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Developmental shifts in social cognition: socio-emotional biases across the lifespan in rhesus monkeys

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Abstract

Humans exhibit a suite of developmental changes in social cognition across the lifespan. To what extent are these developmental patterns unique? We first review several social domains in which humans undergo critical ontogenetic changes in socio-cognitive processing, including social attention and theory of mind. We then examine whether one human developmental transition—a shift in socio-emotional preferences—also occurs in non-human primates. Specifically, we experimentally measured socio-emotional processing in a large population of rhesus macaques (*Macaca mulatta*) ranging from infancy to old age. We tested whether macaques, like humans, also exhibited developmental shifts from a negativity bias at younger ages, indicating preferential attention to negative socio-emotional stimuli, to a positivity bias at older ages. We first assessed monkeys' ($n = 337$) responses to negative socio-emotional stimuli by comparing their duration of looking towards photos of negative conspecific signals (threat displays) versus matched neutral expressions. In contrast to the pattern observed in humans, we found that older monkeys were more attentive to negative emotional stimuli than were younger monkeys. In a second study, we used the same method to examine monkeys' ($n = 132$) attention to positive (affiliative displays) versus matched neutral expressions. Monkeys did not exhibit an overall preference for positive stimuli, nor major age-related changes in their attention. These results indicate that while monkeys show robust ontogenetic shifts in social preferences, they differ from humans by exhibiting an increasing negativity bias with age. Studies of comparative cognitive development can therefore provide insight into the evolutionary origins of human socio-cognitive development.

Significance statement

Humans are characterized by complex and flexible social behavior. Understanding the proximate psychological mechanisms and developmental processes that underpin these social behaviors can shed light on the evolutionary history of our species. We used a comparative developmental approach to identify whether a key component of human social cognition, responses to emotionally-charged social stimuli, are shared with other primates. Humans exhibit important shifts in this aspect of our social cognition: younger individuals attend more to negative stimuli, whereas older adults tend to focus on positive information. These shifts are thought to appropriately tailor our age-dependent social goals. We found that, unlike humans, rhesus monkeys show an increasing negativity bias with age. By examining primate cognition across the lifespan, this work can help disentangle how complex forms of social behavior emerge across species.

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Introduction

Human social behavior is strikingly different from that of other species. We speak languages, routinely cooperate with others, pass cultural knowledge down through generations, and live in complex societies. What are the origins of these social capacities? Cognitive scientists have generally used two main approaches to answer this question. First, comparative psychologists have addressed the evolutionary roots of human cognition by pinpointing which abilities are uniquely human and which are shared more broadly with other animals. This comparative perspective can further test which aspects of different species' natural history promote complex, flexible skills to illuminate their ultimate function. Second, developmental psychologists have examined the ontogenetic roots of human cognition, exploring when and how different abilities emerge over human development. This developmental perspective can provide new insights into the earliest forms of human sociality, as well as the experiences necessary to foster different cognitive abilities. Comparative and developmental studies of cognition therefore provide distinct but complimentary contributions to our understanding of the biology of behavior (Tinbergen 1963; Bateson and Laland 2013).

Recently, a new line of research has begun to integrate comparative and developmental methods in order to examine the origins of human cognition. Work using this comparative cognitive developmental approach aims to compare the ontogeny of different cognitive abilities across the life course in different species, integrating evolutionary perspectives into developmental psychology (Bjorklund and Bering 2003; Gomez 2005; Tomasello and Carpenter 2005; Matsuzawa et al. 2006; Matsuzawa 2007; Bjorklund 2018). Tracing the development of complex abilities across species using the comparative method can illuminate when and how differences in social cognition emerge, providing new insights into the evolution of human social behavior (Rosati et al. 2014).

Studies of comparative cognitive development are also critical for testing hypotheses about the emergence of uniquely human cognition, in part because several prominent theories propose that some of our species' special cognitive abilities are directly linked to a human-like pattern of development. Several specialized or unique life history features characterize both early development and aging in humans, including an extended juvenile period, menopause or reproductive senescence, and a longer lifespan (Bogin and Smith 1996; Robson and Wood 2008; Bogin 2010; Leigh 2012; Schwartz 2012). Crucially, these life history characteristics are different from those observed in other primate species. For example,

macaques show relatively faster growth and brain maturation during the juvenile period, no period of reproductive cessation, and a shorter absolute lifespan than humans (Bogin and Smith 1996; Bogin 1999; Leigh 2004; Alberts et al. 2013). In this way, uniquely human cognitive development may be yoked to our specialized life history characteristics: our longer juvenile period can allow for a longer time for cognitive skill acquisition, and an increased lifespan allows these slowly developing skills to be exploited and ultimately pay off over the lifespan (Bjorklund and Green 1992; Janson and van Schaik 1993; Kaplan et al. 2000; Bjorklund and Bering 2003; Schuppli et al. 2012). Consequently, comparisons of cognitive development across different primate species can test whether specific aspects of our human life history are responsible for the cognitive patterns that emerge in our species.

However, comparative developmental research on cognition is often challenging to implement. For example, most work in comparative social cognition focuses on whether a given cognitive capacity is present (or absent) in adult or mixed-aged individuals of a given species (e.g., Hare et al. 2000, 2001; Flombaum and Santos 2005; Kaminski et al. 2008; Marticorena et al. 2011; Canteloup et al. 2016; Krupenye et al. 2016). The rarity of developmental studies is due in part to limitations on sample size and access to populations of individuals that vary in age. Fortunately, however, researchers have increasingly overcome these limitations to examine developmental processes in non-human primates. Some work, for example, has circumvented sample size issues by tracing the development of a small number of individuals longitudinally in a fine-grained fashion (Okamoto et al. 2002; Tomasello and Carpenter 2005; Matsuzawa et al. 2006; Tomonaga 2006; Okamoto-Barth et al. 2008). Other studies have examined early development in larger cross-sectional samples (Ferrari et al. 2000; Tomasello et al. 2001; Ferrari et al. 2008; Teufel et al. 2010; Simpson et al. 2015, 2016a; Paukner et al. 2018). Finally, more recent work has taken a lifespan approach to examine the full trajectory of primate social cognition during aging as well (Lacreuse et al. 2014; Rosati et al. 2016; Fischer 2017; Rosati and Santos 2017). Together, this kind of work can identify whether certain human cognitive capacities and developmental processes are shared with other primates, as well as how cognition unfolds across different species in general.

Here, we first review several domains in which a comparative developmental approach can reveal important insights into potentially uniquely human social abilities. Research on primate social cognition has already begun using studies of non-human primate development to refine theories about human lifespan development in some domains. After reviewing

recent work using this comparative developmental approach, we then focus on socio-emotional processing. This is a domain of social cognition that has received little attention from comparative developmental research, but which bears on several hypotheses about human social function. Finally, we present two empirical studies of socio-emotional processing in rhesus monkeys (*Macaca mulatta*) to directly test whether this non-human species shares human-like shifts in social cognition across the lifespan.

Gaze following and social attention

The ability to follow gaze—to align one's own gaze with another individual's direction of attention—is foundational to many human social behaviors. For example, gaze following abilities are linked to the onset of human-unique skills such as theory of mind, language, and cultural learning more broadly (Brooks and Meltzoff 2005; Flom et al. 2007; Brooks and Meltzoff 2008; Senju and Csibra 2008; Csibra and Gergely 2009; Csibra 2010; Wellman 2011). In atypical development, such as autism, children exhibit early deficits in social attention and often face challenges in both communication and theory of mind abilities (Dawson et al. 2004; Volkmar et al. 2005; Toth et al. 2006; Klin et al. 2009). This crucial human skill emerges very early in life: infants reliably follow gaze at around 6 months (D'Entremont et al. 1997) and by 18 months can flexibly follow other individuals' gaze to distant targets and around barriers (Moll and Tomasello 2004; Moll and Tomasello 2006). There is also evidence that this skill shows continued change through adulthood and into old age. For example, older adults show decreased responsivity to social gaze cues, paralleling general shifts in social processing during aging (Slessor et al. 2008, 2016; Kuhn et al. 2015). Overall, this indicates that gaze following is a crucial human social capacity with robust age-related change across the human lifespan.

Despite the importance of gaze following for human-unique cognitive skills, humans are not the only species that follows gaze. Indeed, gaze following is a phylogenetically widespread behavior that is observed in many diverse species including apes, monkeys, lemurs, and even some more distantly related animals (Braeuer et al. 2005; Okamoto-Barth et al. 2007; Rosati and Hare 2009; Shepherd 2010; MacLean and Hare 2012; Kano and Call 2014). One important question is how non-human primates develop these gaze following skills. Does primate gaze following trace the same patterns as seen in humans, or does primate gaze following emerge via different ontogenetic processes?

Some evidence suggests that despite similarities between human and non-human primate gaze following at maturity, non-human primates may develop gaze following over different trajectories than humans do. First, many non-human primates do not seem to develop gaze-following capacities in infancy. Pigtailed macaques (*Macaca nemestrina*), for example, exhibit major delays in gaze following relative to humans, with responses to some kinds of gaze cues (e.g., eye direction) only occurring robustly in adulthood (Ferrari et al. 2000, 2008). Similarly, chimpanzees (*Pan troglodytes*) do not show basic co-orienting responses until they are several years old, and more complex inferences about others' line of sight around barriers may not emerge until even later (Tomasello et al. 2001; Braeuer et al. 2005; Okamoto-Barth et al. 2007; Wobber et al. 2014). This evidence indicates that some non-human primates develop gaze following abilities over a slower time course than humans do. This aligns with the proposal that non-human gaze following emerges only after a period of more extensive experience with relevant social interactions, which differs from what occurs in humans for whom gaze following emerges fairly early in development (Ferrari et al. 2008).

However, other non-human species show developmental changes in gaze following that are surprisingly similar to humans, despite differences in their social behavior or life history characteristics. For example, rhesus macaques, unlike other closely related macaque species, appear to following gaze within the first year of life (Tomasello et al. 2001). This pattern was confirmed by another large-scale study of gaze following development, showing that rhesus monkeys exhibit parallels in many of the same important developmental milestones that humans do, including early emergence of gaze following responses in infancy, the emergence of sex differences in responsivity in adulthood, and declining propensity to follow gaze in old age (Rosati et al. 2016). These findings indicate that gaze following in rhesus macaques follows a remarkably human-like trajectory, even though macaque life history characteristics are quite different from humans in terms of both early development and aging (Bogin and Smith 1996; Leigh 2004; Alberts et al. 2013).

Conversely, species that are quite closely related and share many life history and social features may nonetheless differ in their patterns of social development. For example, Barbary macaques (*Macaca sylvanus*) are closely related to rhesus macaques. While this species also shows early-emerging gaze following responses (Teufel et al. 2010), they do not show sex differences in gaze following and further maintain juvenile-like levels of gaze following into old age (Rosati and Santos 2017)—unlike both rhesus macaques and humans. One possibility is that differences in social tolerance, rather than life history, drive these differences in cognitive development. Whereas both macaques species have a similar life history and general social organization, they notably differ in social style: rhesus macaques are a more despotic, competitive species, whereas Barbary macaques are more socially tolerant (Thierry 2007). In fact, there is similar evidence for differences in adult gaze following in ape species that differ in social tolerance (Kano and Call 2014; Kano et al. 2015).

Together, this research on the origins of non-human primate gaze following reveals complicated patterns where some—but not all—primate species show human-like changes in gaze following despite drastic differences in life history. Conversely, even species with very similar life history, such as different macaque species, may diverge in developmental patterns.

Theory of mind

A second domain in which a cognitive developmental approach has provided important insights into the mechanisms underlying uniquely human cognition is "theory of mind." One striking feature of human cognition is that we explain the behavior of other individuals in terms of their unobservable mental states—their perceptions, desires, knowledge state, and beliefs. This capacity to conceive of others as having minds emerges on a now well-understood time course that begins in infancy and extends into childhood (Wellman and Liu 2004). Work using looking time methodologies, which measure looking behavior as an index of cognitive processes in non-verbal populations, has demonstrated that humans begin representing others' actions in terms of mental states within the first year of life. By 9 months of age, for example, infants expect others to behave in accord with their goals and intentions (Gergely et al. 1995; Woodward 1998; Woodward et al. 2001). Infants also recognize that agents act on the basis of their own visual perspective (Luo and Johnson 2009) and successfully represent what other individuals know (Vouloumanos et al. 2014). Later, around 15 months of age, infants begin predicting that people will act on the basis of their beliefs (Onishi and Baillargeon 2005). This early pattern of theory of mind development observed using looking tasks is mirrored when toddlers and older children are tested with more explicit reasoning tasks, asking children to make a judgment concerning how others will act. In these contexts, younger children are capable of representing others' knowledge and intentions but fail to reason about others' beliefs (Wellman et al. 2001; Wellman and Liu 2004; Wellman 2011). Indeed, children begin accurately representing others' false beliefs (e.g., beliefs that do not align with the true state of the world) in explicit tasks only around 4 years of age (Wellman et al. 2001), indicating that this aspect of theory of mind emerges last in a sequence of abilities.

These early-emerging theories of mind capacities are thought to underpin more complex forms of human social behavior, including cultural learning and cooperation (Tomasello et al. 2005; Tomasello and Carpenter 2007). For this reason, whether non-human primates share cognitive capacities for representing other minds has been a topic of intense interest (Call and Tomasello 2008; Rosati et al. 2010; Martin and Santos 2016). In fact, there is good evidence that other primates share some of the components of a human-like theory of mind. First, other primates think about others' actions in terms of goals and intentions (Call et al. 2004; Phillips et al. 2009; Buttelman et al. 2012). Second, there is strong evidence that many primate species can reason about the perception of others, including what others can see or even hear (Hare et al. 2000; Flombaum and Santos 2005; Hare et al. 2006; Melis et al. 2006; Santos et al. 2006; Braeuer et al. 2007; Sandel et al. 2011). Finally, some primates can use their knowledge about others' perspectives to assess what others do or do not know about the world (Hare et al. 2001; Kaminski et al. 2008; Marticorena et al. 2011; Martin and Santos 2014). Thus, many primate species seem to acquire several human cognitive milestones for representing others' goals, intentions, perceptions, and knowledge states.

In contrast, there is currently limited evidence that non-human primates understand that other individuals can hold false beliefs about the world. Most studies have observed that non-human primates fail to track others' beliefs in a variety of different explicit tasks, for example where individuals can use information about other's beliefs to outwit them in a competitive context (Krachun et al. 2007; Kaminski et al. 2008; Marticorena et al. 2011; Martin and Santos 2014; but see Buttelman et al. 2017). The main exception is recent evidence using eye-tracking methods to show that apes may track implicit belief states, measuring whether they anticipate other's actions when they hold false beliefs (Krupenye et al. 2016). However, there is still no evidence that non-human primates can engage in the sorts of explicit false belief reasoning seen in older human children and adults. Consequently, the sorts of theory of mind skills that emerge later in human development—such as explicit false belief representations—may not be present in other primates. Taken together, this pattern of theory of mind performance in primates suggest that other species may share the sorts of theory of mind capacities that humans develop early in life—a sensitivity to others goals, perceptions, and knowledge states—but that they may lack the cognitive abilities that humans acquire later in development.

Less work to date has explored how adult non-human primates develop theory of mind capacities compared to work on gaze following, but there are hints that non-human primates may develop their theory of mind capacities at later relative and absolute ages compared to humans. Human and non-human primate infants show similar attention to social agents at very young ages (Myowa-Yamakoshi et al. 2003; Tomonaga et al. 2004; Myowa-Yamakoshi et al. 2005; Matsuzawa et al. 2006; Tomonaga 2006; Ferrari et al. 2009), but then begin to diverge. For example, apes may not develop a robust understanding of intentional action until around 2 to 3 years of age (Tomasello and Carpenter 2005; Wobber et al. 2014)—and such early differences in theory of mind abilities that could have cascading effects on later-emerging social skills such as cultural learning. Indeed, a comparison of

cognitive development in 2-to-4-year-old humans, chimpanzees, and bonobos found that human children exhibited earlier proficiency in theory of mind tasks such as goal understanding and showed greater improvement longitudinally in their performance when compared to non-human apes (Wobber et al. 2014). Overall, this line of work shows how comparative developmental studies can tease apart when and why humans and other primates diverge in their theory of mind understanding over ontogeny.

Socio-emotional processing

A final important domain of social cognition concerns the emergence of socio-emotional processes. In particular, changes in socio-emotional processing across the lifespan in humans have been the focus of intense interest in social psychology. This work has revealed that humans exhibit robust changes in preferences for social and emotional stimuli as they age. Whereas children and younger adults exhibit a "negativity" bias, selectively attending to and remembering negative stimuli and events, older adults rather exhibit a positivity bias (Carstensen et al. 2003, 2011; Charles et al. 2003; Mather and Carstensen 2003; Carstensen and Mikels 2005; Mather and Carstensen 2005). For example, older adults exhibit more interest in and attention to images of positive facial expressions (happy faces) compared to negative faces (angry or sad faces)—whereas younger adults may show no preference, or even a preference to attend to negative faces (Mather and Carstensen 2003, 2005; Isaacowitz et al. 2006a, b, 2008; Spaniol et al. 2008). Similarly, infants and young children demonstrate a strong negativity bias across several types of social contexts (see Vaish et al. 2008 for a review).

An influential explanation for why humans exhibit these characteristic shifts is socio-emotional selectivity theory. This theory proposes that lifespan changes in emotional processing stem from a particular human cognitive feature, namely our rich understanding of time and our own mortality (Carstensen et al. 1999; Carstensen 2006). Under this view, older adults have a shorter "time horizon" than do younger adults, and therefore shift their goals to maximize emotional satisfaction by prioritizing positive emotional events and preserving enduring social relationships. In contrast, younger adults prioritize future opportunities for relationships and therefore engage in information-seeking by testing out a greater variety of social partners. As such, younger individuals may tolerate more negative experiences—the price that must be paid to successfully forge new social relationships. In this view, a sense of time drives these shifts, because old age inherently limits future opportunities to build or develop relationships. Additional support for this claim comes from studies examining how adults make social choices when they anticipate an imminent ending to their interaction. In fact, younger adults, much like older adults, prefer positive, familiar social partners over

novel social partners when they consider situations that have a clear end date, such as who they would like to interact with if they were soon moving across the country (Fredrickson and Carstensen 1990) or when graduating college (Fredrickson 1995). Similarly, young adults facing a terminal illness exhibit social preferences more like older adults (Carstensen and Fredrickson 1998). That is, younger adults appear to exhibit socio-emotional biases more similar to older adults when faced with limited time horizons.

To date, there has been little research on socio-emotional selectivity in non-human animals. The main exception is a recent set of studies that examined socio-emotional processing shifts in Barbary macaques of different ages (Almeling et al. 2016, 2017; Fischer 2017). This work revealed that older Barbary macaques are less likely to engage in novel object exploration than younger monkeys, but still retain great interest for social information, suggesting a shift to greater socio-emotional interest with age. Other studies have examined rhesus monkeys' interest in emotional stimuli very early in development, to examine how early life experiences shape socio-emotional processes (Simpson et al. 2015; Paukner et al. 2018). For example, the infant sons of high-ranking rhesus mothers look more at faces than did sons of low-ranking mothers, whereas daughters' interest was not affected by their mother's rank (Paukner et al. 2018). However, no work to date has experimentally measured attention to socio-emotional stimuli across the lifespan in order to examine how preference shifts from juvenility to old age. As this is some of the key evidence for an increasing positivity bias in humans, comparative developmental work can provide a new test of socio-emotional selectivity theory.

The current study

In the current study, we empirically examined lifespan changes in socio-emotional attention in rhesus monkeys. Our first goal was to test whether this non-human primate species exhibits an emotional bias like that of human: one that shifts from negativity to positivity across the lifespan. As discussed above, a prominent explanation for human shifts in socio-emotional biases attributes these changes to our understanding of our own mortality (Carstensen et al. 1999; Carstensen 2006). According to this *limited future hypothesis*, it is this sense of a clear "end date" that is the proximate mechanism driving this shift. Comparisons with other species can provide a strong test of this idea, as non-human primates do not appear to think about time and mortality in the way that humans do (Fung and Isaacowitz 2016)—and thus other primates should consequently not exhibit a developmental shift from a negative bias to a positive bias like humans. In this way, the socio-emotional selectivity theory makes a specific proximate, psychological explanation for why organisms might exhibit

increasing positivity bias with age: the possession of a sense of time and mortality.

Yet, it is important to note that in addition to proposing a proximate explanation for our emotional biases, socio-emotional selectivity theory also suggests a functional or adaptive explanation concerning how socio-emotional biases support differing patterns of social behavior (Fredrickson and Carstensen 1990; Carstensen et al. 2003; Carstensen and Mikels 2005). Specifically, this theory argues that while younger adults need to seek out and build new social relationships, older adults are more focused on preserving strong existing bonds. Under this *relationship-building hypothesis*, some human shifts in socio-emotional processing might in fact be shared with other species as well, if other species face the same challenges in building new relationships at younger ages like humans do. Indeed, many primates disperse at sexual maturity, and dispersing individuals must cut ties with their prior social partners to join a new group. In this view, a stronger negativity bias may facilitate the formation of new social relationships, including transitions to a new group, in younger monkeys. In contrast, older monkeys may rely more on established relationships. Thus, macaques may also exhibit increasing positivity bias with age but not necessarily use future-oriented cognitive mechanisms to do so as appears to be the case in humans.

An alternative functional perspective, rooted in the specifics of primate versus human social behavior, suggests that other primates may actually show the opposite pattern than that seen in humans: increasing negativity bias with age. First, primates differ from humans in several aspects of their social behavior across the lifespan. For example, agonistic interactions in primates increase between juvenility and adulthood in macaques (Bernstein and Ehardt 1985; Pereira and Fairbanks 2002), and the likelihood of receiving aggression in particular shows a sharp uptick with age (Kulik et al. 2015). Some evidence even suggests that older macaques may be especially targeted for aggression compared to younger mature adults (Almeling et al. 2017). Moreover, aggressive interactions are often preceded or accompanied by negative emotional signals, such as threat expressions. Thus, animals may be tuned into the socio-emotional signals that are most relevant to them given their particular stage of life, and negative socio-emotional expressions directed at an individual are an important signal that they are a potential target of aggression (Hoffman et al. 2007). In this *signal-relevance hypothesis*, consequently, older monkeys may in fact be more focused on socio-emotional signals indicating potential aggression than are younger monkeys, given the greater relevance of such negative signals for their social lives. Along the same lines, humans exhibit specialized life history features in old age, including female reproductive senescence and a longer lifespan, which allow our species to engage in types of grandparenting behavior that is not observed in other primates (Hawkes et al. 1998; Hawkes 2004).

Some have proposed that an increasing positivity bias may facilitate such grandparenting behavior (Carstensen and Loeckenhoff 2003). That is, an increasing positivity bias may be the cognitive mechanisms supporting social behaviors that are unique to humans.

To test these different hypotheses, we presented large samples of free-ranging macaques with images of conspecifics producing different emotional or neutral facial expressions and assessed their attention to and interest in these different kinds of stimuli. In doing so, we were able to devise a new task that mirrored one of the key pieces of evidence for increasing positivity bias with age in humans: differential attention to emotionally valenced faces. For example, prior work with humans has used attention tasks where participants observe photos of faces and must identify where on the screen a dot probe appeared. In fact, younger people are similarly fast to locate the dot when it appears in a location where a positive or negative face was previously presented, whereas older people are faster to notice it when it appears in the location of a positive face (Mather and Carstensen 2003, 2005; Carstensen and Mikels 2005). That is, older adults attend more to positive stimuli, facilitating their detection of new objects or events in the same location. There are similar results from eye-tracking studies measuring naturalistic patterns of gazing at emotional photographs indicating an increasing positivity bias in old age (Isaacowitz et al. 2006a, b).

Like humans, monkeys also have rich repertoires of emotional expressions, and there are deep homologs in emotional processing between humans and macaques (Ono and Nishijo 2000; Parr et al. 2005; Phelps and LeDoux 2005; Gothard et al. 2007; Hoffman et al. 2007). In our studies, we used two types of emotional expressions: threat faces, an aggressive display used in negative behavioral contexts, and lip-smacking, an affiliative display used in positive contexts (Maestripieri and Wallen 1997; Partan 2002; Parr et al. 2010; Bethell et al. 2012). Experimental work indicates that rhesus macaques recognize conspecific facial expressions varying in valence (Parr et al. 2005; Parr and Heintz 2009), and there is particularly strong evidence that threat expressions are salient for macaques (Gothard et al. 2007; Hoffman et al. 2007). For example, conspecific photos of directed threat expressions in macaques robustly engage the amygdala (Hoffman et al. 2007), similar to how expressions of anger with direct eye gaze in humans engage the amygdala and are interpreted as threats directed at the observer (Adams et al. 2003; Adams and Kleck 2005; N'Diaye et al. 2009). We therefore developed a new task that was analogous to prior work with humans involving emotional expressions such as anger (Mather and Carstensen 2003, 2005), in order to test a key prediction of socio-emotional selectivity theory in non-human primates.

In particular, we used a looking time methodology to assess monkeys' interest in looking at emotional stimuli, similar to

prior work measuring naturalistic viewing patterns in humans (Isaacowitz et al. 2006a, b). Looking time methods have been commonly used to examine psychological processes in non-verbal populations, such as infants or animals, by measuring how long an individual looks at different events or stimuli in order to assess their interest or preferences (Spelke 1985; Spelke et al. 1992). This method has further been well-validated as a way to examine cognition in the free-ranging rhesus monkey population examined here (Marticorena et al. 2011; Martin and Santos 2014; Drayton and Santos 2015). In study 1, we first examined how monkeys, ranging from juvenility to old age, responded to negative emotional images. Study 2 then examined monkeys' responses to positive emotional images. If monkeys show human-like shifts in socio-emotional processes, they should exhibit greater interest in and attention to negative images at younger ages, but an increasing bias towards positive images at older ages. These studies thus together allowed us to trace the development of selective socio-emotional biases across the macaque lifespan.

Study 1: negative socio-emotional stimuli

In study 1, we examined how monkeys respond to images of conspecifics producing either a neutral facial expression or a negative facial expression. Across trials, we showed monkeys matched photos of an unfamiliar individual producing either a negative (threat face) or neutral expression. We measured how long they spontaneously chose to view these images to index their interest. If monkeys exhibit human-like patterns of socio-emotional selectivity, then monkeys' interest in the negative threat stimuli should decline with increasing age.

Methods

Subjects

We tested 337 rhesus monkeys living at the Cayo Santiago Biological Field Station in Puerto Rico. The Cayo population consists of approximately 1500 semi-free-ranging monkeys who live on a 38-acre island off the coast of Puerto Rico. Monkeys in this population live in natural social groups, are provisioned daily (in addition to access to plants growing on site), and had ad libitum access to water from natural pools and water troughs. The Cayo Santiago monkeys are highly habituated to human observers and are individually identifiable based on unique combinations of tattoos and ear notches. We were able to determine exact birth dates for all monkeys through the site's long-term census data. Our final sample comprised 161 females and 176 males, ranging in age from 1.4 to 28.5 years. All monkeys were naïve to the particular photos used in this study. Some monkeys in this population may have previously observed photographs of conspecifics in

the context of other research (Higham et al. 2011; Dubuc et al. 2016), although to our knowledge, no prior work involved emotionally valanced photos, the key feature of the current study.

Monkeys had to successfully complete at least two trials (the first pair of photos) to be included in the study but sometimes left the testing area before fully completing the second set of photos. Thus, all 337 subjects completed the first pair of photos (female stimuli) and a subset of 182 monkeys also observed the second two photos (male stimuli). An additional 70 monkeys were approached for testing but did not successfully complete the study because they were interrupted by other monkeys or moved away of their own volition before completing at leat two trials (as monkeys were free-ranging during the tests). One subject was further excluded during coding because they were not attending when the trial started. In the event that the same individual was tested more than once (e.g., because they were not identified until after testing), we analyzed only the responses of their first successful session. Of the 337 monkeys in our final sample, 40 of them did not complete an initial testing attempt but were successfully tested in a later session.

Setup and procedure

Monkeys completed up to four trials in a looking time task in which they could attend to sequence of photos of unfamiliar conspecifics. The first two photos were of a female producing a neutral expression followed by the same female producing a threat expression (see Fig. 1b for an example). The second two trials showed a male producing a neutral expression followed by a threat expression. As prior work indicates that rhesus monkeys detect and show robust responses to conspecific threat expressions (Gothard et al. 2007; Hoffman et al. 2007; Mosher et al. 2011), all monkeys observed the stimuli in a fixed order across trials to facilitate comparisons of age-related variation in responses, the main focus of this study.

Two experimenters ran each session. At the start of testing, the experimenters would first locate a calmly sitting monkey. Experimenter 1 (E1) presented the photo stimuli to the monkey, while experimenter 2 (E2) filmed the monkey's response from behind the presenter. Photos were presented in a white box made of poster board (34 cm high, 16 cm deep, 54 cm wide) with a front-facing "window" (23 cm wide, 30 cm tall). At the beginning of each trial, this window was covered by a purple flap attached with Velcro. Thus, E1 could rapidly remove the cover to initiate a trial, where the monkey could observe a photo through the window (see Fig. 1a and Video S1 for a demonstration). Between trials, the experimenter could replace the flap and therefore exchange the photos out of the monkey's view.

On each trial, E1 sat in front of the monkey, at a distance of 1–2 m away, with the apparatus in front of her, and E2 stood or crouched behind E1 in order to get a direct shot of the
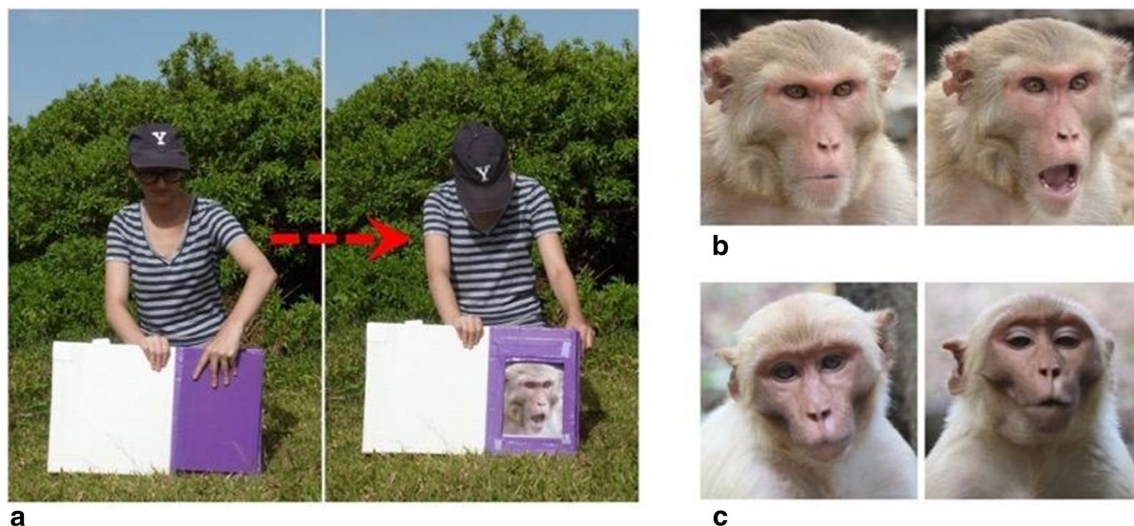
Fig. 1 Setup and stimuli for Studies 1 and 2. **a** We showed monkeys a photo of a conspecific by opening the window on a box apparatus to reveal a photo. **b** In study 1 (negative socio-emotional stimuli) monkeys observed matched photos of conspecifics producing first a neutral monkey's face. E1 first attracted the monkey's attention to the apparatus by tapping it and calling the monkey. Once the monkey oriented towards the window, she removed the cover flap to reveal the photo underneath, while simultaneously saying "now" to mark the start of the trial on the video. During each 10-s trial, E1 held still after initiating the trial, and gazed downwards so her eyes were occluded by a hat (see Fig. 1a). During this time, E2 recorded the monkey's face while timing each 10-s trial on the camera (see Video S1 for an example looking response). After 10 s was up, E2 called "stop" to mark the end of the trial on the video. If the monkey left the testing area or was interfered with (as described above), E1 decided whether to halt the session before all four trials were complete, as she was blind to the monkey's responses because she was looking downwards during the timed 10-s trial.

Photo stimuli

We presented each subject with a series of photos of conspecifics from the Cayo Santiago population. In particular, subjects first saw a female producing neutral and then threat expression across two paired photos, and then a male producing a neutral and threat expression across two more. Photos showed a monkey's face and upper shoulders; they were printed on photo paper mounted on poster board backings so they remained stationary during trials in the viewing window. There were two possible photo sets, each including an adult female and an adult male (the age of the male and female individuals approximately matched across the two sets). As our aim was to present an image of an unfamiliar conspecific to the subject, we matched subjects with a photo set including individuals who did not share either their current or birth

expression (left photo) and then the same individual producing a threat expression. **c** In study 2 (positive socio-emotional stimuli) monkeys observed a conspecific producing a neutral expression and a lip-smacking expression (in counter-balanced order)

group membership with the subject. One photo set included a female born and living in group KK and a male born in R and currently living in group KK at the time of testing; this photo set was therefore not used with individuals born or currently living in R or KK. The second photo set included a female born and living in group V and a male born in S living in V; this photo set was not used with individuals born or currently living in S or V. Together, these two photo sets allowed us to present unfamiliar conspecific to the majority of subjects. In a few cases ($n = 21$ subjects; 6% of the total), it was not possible to match a subject with a photo set that did not share either a birth or current group. In these cases, we typically presented photos who were not current group members. In analyses, we therefore accounted for whether the photo set consisted of outgroup conspecifics; additional analyses indicated that this did not appear to affect results.

Data coding

Two independent coders scored subjects' responses on all trials. We first clipped out individual trials from longer-session videos, and then randomized the order of trials (assigning a new, random trial ID) to blind coders to condition while they were coding. Each coder independently identified the start of the trial (e.g., when E1 said "now"), and then examined the subsequent 10-s period frame-by-frame in the program MPEG Streamclip to assess if the monkey was looking at the photo (e.g., oriented in the direction of the box that they were positioned in when E1 said "now"). The reliability coder had high reliability with the primary coder for duration of looking across trials ($r_\text{p} = 0.96$). As our questions and analyses focused on relative looking to the two expressions (neutral versus

threat) within a pair of photos, we only coded monkeys' responses to either the first two trials or to all four trials (e.g., if an individual completed three trials and walked away, we only coded and analyzed their first two trials).

Statistical analyses

Our analyses focused on (1) total duration of looking across trials and (2) a difference score accounting for a subject's negativity bias. The difference score indexed how monkeys allocated their looking at the threat versus neutral expression of a given conspecific (threat looking time–neutral looking time). This sort of simple difference score is commonly used in looking time research with infants (Spelke et al. 1992); the logic of this score is that it indexes the duration of time that spent looking at the emotional photo while accounting for overall differences in duration of looking at the neutral photo across individuals. We also examined a "weighted" difference score, calculating a proportional change in attention (threat looking time–neutral looking time/neutral looking time), which is more focused on relative changes in attention (Bornstein and Sigman 1986).

Across analyses, we first implemented a basic model where we accounted for control variables; in this study, we accounted for *photo set* (which of the two sets of stimuli presented), *outgroup photos* (whether monkeys saw unfamiliar conspecifics in the stimuli), and subject's *sex* across all models. We accounted for subject's sex because prior work indicates that male and female rhesus monkeys may differ in their interest in emotional facial expressions (Simpson et al. 2016a; Paukner et al. 2018), differ in their sensitivity to social cues such as gaze direction (Rosati et al. 2016), and finally exhibit differences in rates of received aggression (Kulik et al. 2015). We then compared the base model to a "full" model also accounting for the predictors we are focused on in this work. In particular, for analyses of duration of looking, we examined the importance of emotional *expression* (neutral or threat), the subject's *age*, and an *interaction between expression and age*—the main test of whether socio-emotional biases change across the lifespan. In particular, this allowed us to assess if interest in negative emotional stimuli deceased with age as in humans, while accounting for any shifts in viewing (neutral) faces more generally. In our analyses of difference scores (which index relative bias to the emotional photo), we primarily examined whether this socio-emotional bias changes with *age*, but also compared whether monkeys exhibited similar age-related changes for male versus female stimuli. To assess developmental changes in socio-emotional biases, we analyzed these data with age in years as a continuous predictor, but in some figures, we split individuals into age cohorts based on life history transitions in this species: juveniles up to 5 years (sexual maturity), adults up to 15 years, and older monkeys over 15 years, as monkeys

in this population have a median lifespan of 15 years and rarely exceed 25 years (see Hoffman et al. 2010; Rosati et al. 2016).

We implemented statistical models in R version 3.5.0 (R Development Core Team 2018). For analyses of duration of looking across trials, we used linear mixed models implemented with the lmer function from the lme4 software package (Bates 2010), using restricted maximum likelihood for parameter estimation. In analyses, we included random subject intercepts to account for repeated trials within subjects. Note that mixed models can account for unequal repeats across subjects (Baayen 2008), which is important since subjects did not always complete all four trials as they were free-ranging during tests. We compared the fit of different models using likelihood ratio tests (LRT: Bolker et al. 2008); models were refit using maximum likelihood for model comparisons (Zuur et al. 2009), and parameter significance was calculated using the lmerTest package (Kuznetsova et al. 2015). Graphs showing predicted effects and confidence intervals (CIs) from these models were calculated using the effects package in R (Fox et al. 2016). Finally, for an analysis comparing difference scores in response to female stimuli alone, we used linear regressions, as each subject only had one such difference score.

Data availability Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.9s5p4k1.

Results

Our first set of analyses examined total duration of looking to the female photo stimuli (the first two trials, which all subjects completed). Overall, monkeys looked an average of M = $4.29 \pm SE = 0.16$ s at the neutral expression, and 3.59 ± 0.15 s at the threat expression, but there were also clear differences in patterns of looking across age cohorts (see Fig. 2a). Juveniles ($n = 136$) looked 6.58 ± 0.20 s at the neutral expression and 5.24 ± 0.21 s at the threat expression, adults ($n = 168$) looked 2.94 ± 0.17 s at the neutral expression and 2.68 ± 0.18 s at the threat expression, and older adults ($n = 33$) looked 1.75 ± 0.26 s at the neutral expression and 1.43 ± 0.21 s at the threat expression.

To analyze duration of looking to the female stimuli, we first created a basic linear mixed model with our control variables, accounting for *photo set* (which of the two sets of stimuli presented), *outgroup photos* (yes or no), subject's *sex*, and *subject* (as a random factor accounting for repeated measures). Our full model additionally accounted for *photo expression* (neutral versus threat), subject's *age* (in years), and an interaction between *age X photo expression*; the full model provided better fit than the base model [LRT: $\chi^2 = 188.23$, df = 3, $p < 0.0001$]. We then added our predictors of interest sequentially to the base model to test their importance. Model

Fig. 2 Duration of looking times to negative versus neutral stimuli across age cohorts. Monkeys ranging from juveniles to older adults could view paired photographic stimuli of a conspecific producing a neutral or threat face. Graph shows mean duration of looking time towards **a** the female stimuli presented in the first two trials and **b** male stimuli presented on the last two trials, each broken down by subject's age cohort and sex. Error bars indicate standard error
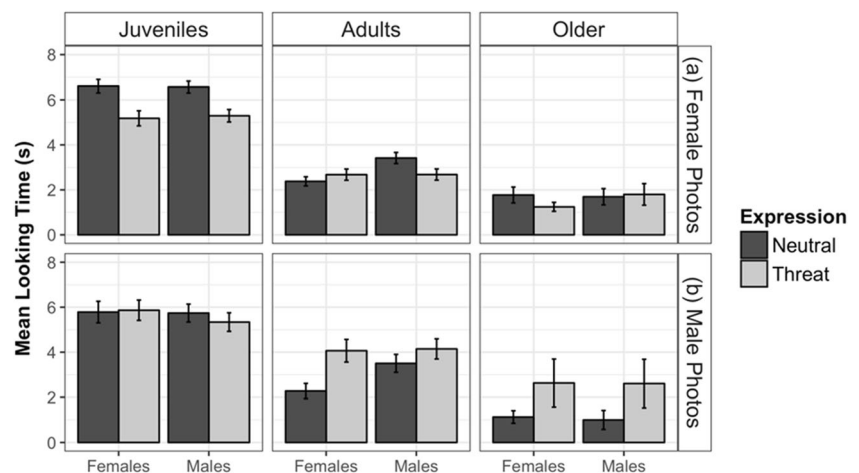
fit was improved by including *photo expression* (neutral versus threat) to the predictors in the base model [$\chi^2 = 24.79$, df = 1, $p < 0.0001$]: overall, monkeys viewed the female neutral photo for longer than the female threat photo. Fit was further improved by including *age* [$\chi^2 = 154.49$, df = 1, $p < 0.0001$]: younger monkeys looked longer overall at the photos than did older monkeys. The key question for socio-emotional selectivity concerns how looking patterns varied with age for the threat photo versus neutral photos. In fact, fit was further improved in the full model incorporating the interaction between *age X expression* [$\chi^2 = 8.95$, df = 1, $p < 0.005$]: the age-related decline in looking times was attenuated for the threat photo compared to the neutral photo. That is, older monkeys showed less of a decline in looking at threat than they did for the neutral photo. In the full model, subject's sex, the photo set, and whether the presented stimuli were outgroup conspecifics were not significant predictors of looking time responses (see Table 1 for parameters).

We next examined duration of looking at the male photos, using the same basic procedure. Overall, the 182 monkeys who completed these trials looked an average of 4.15 ± 0.23 s at the neutral expression and 4.69 ± 0.23 s at the threat expression. As with the female stimuli, there were differences in patterns of

looking across age cohorts (see Fig. 2b): juveniles ($n = 84$) looked 5.76 ± 0.31 s at the neutral expression and 5.58 ± 0.30s at the threat expression, adults ($n = 86$) looked 3.00 ± 0.28 s at the neutral expression and 4.11 ± 0.33 s at the threat expression, and older adults ($n = 12$) looked 1.08 ± 0.23 s at the neutral expression and 2.62 ± 0.73 s at the threat expression. As with the female photo analysis, we first created a basic linear mixed model accounting for *photo set*, *outgroup photo*, subject's *sex*, and *subject* (as a random factor); a comparison to the full model also including *photo expression*, *age*, and an *age × photo expression* interaction revealed that the full model provided better fit [$\chi^2 = 65.53$, df = 3, $p < 0.0001$]. As with the analyses of female photos, we then added these predictors sequentially. The model also including *photo expression* improved model fit [$\chi^2 = 6.42$, df = 1, $p < 0.05$]: for the male stimuli, monkeys overall viewed the threat photo for longer durations than the neutral photo. Fit was further improved by adding *age* [$\chi^2 = 52.42$, df = 1, $p < 0.0001$]: younger monkeys looked longer overall at the photos than did older monkeys. The key question for socio-emotional selectivity was again how monkeys' looking patterns varied with age for the threat photo versus neutral photo. In fact, fit was further improved in the full model also incorporating the

Table 1 Factors influencing looking times to female threat stimuli (study 1). Predictors from the full linear mixed model examining look times (in seconds) to photos of an unfamiliar female producing neutral versus threat expressions. *Age*, expression (neutral or threat), and the *age* × *expression* interaction were added to successive models to test their importance. Baseline reference for predictors indicated in the table; significant predictors are italicized

Factor	Estimate	SE	t	p
Photo set (reference = set 1)	−0.213	0.218	−0.974	>0.33
Outgroup (reference = not outgroup)	0.126	0.456	0.277	>0.78
Sex (reference = female)	0.228	0.218	1.044	>0.29
Age (linear in years)	−0.337	0.025	−13.345	*< 0.0001*
Expression (reference = neutral)	−1.311	0.245	−5.356	*< 0.0001*
Age × expression	0.081	0.027	3.003	*< 0.005*

interaction between *age × photo expression* [$\chi^2 = 6.70$, df = 1, $p < 0.01$]: the age-related decline in looking was attenuated for the threat photo compared to the neutral photo, as with the female photo stimuli. Here, in fact, the older monkeys even showed a relative preference to look at the threat compared to the neutral photo (see Table 2 for parameters from this model).

We then examined each subject's individual negativity bias. To do so, we used the difference score that indexed preference for looking at the threat versus neutral face (negativity bias: threat looking time–neutral looking time); thus, more positive difference scores indicate that individual looked longer at the negative emotional stimuli. In fact, this difference score varied with age for both the female stimuli (juveniles: − 1.34 ± 0.23; adults: − 0.26 ± 0.19; older adults: − 0.32 ± 0.27) and the male stimuli (juveniles: − 0.18 ± 0.33; adults: 1.11 ± 0.29; older adults: 1.55 ± 0.64). To analyze negativity bias difference scores, we first created a basic linear mixed model accounting for *photo set*, *outgroup photos*, subject's *sex*, and *subject* (as a random factor). In a full model, we also added *photo type* (male versus female stimuli), *age*, and an interaction between *age × photo type*; the full model had better fit than the base model type [$\chi^2 = 41.67$, df = 3, $p < 0.0001$]. We then added each predictor to examine how they impacted fit. Including *photo type* to contrast negativity biases for the male versus female stimuli improved fit compared to the base model [$\chi^2 = 26.22$, df = 1, $p < 0.0001$]: monkeys exhibited greater relative attention to the male threat stimuli than the female threat stimuli. The key question for socio-emotional selectivity was whether these difference scores reliably changed with age, indicating shifts in interest and attention to negative stimuli. In fact, fit was further improved in a model also including *age* [$\chi^2 = 14.71$, df = 1, $p < 0.001$]: older monkeys showed more positive difference scores than did younger monkeys, indicating greater interest in the negative emotional images. Finally, we then included the interaction between *age × photo type* to test whether this increasing interest in negative images was more pronounced for male versus female photos. This did not improve model fit [$\chi^2 = 0.74$, df = 1, $p > 0.39$], indicating a similar slope for responses to both types of

images (see Fig. 3, and Electronic Supplementary Materials Table S1 for parameters from the full model). That is, while monkeys showed greater interest in the male photos overall, the patterns of age-related change were similar for both male and female photos. We also performed the same set of analyses using the weighted difference score; this measure that was highly correlated with simple difference score both for female stimuli [$r_p = 0.70$, $p < 0.0001$] and for the smaller subset of subjects who also experienced the male stimuli [$r_p = 0.57$, $p < 0.0001$]. The results from this weighted score similarly indicated that negativity biases increased with age—the key question for socio-emotional selectivity. Here, however, there was also a significant *age × photo type* interaction indicating that the increasing negativity bias was exacerbated for male photos (see Table S2 for details).

As a final check, we also examined whether monkeys who completed only two trials differed in their responses from those who completed all four (see Fig. 4). In particular, we examined the negativity bias difference scores for the female photo stimuli to assess if these subsets of monkeys differed in their responses. We first created a basic linear regression model accounting for *photo set* (which of the two sets of stimuli were presented), *outgroup photos* (yes or no), subject's *sex*, and subject's *age* (in years). In the full model, we also included *completion rate* (only two trials versus all four trials) and an *age × completion* interaction. The full model did not improve fit [$\chi^2 = 0.29$, df = 2, $p > 0.86$; see Table S3 for parameters]. Neither *completion rate* [$\chi^2 = 0.08$, df = 1, $p > 0.77$] or the *age × completion* interaction term [$\chi^2 = 0.21$, df = 1, $p > 0.64$] improved fit individually (see Table S3). Overall, this indicates that there were not major differences in negativity bias towards female stimuli across subjects that completed only the first two female stimuli trials versus all four female and male stimuli trials, suggesting that the data on negativity bias towards the male stimuli from those monkeys who did complete all four trials was likely representative of the larger population. This is in line with the fact that many incomplete sessions were due to exogenous factors, such as other monkeys interfering with or displacing the test subject.

Table 2 Factors influencing looking times to male threat stimuli (study 1). Predictors from the full linear mixed model examining look times (in seconds) to photos of an unfamiliar male producing neutral versus threat expressions. *Age*, *expression* (neutral or threat), and the *age × expression* interaction were added to successive models to test their importance. Baseline reference for predictors indicated in the table; significant predictors are italicized

Factor	Estimate	SE	t	p
Photo set (reference = set 1)	1.697	0.339	5.004	*< 0.0001*
Outgroup (reference = not outgroup)	− 0.162	0.690	− 0.234	> 0.81
Sex (reference = female)	0.145	0.340	0.425	> 0.67
Age (linear in years)	− 0.346	0.044	− 7.896	*< 0.0001*
Expression (reference = neutral)	− 0.277	0.380	− 0.730	> 0.46
Age × expression	0.121	0.046	2.597	*< 0.05*
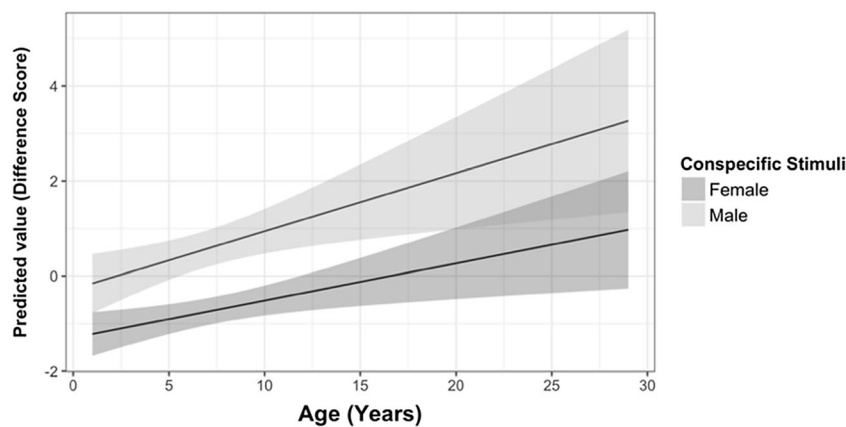
Fig. 3 Changes in negativity bias with age. Each subject was assigned a difference score indexing their negativity bias or relative attention to the threat face compared to the neutral face (threat looking time–neutral looking time); more positive values indicate greater attention to the emotional stimuli. Estimated values are responses to the different photo types (female or male photo stimuli) by subjects' age in years. Estimates are derived from linear mixed models also controlling for subjects' sex, the photo set, whether the photos were outgroup members, and subject identity. Ribbons indicate 95% confidence intervals

Discussion

Our results reveal an age-related shift in how monkeys process negative socio-emotional stimuli across the lifespan. Our analyses of total looking duration revealed two main findings. First, we observed large changes in overall duration of looking with age, as older monkeys generally spent less time looking at the photos overall than younger monkeys did. Second, older monkeys looked relatively longer at the threat expressions (compared to their viewing of the neutral expressions) than did the younger monkeys. When viewing the female stimuli, younger monkeys showed a steep decline in their looking towards the threat photos compared to the matched neutral photo of the same conspecific, whereas this decline was attenuated in older monkeys. When viewing the male stimuli, older monkeys even exhibited increased looking at the threat photo, suggesting an active preference to view these stimuli. As

participants viewed the photos in a fixed order and generally tend to show declines in looking across successive trials in similar looking time tasks, this absolute increase in the duration adult monkeys looked at the male threat photos is especially notable.

Our analyses of the negativity bias difference score provide converging evidence for the conclusion that older monkeys were more interested in the threat images. We found that monkeys showed increased attention to the male stimuli overall, but that this negativity bias increased with age for both male and female stimuli. Finally, additional checks confirmed that monkeys who only saw the first two images showed similar responses to those who completed the whole study. Overall, these findings indicate that older monkeys exhibit an exaggerated negativity bias compared to younger monkeys. Importantly for testing socio-emotional selectivity theory in a comparative context, the pattern we observe in macaques is the opposite of that seen in humans. However, as this study only used negative and neutral social images, it is unclear from these study 1's results if macaques also exhibited a shift in their interest positive socio-emotional stimuli. Thus, in study 2, we examined monkeys' response to positive versus neutral facial expressions.
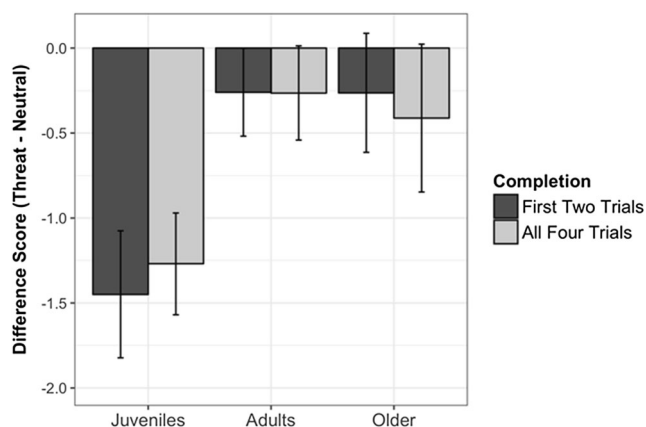
Fig. 4 Negativity bias for female stimuli by study completion. The difference score indexing an individuals' negativity bias for the female photos was compared for individuals who only completed the first two trials versus those that completed the entire study. Error bars indicate standard error

Study 2: positive socio-emotional stimuli

In study 2, we examined how monkeys respond to images of conspecifics producing either a neutral facial expression or a positive facial expression. To do so, we presented monkeys with images of a monkey making either a neutral or lip-smacking expression. Note that overall positive facial expressions are harder to capture in macaques, but lip-smacking is a clear affiliative signal in this species (Maestripieri and Wallen 1997). Due to the practical difficulty of acquiring photos of

monkeys producing this expression, we used only a single paired photo set of a juvenile monkey producing a lip-smacking or neutral expression across successive photos. Consequently, we did not test any individuals from that monkeys' social group to ensure the stimuli were unfamiliar to the subjects. This reduction in available test subjects resulted in a smaller sample size than we used in study 1. In addition, since there is less evidence that rhesus monkeys attend to lip-smacking expressions overall, we counter-balanced the order of the two photos to further assess if monkeys exhibited any overall preference for looking at positive expressions versus neutral ones. Otherwise, we used the same basic methodology as in study 1 to index monkeys' responses to the socio-emotional stimuli.

Methods

Subjects

We tested individuals from the same population as in study 1. Our final sample comprised 132 rhesus monkeys (72 females and 60 males), ranging in age from 0.5 to 27.3 years. Study 2 was initiated more than 1 year after the conclusion of study 1. Thirty-six individuals had previously participated in study 1, between 1 and 3 years previously. Monkeys had to successfully complete both trials (one neutral and one positive) to be included in the study.

Exclusions and repeats

Because we only had one photo set, all monkeys that shared a current or birth social group with the monkey in the stimuli were ineligible for the study. Although we attempted to avoid Group F during data collection, we did collect partial or otherwise successful sessions on 39 additional individuals that were identified as current or previous Group F members either during ($n = 4$) or after ($n = 35$) data collection. These subjects were excluded prior to coding. Another 51 monkeys were approached for data collection but were excluded because subjects walked away ($n = 28$), stopped attending ($n = 14$), were displaced ($n = 6$), or due to experimental error ($n = 3$). Finally, 22 subjects completed more than one successful session. However, we only coded and analyzed the data from their first session.

Procedure and stimuli

We used the same basic procedure as in study 1 with a few critical changes. First, all subjects only completed two trials (instead of up to a total of four) due to the number of lip-smacking stimuli we were able to obtain. Accordingly, we only presented matched photos the same juvenile female individual making either a neutral or an affiliative facial expression (see Fig. 2); we used a juvenile individual in this study because it was difficult to elicit a lip-smacking photo from adults in this population. Finally, the order of the stimuli valence (neutral or positive) was counter-balanced such that half of the subjects saw the neutral face followed by the positive face and other half saw the opposite order. The apparatus was otherwise identical to that in study 1 except that the window covering was blue.

Data coding and statistical analyses

Procedures for data coding were the same as for study 1. Two independent coders scored subjects' responses on all clips, and the reliability coder had high reliability with the primary code for the duration of looking across trials ($r_p = 0.91$). As in study 1, our analyses focused on (1) total duration of looking across trials and (2) a difference score, here accounting for a subject's positivity bias (affiliative looking time–neutral looking time). The difference score indexed their interest in looking at the affiliative versus neutral expression. As in study 1, we also examined a weighted difference score (affiliative looking time–neutral looking time/neutral looking time). We also used the same general approach as in study 1 for statistical analyses. To analyze looking times, we again implemented linear mixed models with random subject intercepts to account for repeated trials within subjects. We used linear regressions to analyze the different scores (as each subject only had one difference score in this study).

Results

Our first set of analyses examined total duration of looking to the photos. Overall, monkeys looked an average of $M = 4.04 \pm SE = 0.23$ s at the neutral expression and 3.89 ± 0.22 s at the affiliative expression. As in study 1, there were differences in overall rates of looking across age cohorts (73 juveniles; 38 adults, and 21 older adults; see Fig. 5). To analyze duration of looking, we first created a basic linear mixed model accounting for subject's *sex*, *trial number* (1 or 2), and *subject* (as a random factor accounting for repeated measures). We then added *photo expression* (neutral versus affiliative), *age*, and an interaction between *age × photo expression* in the full model, which improved model fit [$\chi^2 = 60.01$, df = 3, $p < 0.0001$]. Examining these predictors individually revealed that model fit was not improved by including *photo expression* compared to the base model [$\chi^2 = 0.85$, df = 1, $p > 0.35$]: that is, overall monkeys viewed the emotional and neutral photos for similar durations. However, fit was improved by adding *age* [$\chi^2 = 58.51$, df = 1, $p < 0.0001$]: younger monkeys looked longer overall at the photos than did older monkeys, similar to
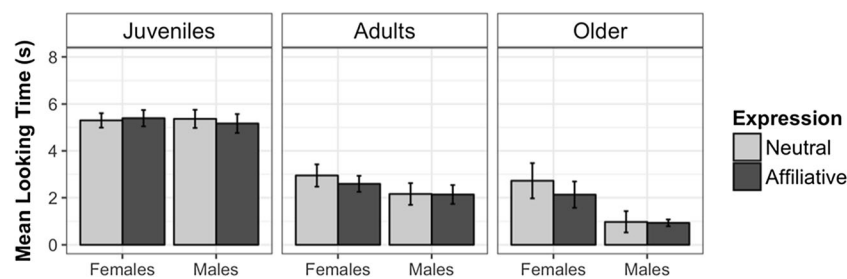
Fig. 5 Duration of looking times to positive versus neutral stimuli across age cohorts. Monkeys ranging from juveniles to older adults could view paired photographic stimuli of a conspecific producing a neutral or affiliative face. Graph shows mean duration of looking time towards the different stimuli, each broken down by subject's age cohort and sex. Error bars indicate standard error

our results in study 1. The key question for socio-emotional selectivity concerns how monkeys' looking patterns varied for the affiliative photo versus neutral photo with age. In fact, unlike in study 2, fit was not further improved in the full model incorporating the interaction between *age × photo expression* [$\chi^2 = 0.65$ df $= 1$, $p > 0.41$], indicating that there were no major age-related differences in interest in the affiliative photo versus the neutral photo (see Table 3 for parameters from the full model). That is, while there were overall age-related changes in looking to the stimuli in general, there were no age-related changes in preferences to look at the affiliative versus neutral images.

We then examined each subject's individual positivity bias using a difference score that indexed relative preference for looking at the affiliative versus neutral face (affiliative Looking time–neutral looking time), such that more positive scores again indicated greater attention to the emotional stimuli. Collapsing across all subjects, juveniles exhibited a difference score of -0.05 ± 0.28; adults of -0.19 ± 0.24, and older adults of -0.43 ± 0.44. To analyze positivity bias difference scores, we first created a basic linear model accounting for *trial order* (affiliative versus neutral photo first) and subject's *sex*. This revealed a strong effect of order [estimate $= -1.92$, SE $= 0.32$, $t = -5.854$, $p < 0.0001$]: monkeys showed a greater positivity bias if they saw the affiliative photo first compared
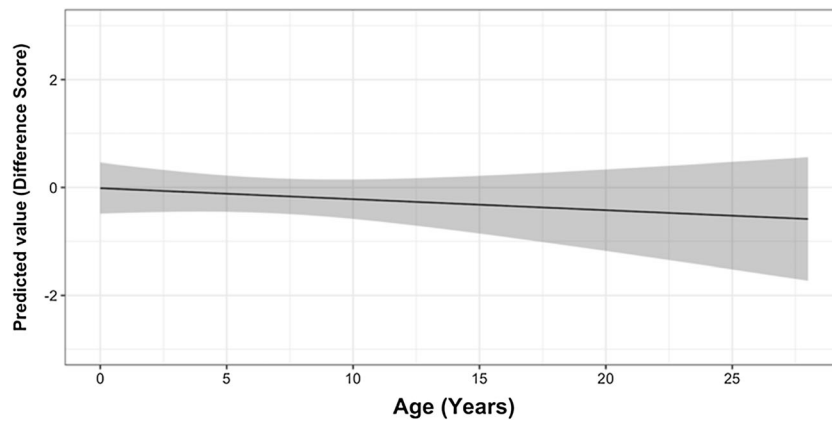
to the neutral photo first. However, model fit was not improved in a full model also incorporating *age* and an *age × order* interaction [$\chi^2 = 3.37$, df $= 2$, $p = 0.19$]. Examining these predictors individually, model fit was not improved by adding *age* to the base model [$\chi^2 = 0.64$, df $= 1$, $p > 0.42$]: monkeys exhibited similar positivity biases across ages, the main test for changes in socio-emotional biases with age (see Fig. 6). Finally, including an *age × order interaction* revealed a trend for improved model fit [$\chi^2 = 2.73$, df $= 1$, $p = 0.098$]; this trend suggests that younger monkeys tended to have a greater positivity bias than older monkeys in the condition where they viewed the emotional photo first, compared to when subjects saw the neutral photo first (see ESM Table S4 for parameters from the full model). However, it is important to note the overall fit of this model was not greater than the base model without these predictors. We also performed the same analysis using the weighted difference score and found largely similar results. As in study 1, this measure was highly correlated with the simple difference score [$r_p = 0.56$, $p < 0.0001$]. Here, the inclusion of age again did not provide an overall improvement in model fit [$\chi^2 = 2.47$, df $= 1$, $p = 0.12$], indicating no overall changes in positivity bias with age. The full model including an *age × order* interaction trended towards better fit compared to the base model but did not reach significance (see Table S5 for details).

Discussion

The results from study 2 align with those from study 1, demonstrating that monkeys do not show human-like shifts from a negativity bias to a positivity bias. In particular, we did not find clear evidence that older monkeys exhibited increased attention to the positive socio-emotional images. As with study 1, younger monkeys overall looked longer photos in general compared to older monkeys. However, monkeys did not exhibit consistently greater interest in looking at positive images at any age. Overall, this pattern of performance suggests that neither older nor younger monkeys exhibited a strong selective preference for viewing positive social stimuli.

Table 3 Factors influencing looking times to affiliative stimuli (study 2). Predictors from the full linear mixed model examining look times (in seconds) to photos of an unfamiliar female producing neutral versus lip-smacking expressions. Age, expression (neutral or threat), and the *age × expression* interaction were added to successive models to test their importance. Baseline reference for predictors indicated in the table; significant predictors are italicized

Factor	Estimate	SE	t	p
Trial (reference = trial 1)	-0.972	0.164	-5.919	*< 0.0001*
Sex (reference = female)	-0.587	0.335	-1.751	$= 0.082$
Age (linear in years)	-0.211	0.029	-7.257	*< 0.0001*
Expression (reference = neutral)	-0.012	0.237	-0.050	$= 0.96$
Age × expression	-0.021	0.026	-0.800	> 0.42

Fig. 6 Changes in positivity bias with age. Each subject was assigned a difference score indexing their positive bias or relative attention to the affiliative face compared to the neutral face (affiliative looking time–neutral looking time); more positive values indicate greater attention to the emotional stimuli. Estimated values for responses by subjects' age in years. Estimates are derived from linear models also controlling for subjects' sex. Ribbons indicate 95% confidence intervals

General discussion

We measured rhesus monkeys' looking time to emotionally valenced versus matched neutral images and found that monkeys exhibit some robust shifts in socio-emotional biases across the lifespan. First, study 1 showed that macaques exhibit increased attention to negative threat expressions compared to neutral expressions as they age. This effect was found both in our analyses of duration of looking times and when analyzing difference scores indexing individual monkeys' negativity biases. Moreover, we observed that this negativity bias increased with age in response to both female and male conspecific photos, although there were some important differences in reactions to the two types of stimuli. In particular, younger monkeys actively avoided looking at female threat photos (relative to neutral photos) whereas older monkeys showed less of a decline. In contrast, older monkeys actually increased their looks to male threat photos compared to male neutral photos—suggesting an active preference for viewing these negative images. The results from study 2, in contrast, revealed no consistent age-related changes in monkeys' interest in positive lip-smacking expressions compared to neutral expression: monkeys exhibited similar durations of looking at both images across ages, and there were also no robust age-related changes when analyzing difference scores indexing an individual's positivity bias.

Overall, these results indicate that rhesus monkeys exhibit developmental changes in socio-emotional attention that differ from the patterns in humans in several respects. Older adult humans show a bias to preferentially attend to neutral over negative faces (including angry faces—the most direct analog of the rhesus threat face used here), as well as a bias to attend to positive (happy) faces over neutral faces; younger adults do not show these signatures of a positivity bias (Charles et al. 2003; Mather and Carstensen 2003, 2005; Isaacowitz et al. 2006a, b). In contrast, we found that older monkeys

preferentially attend to threat faces versus neutral ones and detected no major age-related changes in responses to the affiliative stimuli. The fact that monkeys do not develop an increasing positivity bias with age aligns with the predictions of the *limited future hypothesis*, which proposes that sophisticated notion of time horizons and mortality may underpin these socio-emotional shifts in humans (Carstensen et al. 1999; Carstensen 2006). Specifically, our work lends some credence to proposals from socio-emotional selectivity theory arguing that shifts in human emotional processing over development stem (mechanistically) from our rich understanding of time and our own mortality: since monkeys lack this ability to think about a shorter "time horizon," they should then fail to show a pattern of increased attention to positivity over time. However, it is important to note that this view suggests that non-human animals in general should not exhibit increasing positivity bias with age, so examining a more diverse set of species is crucial to test this idea more broadly.

While socio-emotional selectivity theory predicts that non-humans will *not* show human-like patterns of increasing bias towards positive emotions, it does not otherwise provide a specific prediction for what patterns animals would in fact show. Our two functional hypotheses, in contrast, derive specific predictions based on potential patterns of adaptive social behavior. The *relationship-building hypothesis* suggests that younger monkeys may also need to invest in new social relationships more so than older monkeys, similar to humans. In this view, younger moneys would show greater negativity biases to drive motivation for forming new social bonds. In contrast, the *signal-relevance hypothesis* suggests that different age classes of monkeys will preferentially attend to emotional signals that are most likely to be directed at them and therefore have the greatest personal relevance. As aggressive interactions increase with age in rhesus monkeys, older monkeys may therefore be especially tuned into threats of aggression, unlike in humans. In general, our results support this

second hypothesis concerning signal relevance: older monkeys exhibited greater interest in the negative threat expression than did younger monkeys, with no major age-related changes in interest in the positive expression. That is, monkeys' patterns of attention to these photos appear to map onto changing patterns of aggression across the lifespan.

In general, our results indicate that rhesus monkeys are more responsive to negative (threat) facial expressions than positive (affiliative) facial expression when compared to matched neutral photos —monkeys actively modulated their looking at the threat photo relative to a neutral photo by avoiding looking at it or increasing looks to it, depending on the individual's age. In contrast, monkeys exhibited similar viewing patterns for the positive lip-smacking expression compared to a neutral conspecific photo. This difference in response to the two kinds of stimuli does not appear to be due to differences in overall interest in the photos. While these two studies did involve stimuli from different conspecifics (e.g., unfamiliar adults were presented in study 1, whereas an unfamiliar juvenile was presented in study 2), overall durations of looking at these different photo sets were similar across the two studies. As such, it seems like the main difference in monkeys' responses was the pattern of allocating attention across the matched emotional and neutral photos, not overall interest in viewing the different social models. Some evidence indicates that whereas humans exhibit decreasing responses to negative emotional stimuli with age, responses to positive stimuli remain relatively constant (Change et al. 2007). Thus, monkeys may also show relatively constant responses to positive stimuli, like humans, but rather show increasing interest in negative stimuli unlike humans.

One consideration for interpreting the results from the two studies is that the threat expression and the lip-smacking expression have some crucial differences. In particular, lip-smacking is a more fluid and dynamic expression—even sharing some similarities with human speech (Morril et al. 2012). As such, capturing the lip-smacking expression may have been more difficult in a static photo than for the threat expression. Thus, while it is clear from previous work that rhesus monkeys can make and discriminate affiliative facial expressions, they may not have discriminated the static lip-smacking photo from the neutral photo. Future work may thus profit from using dynamic videos of facial expressions or social interactions, rather than static facial expressions like we used in this study. This would also potentially allow for facial expressions to be displayed with their accompanying vocalizations (Partan 2002), which can be especially salient for threat displays. A final possibility is that even if monkeys did perceive the lip-smacking photo as such, the positive and negative photos may not have been equivalent in terms of intensity of the emotion. In fact, this is an important issue in human studies as well, as negative emotional images generally tend to be rated as more intense than positive ones (Ito et al. 1998).

Across both studies, we also found that younger monkeys generally attended to the social stimuli for longer durations than did the older monkeys, as evidenced by their overall longer looking times. It is important to note that our experimental design allowed us to examine relative looking to emotional faces versus neutral faces in the same individual, thereby accounting for any individual variation in interest in photos overall. In addition, this pattern of decreased *overall* looking times with age is one we have found in several recent studies, including work involving non-social stimuli (Hughes and Santos 2012). As such, the meaning of this increased looking responses in juvenile monkeys in the current study is unclear and may reflect general levels of interest in novel stimuli overall rather than any particularly socio-emotional process per se.

Interestingly, we did not find major differences in how male and female monkeys responded to the emotional facial expressions. This is in contrast to other primate work on early infant development suggesting differences in how male and female infants look at faces (Simpson et al. 2015, 2016a, b; Paukner et al. 2018; although note that we did not test such young infants in the current study). Moreover, rhesus monkeys in this population do exhibit sex differences in related aspects of their social cognition, such as gaze following: females are more responsive than are males (Rosati et al. 2016; Rosati and Santos 2017). Furthermore, one might expect that patterns of socio-emotional interest in threat expressions would map onto actual risk of receiving aggression from conspecifics. In rhesus monkeys, aggression tends to be higher within same sex and age cohorts (Kulik et al. 2015). As such, males might be more attentive to the male threat photos and females to the female photos. Along the same lines, dispersal in rhesus monkeys is sex-biased such that males are more likely to disperse, whereas females tend to remain in their natal group (Greenwood 1980; Bercovitch 1997). Consequently, females might benefit more from investing in relationships in their current group at younger ages. We observed, however, that males and females generally evidenced similar responses to the different photos, such that both sexes exhibited increases in looking towards the threat expressions with age. It is important to note that while infant and juvenile monkeys exhibit less agonistic interactions than older monkeys, younger monkeys do receive both contact aggression, as well as vocal aggression such as threat displays (Bernstein and Ehardt 1985). Natural aggression patterns might partially account for the differential responses we observed in infants to male versus female threat expressions. In fact, adult male rhesus monkeys tend to direct their aggression to adolescent and adult males, whereas adult females will more readily attack infants and juveniles (Bernstein and Ehardt 1986). Along these lines, younger monkeys seemed to find the female threat photo more aversive than the male photo, as evidence by their relatively decreased looking rates.

Overall, the current work indicates that rhesus monkeys do not exhibit human-like patterns of socio-emotional bias in their responses to emotional faces: whereas humans show a shift towards a positivity bias with age, monkeys exhibit an exacerbated negativity bias. This suggests that while patterns of human social relationships and social interest may have parallels in non-human primates (Teufel et al. 2010; Almeling et al. 2016, 2017; Fischer 2017), specific psychological mechanisms supporting socio-emotional processing may not be shared between humans and non-human primates. More broadly, the patterns of changes seen in rhesus monkey socio-emotional processing compared to humans can provide new insights into the links between human life history evolution and human cognitive development. The current work did support the possibility that life history patterns might co-vary with some aspects of cognitive development, as rhesus macaques—who have very different life history characteristics than humans—also exhibited quite divergent patterns of socio-emotional preferences across their lifespan. Future work could therefore test whether species that share more features of their life history with humans, such as apes, also exhibit an increasing negativity bias with age, or whether they show the increasing positive bias seen in humans. More generally, this work illustrates how comparative studies of cognitive development across different species varying in socio-ecology and life history can illuminate the origins of human social behavior and pinpoint why and how humans behave the way we do.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflicts of interest.

Ethics approval All non-invasive behavioral tests were approved by the Institutional Animal Care and Use Committee (IACUC) for Yale University (no. 2014-11624), as well as the Cayo Santiago IACUC (#8310106) administered through the University of Puerto Rico Medical Sciences Campus. All tests adhered to site guidelines for animal research.

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