whether major differences in social tolerance in two closely related macaque species can impact a core sociocognitive ability, the capacity to recognize what others see. Specifically, we compared the performance of Barbary macaques (*Macaca sylvanus*, $n = 80$) and rhesus macaques (*Macaca mulatta*, $n = 62$) on a standard test of visual perspective understanding. In contrast to the difference in performance, one might expect from these species' divergent socioecologies that our results show similar performance across Barbary and rhesus macaques, with both species forming expectations about how another agent will act based on that agent's visual perspective. These results suggest that differences in socioecology may not play as big of a role in the evolution of some theory of mind capacities as they do in other decision-making or foraging contexts.

Keywords Non-human primates · Social cognition · Theory of mind · Macaques · Phylogenetic comparative psychology

Introduction

In recent decades, comparative psychology research suggests that species' social and physical environments shape their cognitive capacities. Indeed, social and ecological differences can drive robust cognitive differences in otherwise very closely related species (for a review, see MacLean et al. 2012). These types of ecologically based cognitive differences are especially salient in non-human primates (hereafter, primates), where researchers have uncovered a number of domains in which primates develop cognitive abilities that align with the specific problems they naturally face in their own ecological niches (Rosati 2017; e.g., chimpanzees and bonobos in Wrangham and Pilbeam 2001).

Most of the species-specific differences in cognition observed to date have been cases of non-social cognitive abilities that vary across species with divergent feeding ecology. Foraging primates vary in the extent to which they need to wait to obtain their food sources (e.g., time-intensive

gummivorous foraging versus herbivorous or insectivorous foraging with immediately consumable rewards), engage in safe or risk-taking behavior (e.g., hunting live prey versus foraging plants), and navigate complex environments (e.g., a dense forest versus an open savannah). Thus, one might expect that species with varying diets would show differences in a set of relevant cognitive skills, such as temporal discounting, risk-taking, and spatial navigation. Indeed, researchers have observed that feeding ecology seems to play a role in the evolution of a variety of such cognitive abilities. For instance, species that have to wait or work for their food in the wild show similar patterns in an experimental cognitive task, waiting significantly longer for a better reward in tests of temporal discounting as compared to closely related species that eat foods with a more immediate payoff (Stevens et al. 2005; Rosati and Hare, 2013). Researchers have observed the same pattern of results in the domain of risk preferences, where species that experience more risk as part of their natural diet similarly show a preference for more risky options in an experimental setup than closely related species that feed on more abundant resources (Heilbronner et al., 2008; Rosati and Hare 2012a). Similarly, others have found that spatial cognitive capacities can be shaped by species' specific ecological differences, such as the degree to

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which their main food source is abundantly distributed in their environments. Species who forage on fruit and other sparsely available foods face a harder spatial navigation challenge than species that consume abundantly available leaves (Rosati 2017), and consequently show better spatial navigation and memory abilities than those species whose diet is abundantly distributed (Rosati et al. 2014; Rosati and Hare 2012b).

Taken together, this work shows that a species' natural foraging ecology matters a lot for the evolution of its non-social cognitive abilities. Nevertheless, foraging problems are not the only factor at play in a species' natural ecology. While early comparative work focused mostly on the role that diet and foraging ecology played in species differences in cognitive abilities, more recent work has begun to explore how differences in the *social* environment can shape a species' cognition. Researchers have long suspected, for example, that a species' group size might influence its sociocognitive abilities (Dunbar 1998). The so-called social brain hypothesis was originally developed as an explanation for the tendency of brain size to scale as a function of group size, especially in primate species (Shultz and Dunbar 2007; Dunbar and Shultz 2007a, b). Due to increased pressure and experience to overcome social challenges like intra- and intergroup conflicts and cooperative breeding, and similar demands that come with living in large complex social groups, some have argued that species living in big groups should show superior social cognition to small group or individualistic living species (Dunbar 2009; Shultz and Dunbar 2007; Dunbar and Shultz 2007a, b). MacLean et al. (2013) were among the first to test this directly, exploring whether group size affected lemurs' ability to recognize what others see. They compared five lemur species on a visual perspective taking test in which subjects have the opportunity to steal food from human experimenters who can and cannot see them (see Flombaum and Santos 2005; Hare et al. 2000 for a similar task). They found that species with larger group sizes performed better on the competitive stealing task as compared to those species with smaller group sizes. However, they found no relationship between group size and task performance in a non-social task (MacLean et al. 2013). Group size has such a powerful influence on social cognition that lemur species with larger group sizes (e.g., ring-tailed lemurs, *Lemur catta*) perform more similarly to monkeys on this and other social tasks than to other species of lemurs (Sandel et al. 2011; Jolly 1966).

Another aspect of a species' social environment that is thought to affect cognition concerns a species' social tolerance. Some species are more despotic, characterized by their high and unbalanced rates of aggression, low rates of reconciliation, and kinship bias for affiliative interactions than other more tolerant species (Aureli 1997; Thierry 1985). A number of accounts of human cognitive evolution hint

that such differences in tolerance may be important for the evolution of complex social cognitive abilities (e.g., Hare et al. 2012; Cieri et al. 2014) like cumulative culture, social learning, and language (Sánchez-Villagra and van Schaik 2019; Thomas and Kirby 2018; Benítez-Burraco and Progovac 2020). For example, some scholars have argued that more despotic, competitive social environments could lead to the evolution of richer social cognitive skills (Byrne and Whiten 1990; Byrne 1994, 1996). This account—which has been christened the *Machiavellian intelligence hypothesis*—would predict that more despotic and competitive social environments could serve as a catalyst for developing more sophisticated sociocognitive skills (Humphrey 1976; de Waal 2007; Byrne and Whiten 1990). Conversely, others have argued for the opposite view, claiming that sophisticated social cognition results from environments in which cooperation is promoted (Hare et al. 2012; Hare 2017), a view that some have called the “self domestication” or “survival of the friendliest” account (e.g., Hare and Woods 2020). For this reason, scholars have begun exploring whether species differences in social tolerance map onto differences in cognitive abilities across closely related species.

A growing body of work hints that tolerance differences at the species level may give rise to a number of species differences in social cognitive capacities. Most of this work comes from our closest living relatives, chimpanzees, and bonobos. For example, though closely related, bonobos and chimpanzees show different levels of tolerance both within and between social groups, with chimpanzees exhibiting much less tolerance and reconciliation than bonobos (Wrangham and Pilbeam 2001; but see Jaeggi et al. 2010). Bonobos show a stronger preference to look at social stimuli like faces and eyes than chimpanzees (Kano et al. 2015), gaining more experience from a younger age at reading and interpreting the social cues of other agents like gaze direction and facial expression, as compared to chimpanzees. Bonobos also show more prosocial preferences than chimpanzees across the lifespan, with bonobos showing more willingness to share food in adulthood (Hare and Kwetuenda 2010) than chimpanzees, which only exhibit food sharing in early life (Silk et al. 2005; Jensen et al. 2006). This switch toward intolerance in chimpanzees seems to emerge early in the chimpanzee development (Wobber et al. 2010) suggesting that the species differences observed in adults result from species-specific developmental changes.

A limited body of work has investigated the same question in non-ape primate species. For example, Joly et al. (2017) compared several aspects of social and non-social cognition in four macaque species. The macaque genus shows a clear linear spectrum from more tolerant to more despotic species (Thierry 2007; Thierry et al. 2000, 2004), making this genus particularly useful for testing predictions about how social tolerance shape cognition. Joly et al.

(2017) found that the different species showed similar levels of performance on non-social tests of causality, numerical reasoning, and spatial memory, but did exhibit performance differences on at least some tests of social cognition. For example, the different macaque species performed differently on a social object choice task, in which subjects had to follow an experimenter's pointing cue toward different hiding locations to receive a food reward. Tolerant species were more likely to succeed at the task, as compared to less tolerant species, which the authors argued showed that tolerant species have better social cognition as compared to despotic species; interestingly, however, the tolerant and despotic species showed no differences in performance in the other tasks assessing social cognition.

In another experiment, Rosati and Santos (2017) found a difference in one social cognitive ability between tolerant and intolerant species, but only when evaluating developmental differences. In their experiment, they compared gaze-following rates across the lifespan in tolerant Barbary macaques (*Macaca sylvanus*) to that of despotic rhesus macaques (*Macaca mulatta*). Adults in both species do not seem to differ in their propensity to gaze follow. However, their findings show an important developmental difference between the two species; rhesus monkeys show marked decline in the degree of gaze following across the lifespan, while Barbary macaques maintain juvenile levels into late adulthood. This pattern across macaques is mirrored in chimpanzees and bonobos, whose gaze-following patterns mirror those found in macaques (Herrmann et al. 2010), with more tolerant bonobos outperforming chimpanzees on tasks requiring gaze following and more complex social skills, but not on tasks assessing physical and causal skills.

Building off this work and to further explore the extent to which tolerance shapes complex social cognition abilities, we compared whether two species of macaques that vary in their social tolerance (see Thierry 2007; Thierry et al. 2000, 2004) also vary in their capacity to understand another agents' visual perspective (Marticorena et al. 2011). We chose to compare the performance of Barbary macaques and rhesus macaques, because these two macaque species are on either end of the tolerance spectrum. Rhesus macaques have lower levels of social tolerance and social life is characterized by more hierarchical steepness, more violent inter- and intragroup encounters, and even more sophisticated facial expressions indicating submission (Thierry et al. 2004) than species like Barbary macaques (Matsumura 1999). Visual perspective taking is the ideal cognitive ability to study this difference due to the two competing hypotheses about the effect of social tolerance on social cognition evolution. Specifically, the Machiavellian Intelligence Hypothesis (Humphrey, 1976; de Waal 2007; Byrne and Whiten 1990) and the Self-Domestication Hypothesis (Hare et al. 2012; Hare 2017) each make a prediction about how agents

operate differentially to navigate the challenges that come with group living: the former suggests that social success results from an individual's ability to *exploit* the cues of others, while the latter suggest that an individual's ability to *cooperate* using the cues of others is what needed to succeed at group living. Thus, by comparing two species that vary in their despotism (Matsumura 1999), we can test whether experience exploiting versus cooperatively using the visual cues of others results in better visual perspective taking abilities.

In our experiment, we compared the performance of rhesus and Barbary macaques on a well-validated looking time measure of visual perspective taking, one that has been successfully used to test both human infants (e.g., Onishi and Baillargeon 2005; Luo and Baillargeon 2007; for a review, see Baillargeon et al. 2010) and non-human primates (e.g., Arre et al. 2020; Horschler et al. 2019; Marticorena et al. 2011; Martin and Santos 2014). Specifically, we collected a new dataset in a population of Barbary macaques and compared that to a previously published dataset from a population of rhesus macaques who were tested on an identical task (Marticorena et al. 2011, Experiment 1). In this task, subjects watch as an agent (a human experimenter) acts either consistently or inconsistently with what she is previously seen. Monkeys watched as a human experimenter saw a desired object move into one of two boxes and then searched for the hidden object. If subjects expect that the experimenter should act consistently with her visual perspective, then they should look longer when she reaches for that object in the empty box than when she reaches for the object in the box where both she and the subject saw the object enter. Subjects' expectations about this event are then measured using looking time to the experimental setup.

The logic of the looking time method is that subjects will look longer at an unexpected event that violates their expectations than at a control expected event. Looking time measures have been used widely in the developmental literature for decades to test human infants' expectations about both the physical (Baillargeon 1995; Baillargeon 1987; Sobel and Kirkham 2006; Hood et al. 2000; Feigenson et al. 2002; Wynn 1992) and social world (Onishi and Baillargeon 2005; Luo and Baillargeon 2007; Luo 2011) and for the last 3 decades have also been used to study expectations in non-human primate subjects both those involving physical objects (e.g., Cheries et al. 2006; De Petrillo and Rosati 2019; Munakata et al. 2001; Santos et al. 2005a, b; Santos and Hauser 2002; Shutts et al. 2009) as well as the actions of social agents (e.g., Arre et al. 2020; Martin and Santos 2014; Horschler et al. 2019; Drayton and Santos 2016; Santos and Hauser 1999). Moreover, several previously published studies have included control conditions that test for deflationary explanations of subjects' performance. These control experiments have shown that subjects show this pattern of looking longer

at an unexpected reaching event only in cases in which the agent has seen the objects' movements and thus knows where the object is (e.g., Marticorena et al. 2011; Horschler et al. 2019). In this way, the method that we use here has long been considered a valid test of visual perspective understanding both in the comparative and developmental psychology literatures.

Methods

Subjects

We compared the performance of two species of macaques: rhesus macaques ($n=62$; 22F, 40M; mean 8.18 years) from a previously collected dataset (Marticorena et al. 2011, Experiment 1) and Barbary macaques ($n=80$; 39F, 41M; mean 10.5 years) (for a full subject breakdown by age, sex, and condition, please see Table 1). Our population of Barbary macaques lived at the Trentham Monkey Forest in Trentham, England. Monkeys at this site are provisioned daily, given ad libitum access to water, and receive otherwise no medical intervention. The park is open to the public, so the monkeys are habituated to humans via the park visitors and site staff, and cognitive and behavior work has been conducted there for the last few decades. Monkeys at the park live in two social groups with individuals diverse in age and rank.

We also used data from a previously published study Marticorena et al. (2011) on a population of rhesus macaques living at the Cayo Santiago Biological Field Station in Punta Santiago, Puerto Rico (Rawlins and Kessler 1986). Monkeys in this population inhabit a small island off the east coast of Puerto Rico, where they are provisioned daily, given ad libitum access to water, and receive otherwise no medical intervention. Research has been conducted at the field site for over 80 years (for a review, see Drayton and Santos 2016), including studies using similar looking time methods (Marticorena et al. 2011; Hughes and Santos 2012; Martin and Santos 2014; Drayton and Santos 2018; Horschler et al.

2019; Arre et al. 2020). The monkeys on the island live in six social groups, which include individuals diverse in age and rank.

In total, we successfully tested (80) Barbary macaques. We approached another 33 Barbary monkeys that did not successfully complete the session, either because the subject was interfered with or displaced by another monkey (2), stopped attending to the stimuli (4), walked away (1), or had seen the entire study at an earlier date (26). The session success rate (71%) is similar to that of previously published cognitive testing with free-ranging monkey populations (Bettle and Rosati 2019; Marticorena et al. 2011; Hughes and Santos 2012; Martin and Santos 2014; Drayton and Santos 2018; Horschler et al. 2019; Arre et al. 2020). Consistent with other recent cognitive studies completed at Cayo Santiago and Trentham Monkey Forest (Bettle and Rosati 2019; Drayton and Santos 2017, 2018; Horschler et al. 2019; Arre et al. 2020), subjects were not enticed or rewarded for their task performance in any way. All subjects were free to walk away from the testing situation at any point during the experimental session.

Apparatus

In the experiment, we presented monkeys with a series of events taking place on a stage built from foamcore (Fig. 1). As in the previously published study (Marticorena et al. 2011), our stage was 75 cm long and 25.5 cm deep. We added a large screen (60 cm tall) to the front of the stage, which we used to occlude the entire display from the view of the subject. The back of the stage was 55 cm, approximately the chest height of the presenter when she knelt down behind it. Two small boxes were placed on each side of the stage (15 cm × 15 cm × 15 cm). The two boxes were different colors (blue and orange), and the inner side of each box was left open, but trimmed with fake leaves. This leaf-covered opening allowed a moving object (a plastic lemon) to enter and exit the two boxes, but prevented the subject from seeing the contents of the box. We added a length-wise cut through the center of the stage to create a track, which allowed the lemon to move freely between the two boxes. A handle attached to the lemon beneath the stage allowed the experimenter to surreptitiously manipulate the movement of the lemon, out of view of the subject.

Procedure

The testing procedure was identical across both species; we used the procedure from the original rhesus monkey paper (Experiment 1 of Marticorena et al. 2011) with Barbary macaques.

Two experimenters ran each session. To begin a session, both experimenters approached a calmly sitting monkey.

Table 1 Subject sex and age breakdown by condition within each species

Species	Sex	Condition	<i>N</i>	Age (years)
Barbary macaques (<i>Macaca sylvanus</i>)	F	Expected	19	11.1
		Unexpected	20	11.4
	M	Expected	21	10.1
		Unexpected	20	9.4
Rhesus macaques (<i>Macaca mulatta</i>)	F	Expected	10	8.9
		Unexpected	12	7.17
	M	Expected	22	9.14
		Unexpected	18	7.5

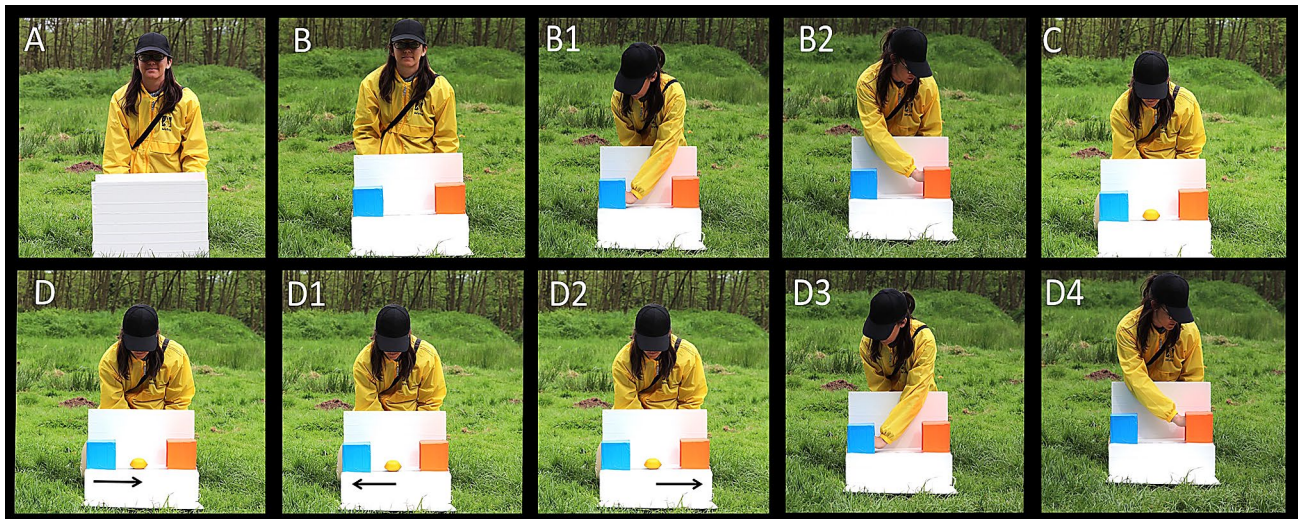


Fig. 1 Experimental apparatus and photos of each trial type. **a** The apparatus with the occluder up. **b** The apparatus with the occluder down. **b1 + b2** Trial 1: Familiarization to action; **c** trial 2: Familiarization to object and **(d–d4)** Trial 3: Test trial: the subject and presenter watch as the lemon exits the blue box (**d**) and either (**d1**) returns to the blue box or (**d2**) crosses the stage and enters the orange

box. The presenter then either acts consistently with her visual perspective, (if **d1** then **d3**; if **d2** then **d4**) reaching the box which she and the subject just watched the lemon disappear into (the expected condition) or acts inconsistently with her visual perspective (if **d1** then **d4**; if **d2** then **d3**), reaching into the box opposite of the lemon (the unexpected condition)

The presenter (E1) knelt roughly 1–3 m away and placed the apparatus between herself and the subject monkey. The cameraperson (E2) then stood beside E1 and began filming the subject. Each study session consisted of three, 10-s trials: two familiarization trials and one test trial (Fig. 1). The cameraperson completed the timing of the trial. At the start of each trial, when the E1 revealed the apparatus main stage, the E1 called out ‘now’ to indicate both that the monkey was looking at the apparatus and that the E2 should begin timing using a stopwatch on the back of the camera. At the conclusion of 10 s, the E2 called out ‘stop’ to indicate the end of the trial.

Within each experimental session, each subject monkey three trials total: two familiarization trials and one test trial. Each trial began approximately 15–30 s after the conclusion of the trial prior, which is about the length of time it takes E1 to lift the occluder and reset the stage. The goal of the familiarizations was to acquaint monkeys with the actions they would see in later in the test trial. In the first familiarization trial (*familiarization to the action*), monkeys watched as the occluder dropped and E1 reached into one of the two boxes (Fig. 1, b1 + b2), called “now” and then held that position for 10 s, during which time the monkeys’ looking was recorded. The E2 called “stop” at the conclusion of the trial. In the second familiarization trial (*familiarization to the object*), monkeys watched as the occluder dropped and E1 looked down at the object (Fig. 1c), a plastic lemon, sitting in the center of the stage for the duration of the trial. As soon as the occluder

dropped, the E1 called “now” and the E2 called “stop” at the conclusion of the 10 s.

In the final trial, the *test trial*, monkeys were randomly assigned to one of two possible outcomes, an expected outcome and an unexpected outcome. In both conditions, the monkeys first watched as the occluder dropped with E1 looking at an empty stage (Fig. 1b). The lemon then emerged from the blue box (Fig. 1d) and then (depending on the side condition) either moved back into that same blue box (*same-side condition*) (Fig. 1d1), or crossed the stage and entered the orange box (*different side condition*) (Fig. 1d2). Consistent with the original study (Marticorena et al. 2011), monkeys were presented with one of two possible test outcome conditions, an expected and an unexpected condition. In the expected condition (Fig. 1d1 then D3, or d2 then d4], E1 reached into the box she just watched the lemon go into (*acting consistently with her visual perspective*), and in the unexpected condition (Fig. 1, d1 then d4 or d2 then d3), E1 reached into the empty box (*acting inconsistently with her visual perspective*). In both conditions, the E1 called “now” when she had completed the reaching motion, and held the reaching position for the duration of the trial until E2 called stop. If subject monkeys tracked the visual perspective of E1 and expected her to act consistently with her visual perspective, then they should look longer when she acts inconsistently with her visual perspective (unexpected condition) and reaches for the object in the empty box than when she acts consistently with her visual perspective

(expected condition) and reaches into the box where she knows the lemon to be. We counterbalanced both the side the object was on (same vs. different side) and the test outcome (expected and unexpected) across subjects. To be considered a successful session, subject monkeys needed to complete all three 10-s trials.

Data coding and analysis

All sessions were coded using MPEG Streamclip (Cinque 2012). Each session was clipped into three 10-s trials and given a randomized identifying code to remove all identifying information (including subject ID, trial number, condition, and session type) from the filename of each individual video clip. The clips begin at the “now” audio cue that E1 gave to start the trial, while the monkey was looking at the experimental setup. Thus, the coder was able to infer the location of the experimental setup by looking at the position of the monkeys’ eyes in the video. Using this initial looking location of the monkey subjects, two independent experimenters coded looking time, or the amount of time the subject attended to the entire experimental setup during each trial, in frames (30 frames per second). Inter-observer reliability was high for both the original rhesus dataset (Pearson’s $R=0.91$) and the Barbary dataset (Pearson’s $R=0.94$), which is consistent with the other studies from these field sites (Drayton and Santos 2017; Rosati et al. 2018; Horschler et al. 2019; Arre et al. 2020).

Additionally, to ensure that any differences or similarities found are not an artifact of coding differences between the two datasets, we had two new coders re-code the entire dataset. The same procedure was used to redact any identifying information. Inter-observer reliability was again high, both between the two new coders (Pearson’s $R=0.92$) and between each of the new coders and the original coder (Pearson’s $R=0.94$ and 0.89 , respectively). Data from the first coder were used for the purpose of the data analysis, though the conclusions are the same regardless of which set of codes was used.

We used RStudio statistical software, Version 1.0.153 (RStudio Team 2020) for data analysis. To test whether Barbary macaques pass the visual perspective taking test, we ran an independent samples t test to see whether looking time across the two conditions (expected and unexpected) varied significantly. To test our main prediction about species differences in task performance, we ran a two-way ANOVA comparing looking time across the two different conditions (expected and unexpected) and species (rhesus and Barbary macaques). Finally, we ran a linear mixed model to look at demographic differences (species, sex, and age) in looking time across all subjects.

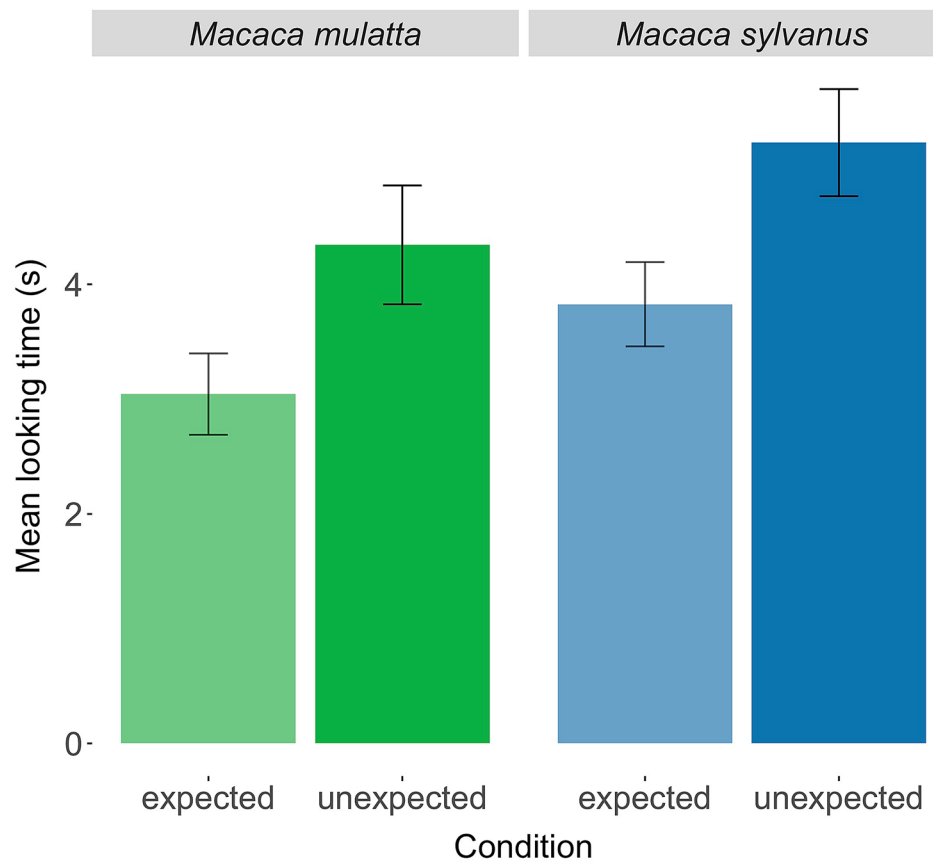
Results

To test whether Barbary macaques make accurate predictions about another agent’s behavior using her visual perspective, we first ran an independent samples t test to investigate the effect of condition on looking behavior in Barbary macaques. If Barbary macaques are able to take the visual perspective of the presenting agent, then they should look longer when the agent acts inconsistently with her visual perspective and reaches for the object in the empty box (unexpected condition) than when she reaches for the object in the correct box (expected condition), where both she and the subject know the object to be. Consistent with this prediction, Barbary subjects ($n=80$) did indeed look significantly longer in the unexpected ($M=5.24$ s, $SD=2.95$) versus the expected ($M=3.83$ s, $SD=2.32$) condition ($t(78)=-2.37$, $p=0.020$, $d=0.530$).

To be sure that monkeys assigned to the inconsistent reach condition were not looking longer across the entire study session, we also confirmed that the looking during the familiarization trials were the same between conditions. Here, we used an independent samples t test, and found no significant difference in average looking time between conditions in the first familiarization trial ($t(78)=0.028$, $p=0.977$; expected condition mean = 4.78 s, $SD=2.94$; unexpected condition mean = 4.76 s, $SD=2.56$). The same was true in the second familiarization trial ($t(78)=-1.194$, $p=0.236$; expected condition mean = 5.10 s, $SD=3.18$; unexpected condition mean = 5.90 s, $SD=2.82$). Given that the looking time did not differ significantly between the two conditions in either of the first two familiarization trials, we can conclude that any differences observed in the test trial reflects actual differences in attention between conditions and were not an artifact of more general differences in subject attention.

We then explored whether Barbary macaques’ performance differed from that of rhesus macaques using a two-way ANOVA ($n=142$; Barbary macaques, $n=80$; Rhesus macaques, $n=62$) to examine the effect of species and condition on looking time. Overall, we found no significant interaction between condition and species ($F(1,138)=0.015$, $p=0.90136$), meaning that a subject’s species had no significant effect on its looking pattern between conditions (Fig. 2). We also looked at the overall differences in looking behavior between species and condition using two independent sample t tests. We found a significant effect of condition on looking time ($t(140)=3.17$, $p=0.001$, $d=0.532$); regardless of species, subjects looked longer on unexpected test trials ($M=4.85$ s, $SD=2.92$) as compared to the expected test trials ($M=3.48$ s, $SD=2.21$). We also tested species

Fig. 2 Mean looking time across species and test condition (expected and unexpected)



differences in overall looking time (regardless of condition). Here, ($t(140) = 1.92, p = 0.057, d = 0.325$); we found no significant difference in the amount of time that Barbary macaques looked at the experimental setup, regardless of condition, ($M = 4.53$ s, $SD = 2.73$) as compared to rhesus macaques ($M = 3.67$ s, $SD = 2.51$).

In our final set of analyses, we investigated two demographic factors (sex and age) and overall looking patterns of monkey subjects in the test trial using a linear mixed model. Our base model included only trial condition (expected baseline) and confirmed our initial finding that subjects look longer in the unexpected, as compared to the expected condition. In all monkey subjects, an initial model adding subject species as a linear predictor did not improve model fit, compared to a base model with only condition as a predictor [SI Table S1; species model versus base model: $F(1) = 2.11, p = 0.1491$.] This pattern of results indicates that rhesus and Barbary subjects did not vary in their looking time in the test trial. We also looked at whether sex affected monkeys' task attention; a model adding subject sex as a linear predictor did not improve model fit, as compared to the base model with only condition as a predictor [SI Table S1; sex model versus base model: $F(1) = 3.65, p = 0.0580$]. This finding shows that male and female subjects of both species did not vary in their looking time by in the test trial. Finally, in line

with previous work comparing rhesus and Barbary macaques (Rosati and Santos 2017), we investigated how age affected monkey attention to the task using a model adding subject age as a linear predictor. Adding age as a predictor to the model did improve model fit, as compared to the base model with only condition as a predictor [SI Table S1; age model versus base model: $F(1) = 8.82, p = 0.004$], indicating that in both conditions, looking time decreased as a function of age (see SI Fig. S1 depicting this effect between age cohorts).

Discussion

Here, we found that Barbary macaques can take the visual perspective of another agent and make an accurate prediction about her behavior. This finding is consistent with a previously collected dataset (Marticorena et al. 2011) on rhesus macaques using the same task. Both Barbary and rhesus macaques look significantly longer in the unexpected condition, in which an agent acts inconsistently with her visual perspective and reaches for an object in an empty box, as compared to the expected condition, where she reaches toward the box that she and the subject both know the object to be. In short, these two species show no differences in their

ability to track other agents' visual perspective, and are both capable of taking the visual perspective of a human agent.

The results presented here are in contrast to some of the existing work investigating how species differences in social tolerance affect social cognition. Previous work in these two species (Joly et al. 2017; Rosati and Santos 2017) found that social tolerance seems to affect several aspects of these species' social cognitive abilities. Joly and colleagues suggest that their results show tolerant macaque species outperform less tolerant species of macaques on some tests of social cognition (Joly et al. 2017). It is important to note that the task at which the experimenters observed the most strong difference between species was a "social object choice task" which required subjects to follow a human's pointing cue, and that in fact, consistent with our findings here, the experimenters found no significant differences in task performance in gaze-following or intention-reading tasks within the same test battery of Joly et al. 2017). Thus, any species differences others have observed may play out as life-long effects (e.g., Barbary macaques but not rhesus macaques maintain high-levels of gaze following into senescence, Rosati and Santos 2017; see also, Rosati et al. 2016) rather than a measurable difference at a single life stage. Our results suggest no difference in adult social cognition performance between these two species despite their large differences in social tolerance, but do not rule out differences within different developmental stages of the two species.

Given these results—and convergent work showing superior social cognitive abilities in tolerant bonobos as compared to despotic chimpanzees (Herrmann, et al. 2010)—we consider a few possibilities for why we found no difference in performance between tolerant Barbary macaques and despotic rhesus monkeys. The first possibility is that the capacity to recognize other agents' visual perspective is not affected by a species' social tolerance in the way that gaze following and other sociocognitive capacities are. The capacity to understand how others will act based on where they are looking is an early emerging capacity in human development (e.g., Luo and Baillargeon 2007; Onishi and Baillargeon 2005), one that many scholars have argued may emerge innately (Baillargeon et al. 2010), perhaps even in non-human primates. It is therefore possible that the capacity to predict others' behaviors based on visual perspective is one that many social species share despite divergent social ecologies.

A second possible explanation concerns potential limitations in the previous studies of species differences in these two species. One of the two previous studies observing differences in social cognition performance across macaque species including Barbary and rhesus macaques (Joly et al. 2017) had relatively small sample sizes ($n = 11$ for both species) at least relative to the studies presented here ($n = 62$ and $n = 80$ for rhesus and Barbary macaques, respectively).

In addition, Joly and colleagues' sample had sex ratios that were relatively imbalanced across species (Barbary: 7F, 4M; rhesus: 2F, 9M). We know from previous work in adults of these species that there are sex differences in social motivation and cognition (e.g., Almeling et al. 2016, 2017; Rosati et al. 2016, 2018; Rosati and Santos 2017). For these reasons, it is difficult to rule out whether the species-level differences Joly et al. observed are indeed differences across species or whether they may instead reflect individual and/or sex differences across the two specific sample populations used in this study, as others have suggested of phylogenetic comparative work using single populations to define a species' cognitive characteristics (Many Primates et al. 2019).

Another possibility concerns the age of subjects we tested. One previous study that observed species differences in Barbary and rhesus macaque social cognition (Rosati and Santos 2017) only observed such differences later in life; specifically, Rosati and Santos (2017) found that older Barbary monkeys living in tolerant social groups seem to maintain their gaze-following abilities in old age, whereas older despotic rhesus macaques show age-related declines (Rosati and Santos 2017; Rosati et al. 2016). Scholars have previously suggested that the varying social tolerance environments might lead to different paces of development (Krupenye et al. 2017), predicting that species in socially tolerant environments may have a delayed development of perspective-taking abilities, because the pressures for refining visual perspective taking abilities are not as intense. Under this view, we would expect younger individuals in more competitive species to show more adult-like perspective taking than younger individuals in more socially tolerant species. Taken together then, this previous work suggests that we might expect developmental differences in rhesus macaques and Barbary macaques. Unfortunately, our current sample did not include a large enough sample of older monkeys of each species to test these predictions specifically. However, we did find that across all subjects' test trials, subject looking time decreased as a function of age, regardless of condition (see SI Fig. S1 depicting this effect between age cohorts); the model adding subject age as a linear predictor did improve model fit, as compared to the base model with only condition as a predictor [age model versus base model: $F(1) = 8.82$, $p = 0.004$]. In other words, regardless of the experimental condition, older subjects are looking less long at the experimental setup in the test trial than younger subjects. Future work should therefore investigate the possibility that despotic macaque species differentially lose their attention to the visual perspective of others across the lifespan relative to more tolerant species.

A final caveat concerns the specific two populations we tested. Both of the macaque groups we tested are free-living, but captive, populations. It is possible that these subjects may not have to compete for as many resources (food, water)

as a wild population. As a result, there is a chance that wild-living animals might show a different pattern of performance than the populations we compared here. Nonetheless, it is worth noting that both of our populations show much of the competition typical of wild populations in our free-ranging setting. Both populations we tested have ample opportunities to compete over social resources like grooming, mating, and infant handling opportunities (Rawlins and Kessler 1986; Maestriperi, and Hoffman 2012; Carne et al. 2011). Furthermore, individuals in these populations engage in physical altercations to resolve hierarchical disputes and also disperse between groups (Boelkins and Wilson 1972). Thus, while our free-ranging subjects may have relatively limited competition over non-social resources, individuals in these populations have ample opportunity to compete socially. Future research, however, could follow up with similar tests in wild-living or captive populations.

In addition, future work could explore how rhesus and Barbary macaques initially develop their visual perspective taking abilities. It is possible that tolerant and despotic species develop this capacity along different ontogenetic trajectories (Rosati et al. 2014; Gómez 2005). Indeed, recent work suggest that rhesus macaques may require some experience before developing the capacity to make predictions about another agent's perspective (Arre et al. 2020), raising the possibility that Barbary macaques may develop this ability earlier than rhesus macaques due to their experiences in a tolerant social environment. In this way, testing whether these two species show divergent ontogenetic patterns, even though they show relatively similar performance as adults, would be a fruitful next step for this line of work.

In conclusion, we observed that two species that vary in their social tolerance do exhibit at least one similar social cognitive ability as adults—the capacity to make accurate predictions based on an agent's visual perspective. This convergence suggests that there may be some social cognitive abilities that are fundamental to any type of social living, and that social tolerance may play less of an important role in the emergence of these capacities. Our results hint that visual perspective understanding may be one such core part of social living that emerges regardless of socioecology.

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Author contributions AMA and LRS contributed funding. AMA and LRS designed the experiment. AMA and ES collected data. AMA analyzed data and created figures. AMA, ES, and LRS wrote the paper.

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Availability of data and materials The data (Arre, 2020) that support the findings of this study are available in the Open Science Framework data repository via a view-only link at https://osf.io/9mz4n/?view_only=398000e76ab64a31aed39844df5faf2e and will be made publicly available upon publication.

Code availability All analyses were done using RStudio statistical software, Version 1.0.153 (RStudio Team 2020). Script can be made available upon request.

Compliance with ethical standards

Conflicts of interest/competing interests The authors declare no conflicts of interest or competing interests.

Ethics approval All research protocols reported in this manuscript were reviewed and approved by the Institutional Animal Care and Use Committee of Yale University (rhesus monkeys: Protocol #2014-11624, Barbary monkeys: Protocol #2014-11615) and the University of Puerto Rico (Protocol #8310106). The research presented in this manuscript adhered to the legal requirements of Puerto Rico and the United Kingdom.

Consent to participate Non-human primate subjects were not enticed or rewarded for their task performance in any way. All subjects were free to walk away from the testing situation at any point during the experimental session.

Consent for publication All authors consent to the publication of this manuscript.

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