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Differences in How Macaques Monitor Others: Does Serotonin Play a Central Role?

Hannah Weinberg-Wolf¹ and Steve W. C. Chang^{1,2,3}

¹Department of Psychology, Yale University, New Haven, Connecticut 06520

²Department of Neuroscience, Yale University School of Medicine, New Haven, Connecticut 06510

³Kavli Institute for Neuroscience, Yale University School of Medicine, New Haven, Connecticut 06510

Abstract

Primates must balance the need to monitor other conspecifics to gain social information while not losing other resource opportunities. We consolidate evidence across the fields of primatology, psychology, and neuroscience to examine individual, population, and species differences in how primates, particularly macaques, monitor conspecifics. We particularly consider the role of serotonin in mediating social competency via social attention, aggression and dominance behaviors. Finally, we consider how the evolution of variation in social tolerance, aggression, and social monitoring might be explained by differences in serotonergic function in macaques.

Graphical/Visual Abstract and Caption



Cover Figure: Serotonin may play a role in balancing macaques' need to monitor others and monitor the environment, ultimately mediating differences in social monitoring across individuals, populations, and species of macaques.

Keywords

Non-human primates; macaques; serotonin; social monitoring; social information

Corresponding author address: Hannah Weinberg-Wolf, Yale University, Department of Psychology, 2 Hillhouse Ave., New Haven, CT 06511, USA.

Introduction

Many species of primates, including humans, live in complex social environments, and must monitor other individuals in order to avoid conflict, share resources, and maintain status within their social groups. Primates thus allocate extensive cognitive resources to monitor conspecifics. However, primates must flexibly balance the need to gain information about social partners with the need to exploit food sources and avoid predation and environmental risks. This review consolidates evidence across the fields of primatology, psychology, and neuroscience to discuss the variability in monitoring others and a potential neuromodulator pathway that underlies this variability.

Individuals within a species vary in their social monitoring strategies. Social monitoring also varies across different populations of the same species, and also across different species. These differences in strategies seem to be dependent on the amount of social monitoring required for an individual to avoid conflict and maintain its dominance rank. Given that serotonin plays a critical role in regulating aggression and dominance rank, we suggest that serotonin, at least in part, also plays a role in social monitoring. We discuss evidence for this hypothesis, synthesizing pharmacological, clinical, and neuroscientific research on serotonin and social attention. Finally, we consider how evolutionary differences in dominance hierarchy despotism and social monitoring may be linked to differences in serotonergic function and genetics across species, particularly in macaques.

Monitoring Others Helps Individuals Navigate Social Environments

For the purposes of this review, we define monitoring others as the act of attending to, looking at, or watching conspecifics. The social information that can be gleaned via monitoring others is not only information directed from conspecific 'A' to oneself (direct-social monitoring), but also information that is independent of oneself, i.e. directed from conspecific 'A' to a third conspecific, conspecific 'B' (indirect-social monitoring, or third-party monitoring) (Figure 1A).

Primatologists historically have studied what primates know about others. Through this work, we know that monkeys can, and do, use social information to represent social relationships including kinship, dominance, and even facial expressions (Cheney & Seyfarth, 1990, 1999; Parr & Heintz, 2009; Parr, Winslow, Hopkins, & de Waal, 2000; Pokorny & de Waal, 2009; Shepherd, Deaner, & Platt, 2006). Monitoring both direct- and indirect- social information allows monkeys to more quickly represent social relationships and this can help them determine which individuals will reciprocate prosocial behavior, preventing them from wasting resources on unreciprocated altruistic behavior (Trivers, 1971). Even more importantly, gaining social information and representing social relationships allows individuals to navigate complex social environments while reducing the need for potentially threatening direct interactions. This is true for many species, but especially for the species of primates that live in complex social groups organized into linear dominance hierarchies (Rowell, 1974). In these societies, like those of macaques, it is crucial for each individual to know their relative dominance rank; aggressing towards a higher-ranking animal can result in injury or death (J. D. Higley, P. T. Mehlman, S. B. Higley, et al., 1996;

Silk, 2007) while inappropriately submitting to lower-ranking animals can result in a loss of resources or decrease in dominance status(Pusey, Williams, & Goodall, 1997; Rowell, 1974; Sapolsky, 2005; Wittig & Boesch, 2003). Physical cues such as size and age are not the most reliable predictors of dominance rank in some primate species, including macaques(Bernstein & Gordon, 1980; Maestripiéri & Wallen, 1997). In these species, where age and size are not perfect predictors of rank, individuals must monitor species-typical social signals(F. de Waal & Luttrell, 1985) to communicate and decipher dominance hierarchies. For example, macaque dominance hierarchies seem to be reflected and signaled by differences in facial expressions(Maestripiéri, 1997; Partan, 2002) and social gaze dynamics(Dal Monte, Piva, Morris, & Chang, 2016).

Indeed, social primates are adapted to seek out, value, and use social information related to faces(Anderson, 1998). Infant rhesus macaques as young as 3 weeks of age are more likely to detect faces and look longer at faces relative to non-social stimuli. By the age of 3 months, this face-prioritizing visual system has been tuned specifically to conspecific faces relative to other primate and animal faces(Simpson et al., 2017) (Figure 1B). In addition, when viewing dynamic video clips of naturalistic scenes, humans and macaques direct their attention to social agents even when these locations are not predicted by a model that only considers low-level visual characteristics (e.g., contrast, stimulus orientation)(Shepherd, Steckenfinger, Hasson, & Ghazanfar, 2010) (Figure 1C).

Laboratory studies also indicate that adult rhesus macaques readily recognize individuals(Pokorny & de Waal, 2009), their facial expressions(Parr & Heintz, 2009) and statuses(Shepherd et al., 2006). Consistent with the value attached to social information, rhesus macaques will work in order to receive social information(Andrews, Bhat, & Rosenblum, 1995; Turrin, Fagan, Dal Monte, & Chang, 2017) and even forgo juice and food rewards in order to gain valuable social information(Deaner, Khera, & Platt, 2005) (Figure 1D). Macaques also reflexively follow the gaze of conspecifics and humans(Drayton & Santos, 2017; Mosher, Zimmerman, & Gothard, 2014; Putnam, Roman, Zimmerman, & Gothard, 2016).

Overall, primates strategically devote cognitive resources to maximize the information they gain by monitoring others. In a naturalistic scene viewing task, macaques were found to view conspecifics earlier and for a longer period of time when they exhibited directed eye gaze and redder sex skin, which both convey particularly important social information(Solyst & Buffalo, 2014). Furthermore, macaques frequently direct attention to the eye region of faces(Dal Monte et al., 2016), scan faces conveying agonistic and affiliative expressions differently(Nahm, Perret, Amaral, & Albright, 1997) and attend to photos of novel conspecifics more than familiar conspecifics(Gothard, Erickson, & Amaral, 2004), likely to maximize gained social information. When foraging for social information, rhesus macaques decide to explore or exploit “patches” that offer varying amounts of novel social information(Turrin et al., 2017), indicating that they employ a strategy in seeking social information. This strategy seems to be guided by social value. For instance, macaques are more willing to forgo juice rewards to observe the perinea of fecund females and the faces of high ranking macaques(Deaner et al., 2005) and more readily follow the gaze of high dominance status individuals(Shepherd et al., 2006).

While social information is important, monitoring others for too long of a period can be risky. For example, direct eye gaze towards another macaque is considered to be a threat (Maestriperi, 1997). Thus, animals also gain dominance related information via attending to third party or to other-other interactions (Qu, Ligneul, Van der Henst, & Dreher, 2017). This allows individuals avoid having to learn about dominance hierarchies via direct competition and thus limit fighting and antagonistic interactions. Rhesus macaques are able to use behavioral cues to identify, responding via joystick, which of two unfamiliar conspecifics in artificially created videos was the dominant individual (Bovet & Washburn, 2003). Another study demonstrated that macaques were not only able to learn which of two novel conspecifics was the dominant individual, but were also able to remember and transfer, responding via touchscreen, this dominance relationship to new videos where the recorded animals provided no dominance information (Paxton et al., 2010).

Monitoring Others – Variability Between Individuals, Populations, and Species

All individuals must judiciously balance the benefits and costs of monitoring conspecifics. Monitoring others can yield valuable information about fecundity, dominance ranks, and third-party environment information. However, excessive monitoring of conspecifics can lead to accidentally aggressing to conspecifics, and prevents individuals from scanning their environment for food or potential threats (Figure 2). This balancing act is reflected as variation in monitoring behaviors, and can be observed in the laboratory and in the wild, across individuals, populations, and species.

Third party monitoring can manifest differently across individuals within a given population according to age, gender, and dominance rank. As rhesus macaques age they tend to modulate gaze following, increasing gaze following into adolescence and then decreasing gaze following into adulthood (Rosati, Arre, Platt, & Santos, 2016). This is likely because juvenile rhesus depend on monitoring other-other interactions to learn relative dominance rankings, but this need decreases with age as individuals gain more knowledge of and become more established in their dominance ranks (Rosati et al., 2016). Adult rhesus males are more vigilant and monitor conspecifics more than females (K. Watson et al., 2015), likely because the dominance ranking of males are more volatile than female rhesus, who exhibit inherited dominance ranks (Holekamp & Smale, 1991). However, adult females follow gaze more readily than adult males (Rosati et al., 2016). Moreover, as macaques age they also modulate rates of direct gaze. Bonnet macaques exhibit increased eye contact from infancy to adolescence, and then decrease direct gaze into adulthood, likely because adult macaques punish direct gaze more as macaques age (Coss, Marks, & Ramakrishnan, 2002).

An individual's dominance rank also strongly influences patterns of social monitoring. Haude found that middle ranking rhesus macaques looked at conspecifics more frequently, but that each of these looking events was for a shorter period of time than low or high-ranking individuals (Haude, Graber, & Farres, 1976). This is likely because the dominance rankings of middle ranking individuals are more volatile, requiring them to be more vigilant towards conspecifics, hence the increased number of looks. However, middle ranking

individuals also need to avoid accidentally aggressing to others during their heightened vigilance, hence the relative short duration of each looking event in order to prevent accidental direct eye contact. Capitanio and colleagues observed a similar effect in pigtailed macaques; middle ranking females spent a relatively longer period of time monitoring conspecifics compared to low- and high- ranking females (J. P. Capitanio, Boccia, & Colaianina, 1985) (Figure 3A). In addition, middle-ranking pigtailed macaques attended most to videos that featured the next highest-ranking females, particularly when they exhibited submissive gestures, which is incongruent to the relative dominance status between the stimulus female and the tested female. Furthermore, the middle-ranking macaques increased aggression in the home cage after viewing these videos, but not other types of videos (J. Capitanio, 1987). Thus, macaques modulate rates of social monitoring depending on their relative dominance relationships and use social information to update their own dominance ranks.

Not surprisingly, social monitoring can also vary across populations and across species. Bonnet macaque populations living in the forest decrease direct gaze as they age, while populations living in urban environments maintain juvenile levels of direct gaze into adulthood (Coss et al., 2002) (Figure 3B). This difference is likely driven by an increased demand to monitor the environment for predators in the forest relative to urban settings. In addition, bonnet macaques in urban settings live in smaller territories and thus live in closer physical proximity to conspecifics, increasing the likelihood of fighting. For this reason, bonnet macaques in urban settings devote more time than their forest counterparts to monitoring conspecifics to avoid ingroup fighting (Coss et al., 2002). Just as bonnet macaques typically decrease directed gaze with age, rhesus macaques decrease gaze following with age. In contrast, the barbary macaque, a highly tolerant species with relatively flat dominance hierarchies, maintains juvenile levels of gaze following into adulthood (Rosati & Santos, 2017) (Figure 3C). This is perhaps because barbary macaques are punished less for direct gaze behavior and do not fear social repercussions relative to their more despotic relatives, i.e. the rhesus and bonnet macaques. Overall, in primate societies, we find variability between individuals, populations, and species in their social monitoring behaviors, with these differences being driven by socioecological and sociobiological distinction.

Serotonin and Monitoring Others

The serotonergic system appears to modulate processes underlying social behaviors and social monitoring and does so in a manner dependent on the prior history of individuals. Modulating central serotonin function with Selective Serotonin Reuptake Inhibitors (SSRIs), precursor augmentations (Acute Tryptophan Depletion (ATD), tryptophan loading, 5-Hydroxytryptophan (5-HTP) loading), or receptor agonism/antagonism has been shown to impact impulsivity, cognitive biases, attention, learning, and memory, with these effects being much stronger for social stimuli, affective processing, and emotional recognition (Mendelsohn, Riedel, & Sambeth, 2009; Merens, Van der Does, & Spinhoven, 2007; Riedel, Klaassen, & Schmitt, 2002; Silber & Schmitt, 2010; Young, 1996). A lot of research, particularly clinical research, has focused on how modulating central serotonin impacts attentional biases to different classes of emotional stimuli and suggest that

decreasing central serotonin with ATD causes negative attentional biases (Fusar-Poli et al., 2007; Klaassen, Riedel, Deutz, & Van Praag, 2002; Munafò, Hayward, & Harmer, 2006; Robinson, Cools, Crockett, & Sahakian, 2010; Roiser et al., 2008), particularly in those at risk of depression, like recovered depressed individuals (Booij et al., 2005; Hayward, Goodwin, Cowen, & Harmer, 2005) or those with a family history of depression (Marsh et al., 2006; van der Veen, Evers, Deutz, & Schmitt, 2007). On the other hand, increasing central serotonin with acute SSRIs and serotonergic precursor loading seems to modulate eye gaze patterns (Jonassen, Chelnokova, Harmer, Leknes, & Landrø, 2015) and decrease negative attentional biases and negative emotional recognition (C. Harmer, Bhagwagar, et al., 2003; C. Harmer, Rogers, Tunbridge, Cowen, & Goodwin, 2003; C. J. Harmer, Mackay, Reid, Cowen, & Goodwin, 2006; C. J. Harmer, Shelley, Cowen, & Goodwin, 2004; Jonassen et al., 2015; Luciana, Burgund, Berman, & Hanson, 2001; Murphy, Longhitano, Ayres, Cowen, & Harmer, 2006), particularly for those at deficit prior to intervention (Bhagwagar, Cowen, Goodwin, & Harmer, 2004). Other studies have investigated the effects of serotonin manipulation on emotional recognition and shown that risk factors and baseline differences in behavior can impact the effect of serotonergic modulations (Bhagwagar et al., 2004; Hayward et al., 2005; Robinson et al., 2010). A single dose of the SSRI citalopram increases the recognition of fearful faces in healthy volunteers but decreases fear recognition in subjects with a history of depression (Bhagwagar et al., 2004) (Figure 4A). Furthermore, decreasing central concentrations with low dose ATD increases the recognition of happy faces in healthy volunteers, but instead decreases the recognition of happy emotions in recovered depressed patients (Hayward et al., 2005) (Figure 4B).

Mirroring the individual variability in serotonin manipulations in human subjects, a recent study from our lab reported that increasing central serotonin via acute administration of the serotonergic precursor 5-HTP modulated rhesus macaques' attention to images in a bidirectional manner (Weinberg-Wolf et al., 2018). 5-HTP increased looking duration in subjects with low starting or baseline attention, yet decreased it in those with high baseline attention. Importantly, while 5-HTP modulated looking duration to both social and nonsocial images, 5-HTP had a greater effect on attention to social images (Figure 5A). In animals that, at baseline, directed less attention to social images, 5-HTP increased attention to social images more than to non-social images. On the other hand, in high baseline social attention animals, 5-HTP decreased attention specifically to social images. Moreover, 5-HTP had the largest impact on attention to facial features that are salient and convey important social information, the eyes and mouth (Figure 5B). 5-HTP increased looking to the eyes and mouth in animals with low baseline attention, but decreased looking to these same regions in animals with high baseline attention. In addition, these effects were greatest for expressive compared to neutral faces, and faces with direct gaze compared to averted gaze meaning that 5-HTP seems to modulate attention to social stimuli as a function of how salient facial expression are and also the relative value of the information they convey. Overall, these findings suggest that central serotonergic function may balance the benefits and costs of monitoring conspecifics dependent on differences between individuals.

Dominance and Aggression: The Role of Central Serotonin

While monitoring others is a crucial component of dominance hierarchies, the establishment and maintenance of these hierarchies often relies on some level of aggressive behaviors. It ensures that individuals can maintain access to limited resources and defend themselves against others (Chiao, 2010; A. S. Clarke & Boinski, 1995; F. B. de Waal, 1986; Qu et al., 2017; Rowell, 1974). However, high levels of aggression are maladaptive and can lead to low social competency and impaired quality of life (F. B. de Waal, 1986; J. D. Higley, P. T. Mehlman, S. B. Higley, et al., 1996; Rowell, 1974). Central serotonin has been implicated repeatedly, and across many species, in regulating maladaptive aggression (Coccaro, 1992; Coccaro et al., 1997; Ferrari, Palanza, Parmigiani, de Almeida, & Miczek, 2005; Garattini, Giacalone, & Valzelli, 1967; Gibbons, Barr, Bridger, & Liebowitz, 1979; Linnoila et al., 1983; Manuck et al., 1998; Valzelli, 1971). While researchers have found that central concentrations of the serotonin metabolite 5-hydroxyindoleacetic Acid (5-HIAA) are overall inversely correlated with aggression in rhesus macaques (J. D. Higley et al., 1992), low CSF 5-HIAA concentrations have been linked specifically to only one subtype of aggression: impulsive aggression, or aggression that is unprovoked or unproductive and will not help an individual maintain access to resources or secure dominance status (J. Higley & Linnoila, 1997). On the other hand, productive aggression, used to maintain dominance rank, has been positively correlated with concentrations of testosterone in male macaques (J. D. Higley, P. T. Mehlman, R. E. Poland, et al., 1996). This relationship is further supported by extensive work, in multiple species, showing that low CSF 5-HIAA concentrations correlate with poor impulse control, impaired social functioning, severe wounding, and even mortality in primates (Fairbanks, Melega, Jorgensen, Kaplan, & McGuire, 2001; J. Higley, S. King, et al., 1996; J. Higley & Linnoila, 1997; J. Higley, Suomi, & Linnoila, 1996; J. D. Higley, Linnoila, & Suomi, 1994; J. D. Higley et al., 1992; J. D. Higley, P. T. Mehlman, S. B. Higley, et al., 1996; J. D. Higley, P. T. Mehlman, R. E. Poland, et al., 1996; P. Mehlman et al., 1994; P. T. Mehlman et al., 1997; Taub & Vickers, 1995; G. Westergaard, Mehlman, Westergaard, Suomi, & Higley, 1999; G. C. Westergaard et al., 2003; Zajicek et al., 2000) (Figure 6A). As a consequence of these impairments, primates with low CSF 5-HIAA concentrations are less likely to acquire and maintain social dominance than those with high CSF 5-HIAA concentrations (J. Higley, S. King, et al., 1996; J. D. Higley et al., 1992; J. D. Higley, P. T. Mehlman, R. E. Poland, et al., 1996; Howell et al., 2013; Kaplan, Manuck, Fontenot, & Mann, 2002; P. T. Mehlman et al., 1997; G. Westergaard et al., 1999; Zajicek et al., 2000) (Figure 6A).

The Relationship Between Despotism and Variability in Serotonergic Alleles

There are 19 sub-species of macaques, each with slightly different styles of dominance hierarchy. Highly despotic species have extremely steep hierarchies whereby a dominant individual almost always wins contests with their subordinates. On the other hand, the dominance hierarchies of tolerant species are less steep and thus dominant and subordinate individuals win contests more evenly (Balasubramaniam et al., 2012; Petit, Abegg, & Thierry, 1997; B Thierry, 1985; Bernard Thierry, 2007; Bernard Thierry, Iwaniuk, & Pellis, 2000). These differences in despotism are categorized along a scale of 1–4 with one being the most despotic and four being the least despotic (Balasubramaniam et al., 2012; Bernard

Thierry, 2007) (Figure 6B). Rhesus macaques are one of the sub-species with the most despotic, or steep, dominance hierarchies (Balasubramaniam et al., 2012; Bernard Thierry, 2007). They exhibit more extreme and higher rates of aggression, along with higher rates of species typical threat and submissive gestures compared to less despotic species, like the Tonkean macaques (*Macaca tonkeana*), who instead exhibit higher rates of affiliative gestures (Petit et al., 1997; Bernard Thierry, 2007). CSF 5-HIAA concentrations are inversely related to aggression levels across macaque species; species with relatively more despotic hierarchies, like rhesus, exhibit relatively lower concentrations of CSF 5-HIAA compared to species with slightly less despotic hierarchies, like pigtailed macaques (G. Westergaard et al., 1999). Not surprisingly, the relationship between individual variations in 5-HIAA and aggressive behaviors seen within a species (J. D. Higley et al., 1992), holds true across species as well (Figure 6A). It is likely that diversity in serotonergic function may contribute to regulating aggression and dominance relationships across individuals, population, and species.

Because of the pressure to know and defend dominance rank, we hypothesize that species with more despotic dominance hierarchies have developed greater intra-group diversity in social monitoring strategies because of greater intra-group differences in social threat (K. Watson et al., 2015). Concomitantly, despotic species of macaques exhibit more variation in genes related to serotonergic function, like the 5-HTT gene encoding for the serotonin transporter (Dobson & Brent, 2013; Wendland et al., 2006), indicating a relationship between variation in socially competent dominance-related behavior and the diversity in serotonergic function (Figure 6C). The relationship between individual differences in these genotypes and monitoring others, vigilance, and dominance has been investigated extensively. While the genetic architecture of these complex behavioral traits is polygenic in nature, evidence suggests that individual differences in these social behaviors are heritable and may be related to genetic variation in the serotonergic pathway (Beevers, Ellis, Wells, & McGeary, 2010; Beevers et al., 2011; Boll & Gamer, 2014; Brent et al., 2013; Canli & Lesch, 2007; Dobson & Brent, 2013; Duncan & Keller, 2011; Gibboni, Zimmerman, & Gothard, 2009; Hariri & Holmes, 2006; K. Watson et al., 2015; K. K. Watson, Ghodasra, & Platt, 2009). Overall, a plausible evolutionary hypothesis is that species that have more diversity in social monitoring due to higher levels of hierarchy despotism also exhibit greater diversity in the genetic encoding of the serotonergic pathway.

Interactions between the Central Serotonin and Oxytocin Systems in Social Monitoring

Oxytocin has been widely implicated in social cognition, influencing multiple stages of social processing, including social attention and valuation (Piva & Chang, 2018). Oxytocin has been shown to increase attention to social stimuli (Dal Monte et al., 2017; Parr et al., 2016), particularly to the eye region (Dal Monte, Noble, Costa, & Averbach, 2014; Kotani et al., 2017), and to also increase gaze following (Putnam et al., 2016; Tollenaar, Chatzimanoli, van der Wee, & Putman, 2013). Increasing central OT also seems to amplify social preferences (Chang, Barter, Ebitz, Watson, & Platt, 2012), regulate social vigilance (Ebitz, Watson, & Platt, 2013; Landman, Sharma, Sur, & Desimone, 2014) and differentially impact

attention and brain activation to different facial expressions (Domes, Steiner, Porges, & Heinrichs, 2013; Liu et al., 2015; Parr, Modi, Siebert, & Young, 2013).

Oxytocin and serotonin are increasingly being studied in tandem. Research has shown that OT receptors are expressed in serotonergic cells in the rodent DRN (Pagani et al., 2015; Yoshida et al., 2009), and that serotonin transporter-containing fibers overlap with oxytocin labeled cells in non-human primates (Emiliano, Cruz, Pannoni, & Fudge, 2007). It has also been shown that increasing central serotonin release via multiple methods, including serotonin receptor agonists, induces OT release in rodents, non-human primates, and humans (Bagdy & Kalogeras, 1993; Jørgensen, Riis, Knigge, Kjaer, & Warberg, 2003; Marazziti et al., 2012). Mottolese and colleagues also found that administering OT, compared to a placebo, increases serotonin binding potential in regions associated with social processing, attention, and valuation in humans: DRN, amygdala/hippocampal complex, insula, and orbitalfrontal cortex (Mottolese, Redouté, Costes, Le Bars, & Sirigu, 2014). This relationship is also present in the macaque brain (Lefevre, Richard, et al., 2017). However, the recruitment of 5-HT by OT seems to be heavily blunted in individuals with Autism Spectrum Disorders, suggesting that the interaction between OT and 5-HT is crucial for typical social behaviors, including monitoring others (Lefevre, Mottolese, et al., 2017). In addition, Dölen and colleagues found that in mice, coordinated activity between OT and 5-HT in the nucleus accumbens is required for social interactions to be reinforcing (Dölen, Darvishzadeh, Huang, & Malenka, 2013). Thus, it has been hypothesized that both oxytocin and serotonin impact social attention and social monitoring in tandem. It would be interesting to further explore the interaction between OT and 5-HT and their effect on social behaviors, specifically social monitoring and aggressive behaviors, in the future.

Conclusions and Future Directions

In this focused article, we examined the relative costs and benefits primates must consider when monitoring other conspecifics. In doing so, we discussed the methods by which primates gather social information and the importance of this information. Monitoring others is guided by its relative costs; accidental aggression to conspecifics and lost opportunities to monitor the environment and gain information about food sources, predation, and environmental risk. Therefore, the ability to balance social and environmental monitoring requires flexibility, a core aspect of behavior that serotonin has been implicated in regulating (H. Clarke, Dalley, Crofts, Robbins, & Roberts, 2004; H. Clarke et al., 2005; Matias, Lottem, Dugue, & Mainen, 2017). Indeed, primates are required to flexibly shift between obtaining useful social information from group members and acquiring valuable information about potential threats and resource opportunities from the environment. Evidence across primatology and psychology supports that social monitoring can greatly vary due to age, gender, and dominance status. Furthermore, it seems that variability in social tolerance explains how, and why, social monitoring differs across populations and across macaque species. The evolutionarily plausible account we present is that individual, population, and species variability in social monitoring and dominance behaviors seems to be, at least in part, linked to variability in serotonergic function and the genetic encoding of the serotonergic pathway. The central serotonin system may have thus played a significant role in shaping social monitoring in primate societies.

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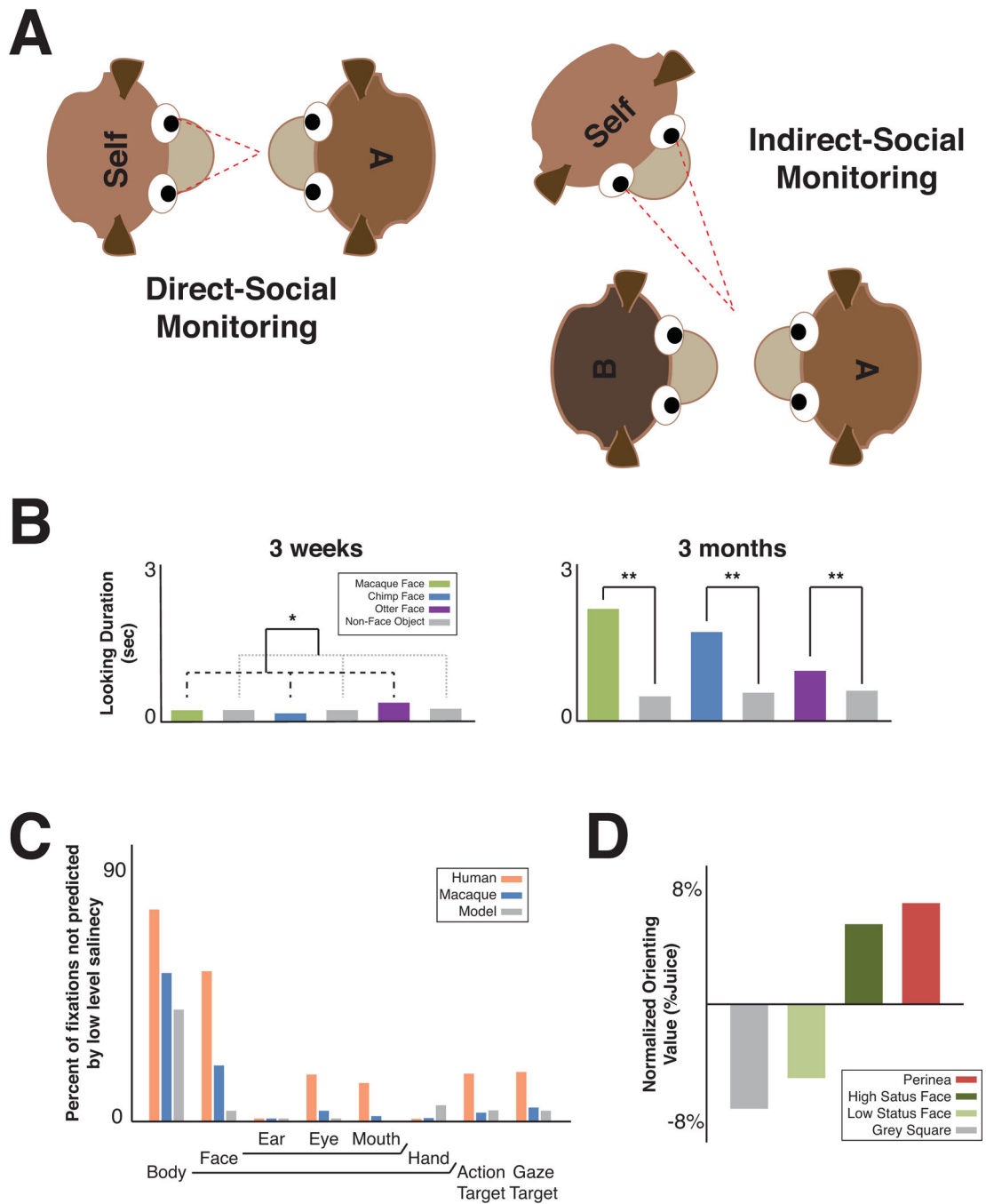


Figure 1: Monitoring others for gaining social information in primates.

A) Many primate species gather social information by either monitoring others when information is directed from a conspecific ‘A’ to themselves (direct-social monitoring) or when information is communicated between conspecific ‘A’ to conspecific ‘B’ (indirect-social or third-party monitoring). **B)** Rhesus macaques detect faces as early as 3 weeks of age, and this detection becomes biased towards conspecific faces by 3 months. When 3-week-old macaques were presented with an image of a macaque, chimpanzee, or otter face in an array with 9 non-face objects they looked at faces (colored bars connected with black

dashed lines) longer than non-face objects (grey bars connected with grey dashed lines). By 3 months, they also looked at macaque faces significantly longer than chimpanzee faces and otter faces. $*p < .05$. $**p < .016$. Reproduced and adapted with permission from(Simpson et al., 2017). **C)** When humans and rhesus macaques view natural scene videos featuring rhesus macaques, humans, or cartoon characters, gaze fixation locations are not simply predicted by a model that only considers low-level visual characteristics (e.g., contrast, stimulus orientation). Instead, the viewed locations often feature social agents and the targets of agents' actions and attention. Reproduced and adapted with permission from(Shepherd et al., 2010). **D)** Rhesus macaques are willing to forgo juice rewards in order to view female perinea and high-ranking male faces, but require extra juice rewards in order to choose to view low-ranking male faces and non-social stimuli. Reproduced and adapted with permission from(Deaner et al., 2005).

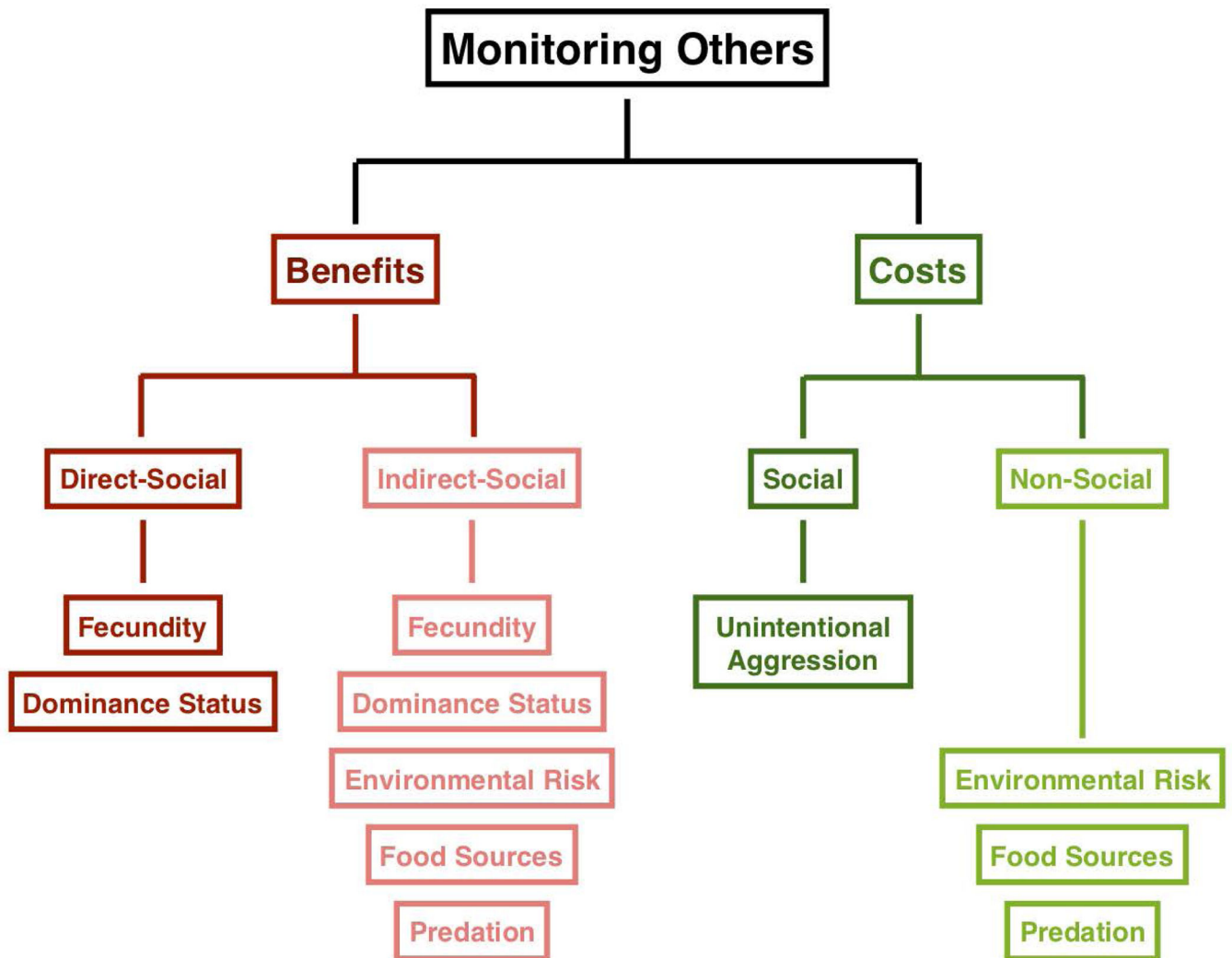


Figure 2: The costs and benefits of social monitoring.

Primates must balance the costs and benefits associated with social monitoring. From direct-social monitoring, primates can gain information about conspecifics fecundity and dominance status. From indirect-social monitoring they can learn not only about fecundity and dominance status, but also environmental risk, food sources, and predation. However, monitoring others for too long can result in the social cost of unintentional aggression. It can also cause a reduction in environmental monitoring which can cause animals to learn less about environmental risk, food sources, and predation.

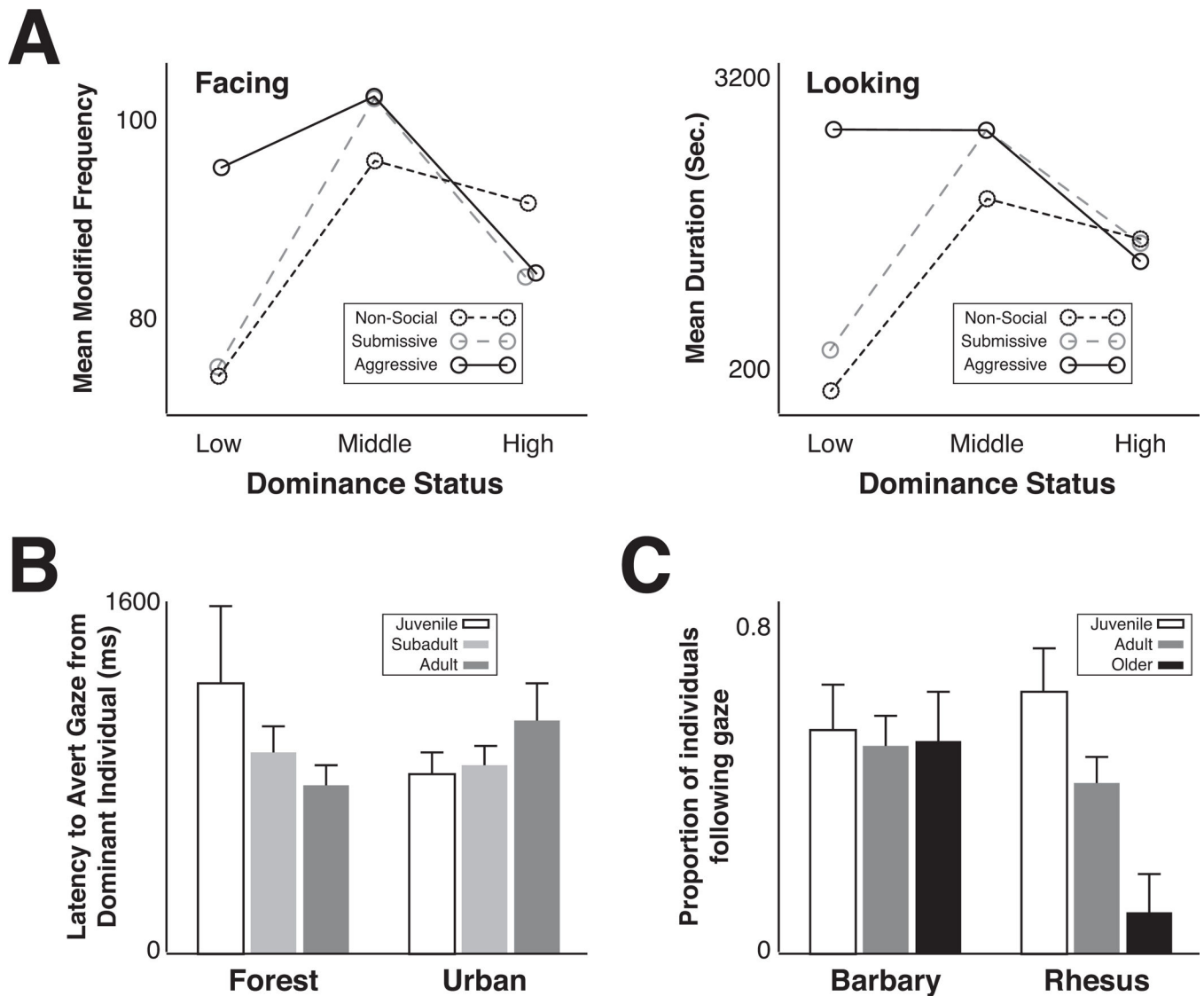


Figure 3: Social monitoring in primates differs across individuals, populations, and species.

A) Left panel: The mean frequency of positioning the body to directly face videos of non-social stimuli, conspecifics exhibiting dominant expressions, and conspecifics exhibiting submissive expressions, for low-, middle-, and high-ranking female pigtailed macaques. Right panel: The mean look duration to these same categories of videos for the same female pigtailed macaques. Middle-ranking females faced the social videos more, and looked at the videos longer, compared to low- and high-ranking females. Reproduced and adapted with permission from (J. P. Capitanio et al., 1985). **B)** While bonnet macaques living in the forest avert eye contact with conspecifics more quickly as they age, bonnet macaques living in urban environments do not. Reproduced and adapted with permission from (Coss et al., 2002). **C)** As despotic rhesus macaques age, fewer of them follow the gaze of an experimenter while tolerant barbary macaques maintain juvenile rates of gaze following throughout their lives. Reproduced and adapted with permission from (Rosati & Santos, 2017).

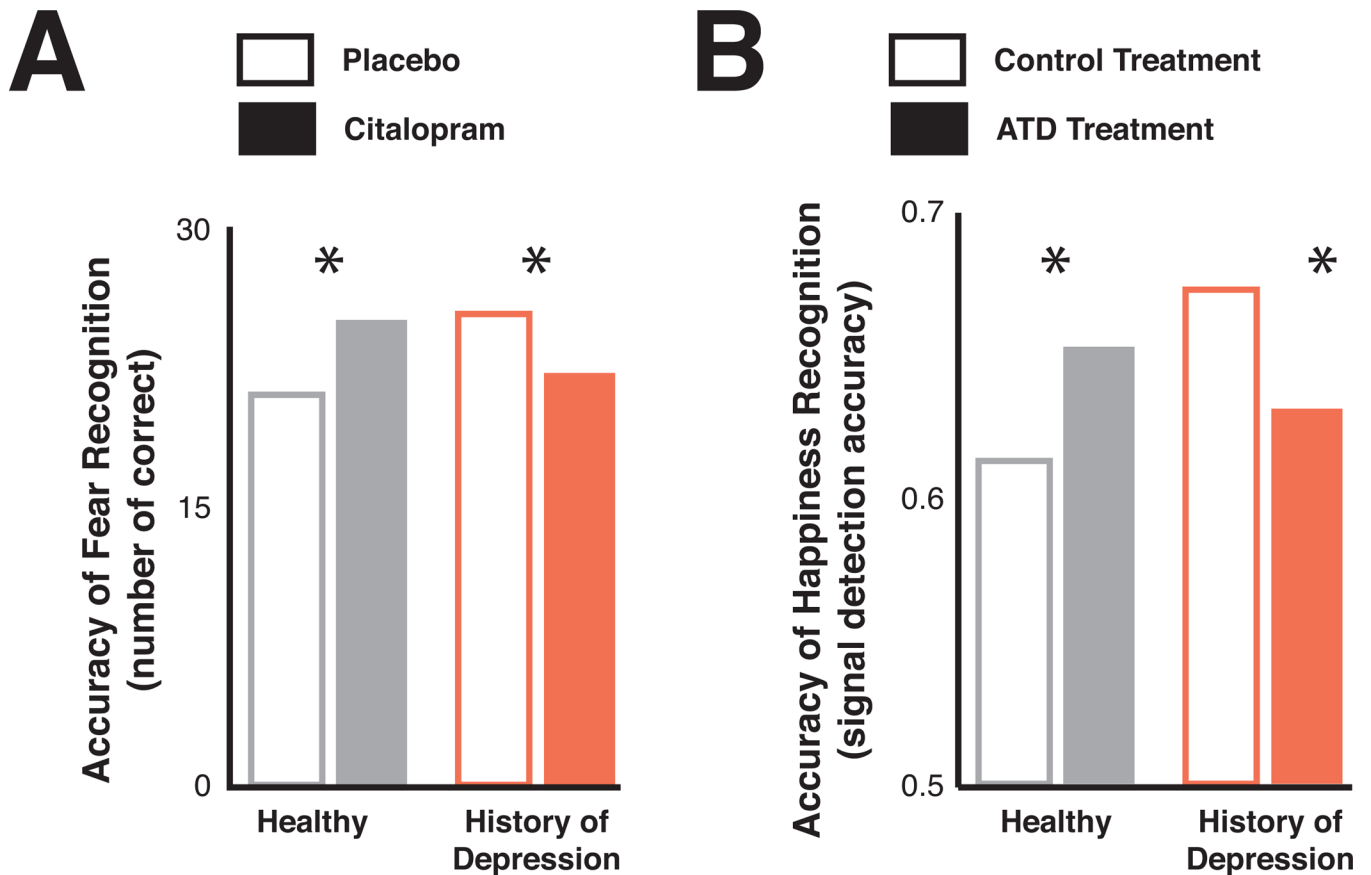


Figure 4: Serotonin differentially impacts emotional recognition dependent on individual differences.

A) The SSRI citalopram (filled bars), compared to placebo (open bars), causes a bidirectional effect on fear recognition depending on whether subjects had a history of depression (red bars; decreases fear recognition due to citalopram) or were healthy volunteers (grey bars; increases fear recognition due to citalopram). Reproduced and adapted with permission from (Bhagwagar et al., 2004). **B)** ATD (filled bars versus placebo open bars) causes a bidirectional effect on the recognition of happy emotions dependent on if subjects were healthy (left graph, grey bars, an increase due to ATD) or recovered depressed (right graph, red bars, a decrease due to ATD). Reproduced and adapted with permission from (Hayward et al., 2005).

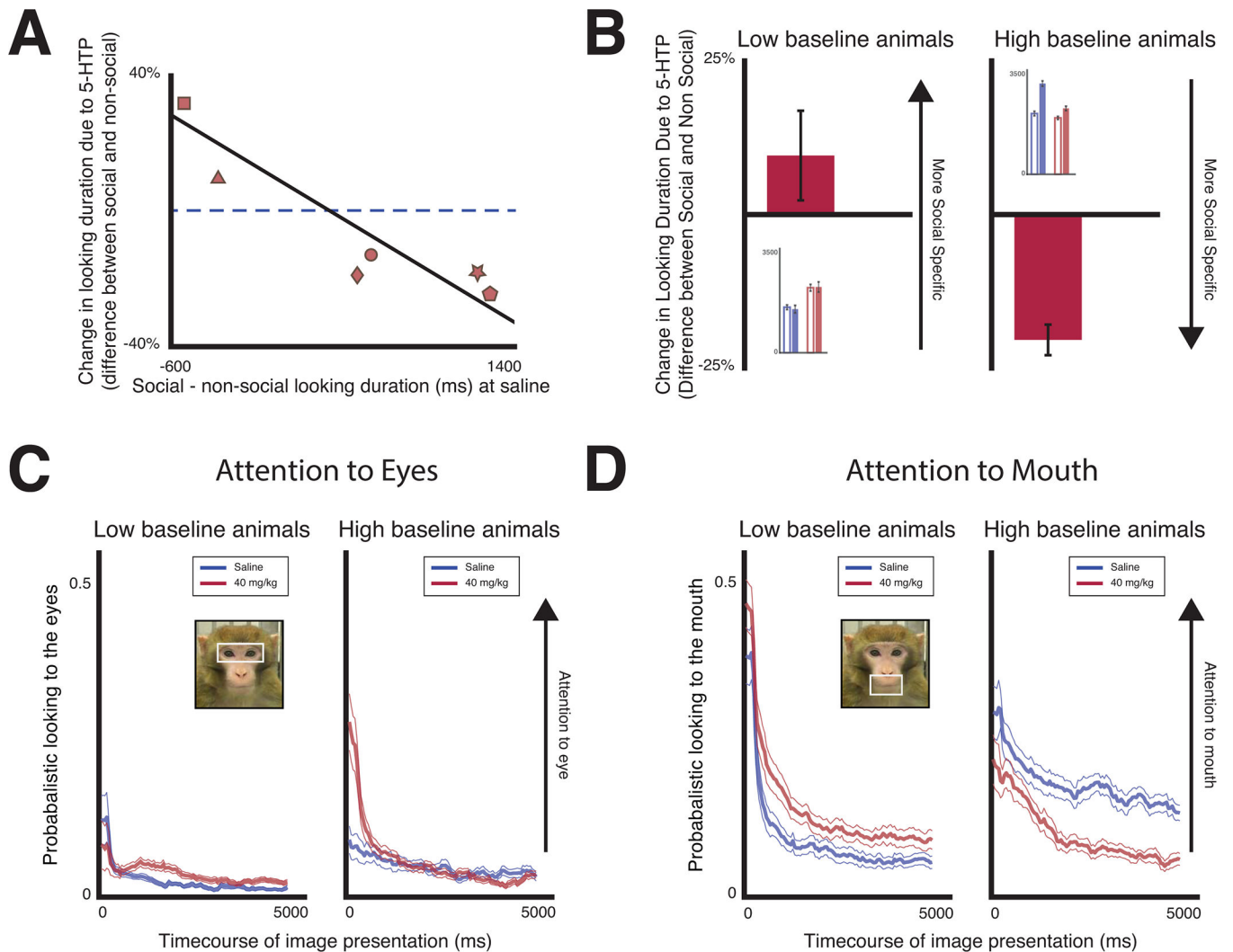


Figure 5: Increasing central serotonin with 5-HTP modulates social attention.

A) Baseline differences in how long rhesus macaques look at social and non-social images are negatively correlated with the differences in how 40mg/kg 5-HTP changes looking duration to social and non-social images relative to saline (blue dashed line). Each shape represents an individual subject's data. **B)** The average differences in the changes in looking duration to social and non-social images due to 5-HTP for low and high baseline animals. The inset shows the raw looking duration to social (filled bars) and non-social images (open bars) for low and high baseline animals during saline (blue) and 5-HTP (red) sessions. Adapted and reproduced with permission from (Weinberg-Wolf et al., 2018). **C)** Average time courses of 5-HTP's bi-directional effect on attention to the mouth for low and high baseline animals. 5-HTP increases attention to the mouth region in low baseline animals but decreases it in high baseline animals. Saline data shown in blue, and 40mg/kg 5-HTP in red. Adapted and reproduced with permission from (Weinberg-Wolf et al., 2018). **D)** Average time courses of 5-HTP's effect on attention to conspecific eyes for low and high baseline animals. While 5-HTP has a large effect on attention to the mouth, it only modestly increases attention to the eye region in low baseline animals while modestly decreases it in

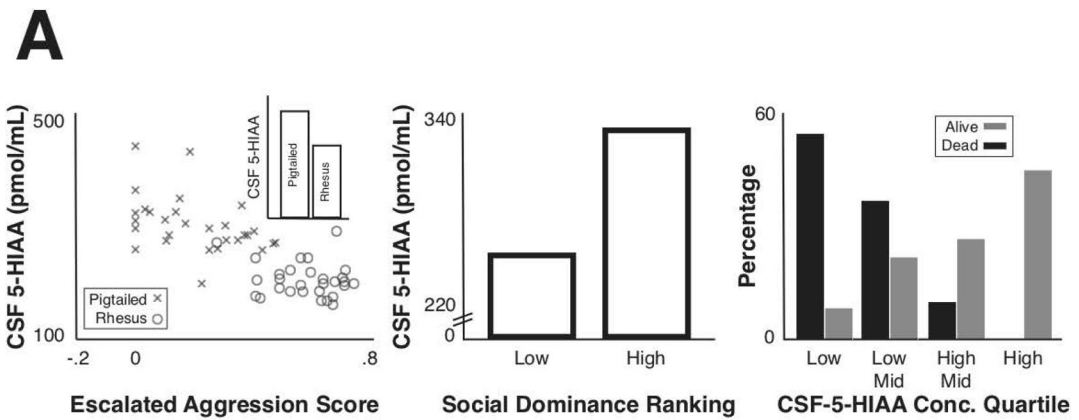
high baseline animals. Saline data shown in blue and 40mg/kg 5-HTP in red. Adapted and reproduced with permission from(Weinberg-Wolf et al., 2018).

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B

Grade 1	Grade 2	Grade 3	Grade 4
Rhesus macaque Japanese macaque (Taiwan macaque)	Longtailed macaque Pigtailed macaque (Assamese macaque) (Tibetan macaque)	Stumptailed macaque Barbary macaque Liontailed macaque Bonnet macaque (Toque macaque)	Token macaque Moor macaque Crested macaque (Muna-Butung macaque) (Booted macaque) (Heck's macaque) (Gorontalo macaque) (Sibert macaque)

C

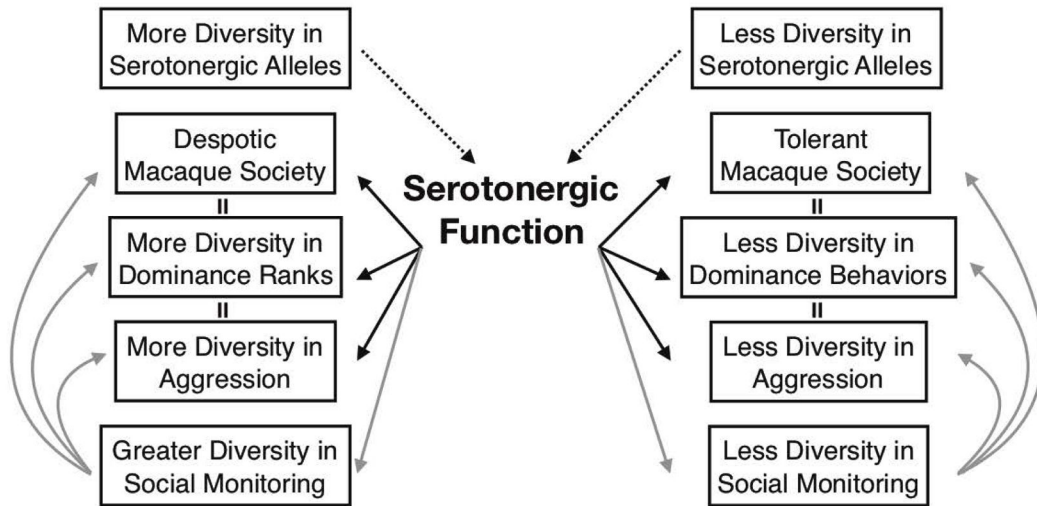


Figure 6: Diversity in social tolerance in macaque species is related to diversity in serotonergic function, and potentially impacts diversity in dominance rank, aggression, and social monitoring.

A) Left Panel: Central concentrations of the serotonin metabolite (5-HIAA) are inversely correlated with escalated aggression scores, or the proportion of all aggressive acts that were characterized by high-intensity aggression, in rhesus macaques and pigtailed macaques. The inset shows that rhesus macaques have lower average CSF-5-HIAA than pigtailed macaques. Reproduced and adapted with permission from(G. Westergaard et al., 1999). Middle Panel: High-ranking female macaques exhibit relatively higher central concentrations of 5-HIAA

than low-ranking females. Reproduced and adapted with permission from (J. Higley, S. King, et al., 1996). Right Panel: Animals with relatively lower concentrations of CSF 5-HIAA are more likely to have died 4 years after sample collection than animals with relatively higher concentrations of CSF 5-HIAA. Reproduced and adapted with permission from (J. D. Higley, P. T. Mehlman, S. B. Higley, et al., 1996). **B)** Macaque species can be categorized according to their social tolerance, varying from grade 4 (most tolerant) to grade 1 (most despotic). Reproduced and adapted with permission from (Bernard Thierry, 2007). **C)** A summary figure illustrating the known relationships between diversity in serotonergic genetics, serotonergic function, social tolerance, and diversity in dominance rank, aggression, and social monitoring across species of macaques. Dotted lines represent the impact of diversity in serotonergic alleles on serotonergic function. Solid black lines represent the impact of serotonergic function on aggression, dominance status, and social tolerance. Grey lines represent the relationship between serotonergic function and social monitoring and the relationship between social monitoring and aggression, dominance status, and social tolerance.