



Tolerant Barbary macaques maintain juvenile levels of social attention in old age, but despotic rhesus macaques do not



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Complex social life is thought to be a major driver of complex cognition in primates, but few studies have directly tested the relationship between a given primate species' social system and their social cognitive skills. We experimentally compared life span patterns of a foundational social cognitive skill (following another's gaze) in tolerant Barbary macaques, *Macaca sylvanus*, and despotic rhesus macaques, *Macaca mulatta*. Semi-free-ranging monkeys ($N = 80$ individuals from each species) followed gaze more in test trials where an actor looked up compared to control trials. However, species differed in ontogenetic trajectories: both exhibited high rates of gaze following as juveniles, but rhesus monkeys exhibited declines in social attention with age, whereas Barbary macaques did not. This pattern indicates that developmental patterns of social attention vary with social tolerance, and that diversity in social behaviour can lead to differences in social cognition across primates.

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A fundamental question regarding the evolution of intelligence concerns how variation in social systems shapes cognitive abilities. Although many theories propose that variation in social cognition stems from the challenges of social life (Dunbar, 1998; Dunbar & Shultz, 2007), little work has tested the specific kind of social interactions that promote sophisticated cognitive capacities. Some proposals have linked complex social cognition to political or 'Machiavellian' social interactions (Byrne & Whiten, 1988; Hare, 2001; de Waal, 1982). Under this competition hypothesis, individuals use social cognitive skills to outcompete or deceive others. Yet other proposals argue that societies characterized by cooperative relationships exhibit more robust social cognition (Burkart, Hrdy, & van Schaik, 2009; Hare, 2017). This tolerance hypothesis is particularly focused on explaining uniquely human cognition. To test the importance of tolerant versus competitive systems for social cognition, we compared the life span development of gaze following abilities in two closely related species with different social styles: more tolerant Barbary macaques, *Macaca sylvanus*, and more despotic rhesus macaques, *Macaca mulatta*.

Social attention, or detection of the locus of another's gaze direction, provides a strong test of the evolutionary relationship

between social behaviour and cognition for several reasons. First, social attention is a foundational component of human social cognition: attending to where and at what others are looking underpins such abilities as joint attention and theory of mind (Emery, 2000; Flom, Lee, & Muir, 2007; Langton, Watt, & Bruce, 2000; Puce & Bertenthal, 2015). That is, information about where others are directing their gaze is potent cue to what they are seeing or thinking, and is therefore important for more complex mentalizing abilities. Second, a basic sensitivity to others' gaze direction is also widely shared across primates; species ranging from strepsirrhine lemurs to monkeys to great apes tend to co-orient with conspecifics or humans, at least in some situations (Rosati & Hare, 2009; Shepherd, 2010). Finally, evidence for both the competition and tolerance hypotheses directly invoke cognitive skills that capitalize on such gaze sensitivity.

Under the competition hypothesis, for example, successful competition may require exploitation of information about others' gaze and visual perspective. Along these lines, more competitive primate species have quite sophisticated abilities to model the perspective of others. Both chimpanzees, *Pan troglodytes*, and rhesus monkeys engage in visual (and auditory) perspective taking to obtain hidden food when competing with a human or conspecific (Flombaum & Santos, 2005; Hare, 2011; Hare, Call, Agnetta, & Tomasello, 2000; Hare, Call, & Tomasello, 2001, 2006; Kaminski, Call, & Tomasello, 2008; Melis, Call, & Tomasello, 2006; Santos,

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Nissen, & Ferrugia, 2006). In contrast, behaviour-reading strategies, where individuals do not directly reason about the subjective mental states of others, seems to account for the performance of more tolerant species, including marmosets (*Callithrix jacchus*), capuchins (*Cebus apella*) and Tonkean macaques, *Macaca tonkeana*, in similar contexts (Burkhart & Heschl, 2007; Canteloup, Piraux, Poulin, & Meunier, 2016; Costes-Thire, Leve, Uhlrich, de Marco, & Thierry, 2015; Hare, Addessi, Call, Tomasello, & Visalberghi, 2003). Additional evidence for this claim comes from direct comparisons of different lemur species. Ringtailed lemurs, *Lemur catta*, which typically live in large groups with anthropoid-like dominance hierarchies, exhibit more robust performance on perspective-taking tasks, outperforming other lemur species that live in smaller family groups (Bray, Krupenye, & Hare, 2014; MacLean et al., 2013; Sandel, MacLean, & Hare, 2011). Finally, chimpanzees are more successful at exploiting social cues specifically in competitive contexts compared to cooperative contexts (Hare & Tomasello, 2004; Herrmann & Tomasello, 2006; but see MacLean & Hare, 2015).

Under the tolerance hypothesis, in contrast, tolerant species should be especially sensitive to gaze cues because they facilitate cooperative interactions. Social tolerance has been specifically linked to robust comprehension of communicative signals, including gaze cues, in domesticated animals. For example, in social tasks in which a human experimenter communicatively informs the participant of the location of hidden food by looking or pointing at its location, domesticated dogs, *Canis familiaris*, and experimentally domesticated silver foxes, *Vulpes vulpes*, outperform wolves, *Canis lupus*, and a control line of undomesticated foxes. Both dogs and the domesticated foxes exhibit greater social tolerance towards humans (Hare, Brown, Williamson, & Tomasello, 2002; Hare et al., 2005; Hare & Tomasello, 2005). Along the same lines, relatively tolerant bonobos, *Pan paniscus*, are more interested in viewing eyes than are chimpanzees (Kano & Call, 2014; Kano, Hirata, & Call, 2015), although they do exhibit more comparable performance in some gaze-following contexts (Brauer, Call, & Tomasello, 2005; Okamoto-Barth, Call, & Tomasello, 2007; see also MacLean & Hare, 2012). More generally, tolerance seems to facilitate the emergence of cooperative interactions: more tolerant chimpanzee dyads are more cooperative than less tolerant dyads, and bonobos outperform chimpanzees in cooperative tasks (Hare, Melis, Woods, Hastings, & Wrangham, 2007; Melis, Hare, & Tomasello, 2006). Finally, humans are characterized by extreme tolerance, joint attention capacities and high levels of cooperation in which gaze cues communicate information about an actor's intentions (Csibra, 2010; Csibra & Gergely, 2009; Senju & Csibra, 2008; Tomasello & Carpenter, 2007; Tomasello, Carpenter, Call, Behne, & Moll, 2005; Tomasello, Hare, Lehmann, & Call, 2007). Indeed, some views argue that competition may be the most important driver of complex social cognitive abilities in other primates, whereas cooperation is specifically important for the emergence of human-unique cognition (Moll & Tomasello, 2007; Tomasello, 2014; Tomasello & Call, 1997).

To test the importance of tolerant versus competitive systems for social cognition in nonhuman primates, we compared the life span development of gaze following in two species of macaques. The genus *Macaca* is a radiation of closely related species that share a similar basic social organization (multimale–multifemale groups, where females stay in their natal group and males disperse), but diverge in social style (Thierry, 2000, 2004). Some macaque species exhibit greater despotism, characterized by steep dominance hierarchies, more intense aggression and formalized submission signals. In contrast, other species are characterized by a relaxed dominance hierarchy, reconciliation after aggression and more affiliative social signals. Across macaque species, this suite of

behavioural traits related to tolerance are strongly linked and tend to covary (Thierry, 2013). Indeed, Thierry (2007) classed macaques into four 'grades' of social styles of increasing tolerance based on this cluster of characteristics. Thus, comparisons of different macaque species can isolate variation in social tolerance across species with otherwise similar social organizations. In the current work, we therefore compared more despotic rhesus macaques (grade 1, the most despotic) with more tolerant Barbary macaques (grade 3). We predicted that rhesus monkeys should exhibit more robust gaze following if competition spurs complex social cognition, whereas Barbary macaques should exhibit more robust gaze following if social tolerance promotes this skill.

We further examined developmental changes in gaze following across the life span of these macaques. Across primate species, younger individuals tend to exhibit greater social tolerance, whereas mature individuals show higher rates of aggression and competition (Pereira & Fairbanks, 2002). Similarly, developmental shifts in social tolerance seem to track developmental shifts in some social cognitive abilities in chimpanzees and bonobos (Wobber, Wrangham, & Hare, 2010). Consequently, patterns of cognitive development provide a second test of the relationship between social tolerance and social cognition. While some prior work has examined the emergence of gaze following within a single primate species (Rosati, Arre, Platt, & Santos, 2016; Simpson, Miller, Ferrari, Suomi, & Pauker, 2015; Teufel, Gutmann, Pirow, & Fischer, 2010; Tomasello, Hare, & Fogleman, 2001), no study has directly compared life span patterns of social attention across different primates. Moreover, qualitative comparisons of different species' ontogenetic patterns in different studies are also somewhat contradictory. Rhesus macaques show high levels of gaze following in the juvenile period that declines with age (Rosati et al., 2016; Tomasello et al., 2001). Yet pigtail macaques, *Macaca nemestrina*, which are somewhat more tolerant than rhesus macaques (Thierry, 2007), exhibit relatively delayed development of gaze following and have been hypothesized to need more social experience to acquire this skill (Ferrari, Coude, Gallese, & Fogassi, 2008; Ferrari, Kohler, Fogassi, & Gallese, 2000). Our study, comparing cognitive development across species with identical methods, allows us to disentangle this issue. We predicted that any species difference should be exacerbated with age, as variation in tolerance is most pronounced in mature individuals.

METHODS

Ethics Statement

All noninvasive behavioural tests were approved by the Institutional Animal Care and Use Committee (IACUC) for Yale University (Barbary: number 2014–11615; rhesus: number 2014–11624), as well as the Cayo Santiago IACUC (rhesus: number 8310106) administered through the University of Puerto Rico Medical Sciences Campus. All tests adhered to site guidelines for animal research. Monkeys who participated in this study live in natural social groups, are provisioned daily (in addition to access to plants growing at their respective sites) and have ad libitum access to water.

Subjects

We tested 80 rhesus monkeys living at Cayo Santiago in Puerto Rico (41 females and 39 males, ranging in age from 1.4 to 22 years), and 80 Barbary macaques living at Trentham Monkey Forest, Stoke-on-Trent, U.K. (41 females and 39 males, ranging in age from 2.1 to 29 years); sample size for age cohorts in each species are shown in Fig. 1. Rhesus data were partially reported in previous work (see

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