

Early Experience Affects the Strength of Vigilance for Threat in Rhesus Monkey Infants

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Abstract

Both human and nonhuman primates exhibit a cognitive bias to social threat, but little is known about how this bias develops. We investigated the development of threat bias in free-ranging infant rhesus macaques (*Macaca mulatta*) at 3 months ($n = 45$) and 9 months ($n = 46$) of age. Three-month-olds did not display bias, but 9-month-olds exhibited increased maintenance of attention to threatening social stimuli. To examine whether the social environment affected this increased vigilance for threat, we collected behavioral data on maternal rank and protectiveness across the first 12 weeks of life for infants tested at 9 months. Among 9-month-olds, those of high-ranking and more protective mothers displayed greater vigilance for threat than those of lower-ranking and less protective mothers. These results demonstrate that infant social cognition is shaped by mothers both directly (via protectiveness) and indirectly (through social rank).

Keywords

cognitive bias, maternal effects, socio-cognitive development, rhesus macaque, primate

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The human mind is far from objective or accurate in the processing of information about the world. Rather, humans show many predictable biases in attention, perception, memory, and decision making (e.g., Kahneman, 2011). Cognitive biases are likely to represent adaptations that aid in survival and reproduction in the environment in which people live (e.g., Haselton et al., 2009; Kenrick & Griskevicius, 2013). For example, it has been shown that humans detect snakes more quickly than flowers or other harmless organisms and allocate more attention to potentially dangerous stimuli as well (LoBue & DeLoache, 2008). The same results have been found for monkeys (Öhman & Mineka, 2001). As the cost of ignoring a threat may be much greater than the cost of ignoring nonthreatening aspects of the environment, both attention to threat (rapid detection) and vigilance for threat (maintenance of attention) are likely to be adaptive.

Cognitive bias for threat in both attention and vigilance is not limited to natural predators or physical

dangers; the social environment is rife with threats as well. Humans demonstrate exceptional attention to and memory for negatively valenced social stimuli (Anderson, Siegel, Bliss-Moreau, & Feldman Barrett, 2011; Kuhbandner, Spitzer, & Pekrun, 2011), including a bias for angry or threatening facial expressions (e.g., E. Fox, Lester, Russo, Bowles, Pichler, & Dutton, 2000; Hansen & Hansen, 1988). The notion that a cognitive bias for threat may be universal and adaptive does not imply that this bias is hardwired or that experience is irrelevant to its development. Bias for threatening faces is not present at birth; human newborns display a preference for looking at happy faces (Farroni, Menon, Rigato, & Johnson, 2007), and vigilance for threat emerges between

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the first 6 and 12 months of age (e.g., Grossman, Striano, & Friederici, 2007; Schupp et al., 2004). Additionally, experience affects bias for negatively valenced facial expressions; 7-month-olds of depressed mothers displayed weaker vigilance for fearful expressions than did infants of the same age raised by nondepressed mothers (de Haan, Belsky, Reid, Volein, & Johnson, 2004), and maltreated children exhibited greater attention to and vigilance for angry faces and voices than did nonmaltreated children (Shackman, Shackman, & Pollak, 2007). However, the way in which early experience affects the development of bias to threat in nonclinical populations remains underinvestigated. Research into experience-dependent aspects of this bias is essential because exacerbated attention to threat and difficulty disengaging from aversive stimuli have been implicated in the etiology of anxiety disorders (Bar-Haim, Lamy, Pergamin, Bakermans-Kranenburg, & van IJzendoorn, 2007), which often emerge early in life (for a review, see Pine, Cohen, Gurley, Brook, & Ma, 1998).

The study of nonhuman primates could contribute to an understanding of the role of experience in the acquisition and expression of biases to social threat. Nonhuman primates, in particular rhesus macaques, are socially and cognitively similar to humans (Frith & Frith, 2007) and are frequently used as a model species for research into the neurobiological mechanisms underpinning cognitive phenomena (e.g., Watson & Platt, 2012), especially the study of anxiety and emotion regulation (Kalin & Shelton, 2003). Rhesus macaques possess several distinct threatening (open mouth), fearful and submissive (fear grimace), and affiliative (lip smack) facial expressions (Maestripieri & Wallen, 1997), and adult rhesus monkeys display attentional bias to threatening faces (Bethell, Holmes, MacLarnon, & Semple, 2012). Whether bias to threat is already present in infancy and to what extent it is influenced by experience is unknown in nonhuman primates. As the mechanisms underlying the effects of experience on bias to threat remain ambiguous (e.g., N. A. Fox, Henderson, Marshall, Nichols, & Ghera, 2005; Strang, Hanson, & Pollak, 2012), an understanding of how experience affects attention and vigilance to threat in rhesus infants could potentially enhance the understanding of these mechanisms in human and nonhuman primates.

The 1st year of life has the highest risk of mortality in primates (Gage & Dyke, 1988), and rhesus monkey infants are vulnerable to social threats (e.g., aggression or kidnapping from other group members; Maestripieri, 1993). As higher levels of anxiety early in life may protect newly mobile individuals from dangerous situations (e.g., Blackford & Pine, 2012), it may be hypothesized that a bias for threatening faces should appear early and be well established by the time infants have become

independent from their mothers (LoBue, Rakison, & DeLoache, 2010; Vaish, Grossman, & Woodward, 2008). However, interindividual variation in the extent to which infants are at risk from conspecifics and in exposure to social threats could lead to individual differences in the strength of bias to threatening faces, which in turn might contribute to variation in the development of anxiety disorders (e.g., Bar-Haim et al., 2007).

Variation in risk and early social experience may depend on the infant's mother. Rhesus mothers directly control their infants' social experiences through their protective or permissive parenting style, which parallels variation in human parenting styles (Maestripieri, 1999). Infant macaques that are restrained or retrieved by protective mothers spend less time interacting with other macaques and are less likely to come near dangerous conspecifics (Maestripieri, 1995, 2001). The dominance rank of rhesus mothers also influences the infant's social experience; infants of high-ranking mothers receive more attention from conspecifics but mainly have affiliative interactions, whereas infants of low-ranking mothers may receive less attention from conspecifics overall but are more likely to be threatened or attacked (Maestripieri, 2001). Thus, the mother's parenting style and her dominance rank might affect individual differences in the strength of attention and vigilance to threatening faces. This hypothesis is consistent with previously demonstrated maternal influences on infant exploration, reactivity to novelty, and social behavior, as well as with maternal influences on the development of neurobiological substrates involved in emotion regulation (for a review, see Maestripieri, Hoffman, Anderson, Carter, & Higley, 2009).

Here, we present the first data on the development of cognitive bias to threat in rhesus macaque infants and the effects of early experience on expression of this bias. We investigated the presence or absence of cognitive bias for threatening faces in 3- and 9-month-olds in a free-ranging population of rhesus macaques. Additionally, we investigated whether bias manifests itself during initial attention capture (in which infants display attention to threat) or during maintenance of attention (in which infants display vigilance for threat), as variation in early life experience has been shown to affect both components of cognitive bias to threat in different ways: specifically, the perception of stimuli during attention capture versus the processing of stimuli when attention is maintained (Bar-Haim et al., 2007). We predicted that infants would show evidence of both components of bias to threat within the 1st year of life, in line with evidence from human infants, and that individual differences in the strength of this bias may be accounted for by variation in maternal characteristics and an infant's opportunities for social experience. Specifically, we tested the prediction that infants whose mothers are lower ranking or

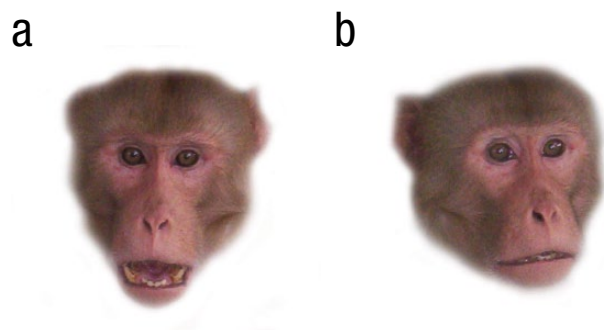


Fig. 1. One of the seven stimulus sets used in the study: an unfamiliar adult male macaque displaying (a) a threatening face and (b) a neutral face.

have a less protective parenting style should display a stronger bias for threatening faces, as they are at higher risk for aggression than other infants.

Method

Study site and subjects

This study was undertaken on Cayo Santiago, a 15.2-hectare island located 1 km off the east coast of Puerto Rico (Rawlins & Kessler, 1986). The Cayo Santiago colony contains approximately 1,000 free-ranging rhesus monkeys (*Macaca mulatta*). Macaques on Cayo Santiago are provided with monkey chow, but they also forage on indigenous vegetation and have sufficient rainwater for drinking. Macaques on Cayo Santiago live in one of nine naturally formed social groups (e.g., Groups R, S, KK, F). Rhesus macaques are seasonal breeders, with the population on Cayo Santiago currently mating during a 6-month window between February and July; the majority of births occur between August and October (Caribbean Primate Research Center, 2013).

Cognitive data were collected on two cohorts of subjects: Cohort 1 consisted of forty-five 3-month-olds (mean age = 15.0 weeks, $SEM = 0.30$) in Groups R, S, and KK born during the 2013 birth season, and Cohort 2 consisted of forty-six 9-month-olds (mean age = 36.8 weeks, $SEM = 0.36$) in Groups R and S born during the 2011 birth season. Subjects were selected based on birth order—each cohort comprised the first 45 (Cohort 1) or 46 (Cohort 2) infants born in the respective birth season. All methods were approved by the Institutional Animal Care and Use Committee at both the University of Puerto Rico and the University of Chicago.

Cognitive-data collection

All infants were tested for cognitive bias to threat using a looking-time paradigm, a commonly used method in

studies of non- and preverbal populations (Spelke, 1985). Individuals were simultaneously shown two previously validated stimuli (Bethell et al., 2012), a threatening face (a photograph of an unfamiliar adult male macaque displaying an open-mouth threatening expression; Fig. 1a) and a neutral face (a photograph of the same male with a non-emotional expression; Fig. 1b). Stimuli were color photographs (8.25 in. long \times 11.75 in. high) presented on a piece of cardboard measuring 48.25 \times 12 in. on which the two photographs were set 32 in. apart. Seven sets of stimuli were used, with one set chosen at random for each individual. Stimuli were covered at the onset of each trial.

A trial was initiated by setting up the cardboard display less than 2.5 m in front of a subject, who was approached while sitting calmly and apart from the group whenever possible. The cameraperson, standing directly behind the presenter and using a handheld camcorder (Canon FS20), started to record as soon as the display was set up and the presenter captured the attention of the subject by tapping the covers on the stimuli. Once the subject had gazed at both right and left covers, the presenter redirected the infant's gaze below the presenter (in the middle of the two stimuli) and then removed the covers to simultaneously expose both stimuli. Infant eye gaze was videotaped for 5 s following stimuli exposure, as previous experiments have demonstrated that the majority of looking behavior occurs in the first few seconds following stimulus exposure (E. Bethell, personal communication, May 10, 2011). During the trial, the presenter and the cameraperson wore visors to cover their eyes and looked toward the ground between the two stimuli to avoid cuing the subject. The locations of the stimuli (e.g., threatening on the left, neutral on the right) were counterbalanced across subjects.

Cognitive-test-video coding

Observers blind to the purpose of the experiment coded video data frame by frame (frame rate = 30 frames per second) using JWatcher software (Blumstein, Evans, & Daniel, 2000). Videos were edited in VideoPad Video Editor (NCH Software, Greenwood Village, CO) so that they began at the onset of the trial and were exactly 5 s in duration. The number of frames during which each infant looked at the threatening and the neutral stimuli were quantified separately. Each video was coded for four primary variables, the looking times at the (a) threatening stimulus during the 1st second, (b) neutral stimulus during the 1st second, (c) threatening stimulus over all 5 s, and (d) neutral stimulus over all 5 s. Two additional variables were created to quantify detection (attention to threat) and attention maintenance (vigilance for threat).

To quantify attention to threat, we subtracted the time spent looking at the neutral stimulus from the time spent

looking at the threatening stimulus during the 1st second following stimulus exposure. To quantify vigilance for threat, we calculated the difference between the looking times at threatening and neutral stimuli over all 5 s. For both variables, a positive value indicated more time spent looking at the threatening stimulus, and a negative value indicated more time spent looking at the neutral stimulus. All videos were coded by an additional coder who was blind to the purpose of the experiment; interobserver reliability for direction of gaze was high (Cohen's $\kappa = .82$). Inconsistencies between observers' codes were resolved through discussion. Following all video coding, the location of each stimulus (threatening on the left and neutral on the right or vice versa) was incorporated into the data set.

Behavioral-data collection

Behavioral data on early life experiences were collected from Cohort 2 only. Across the first 12 weeks of life, these 46 infants were observed for two 30-min periods each week using continuous focal animal sampling (i.e., observing an individual and recording all behaviors and interactions during a set time period; Altmann, 1974). Each session started between 7:00 a.m. and 2:30 p.m., and each week's observations could occur during any 5-day period. Infants were observed using a handheld video camera (Kodak PlaySport Z3). The order in which focal animals were observed was randomized. Videos were coded in Microsoft Excel using an automatic time-stamp function that allowed for measurement of the duration and frequency of each type of behavior, and the number of event behaviors per hour was calculated in Microsoft Access for analysis. Our data set contained 542.5 hr of observational data over the 12-week period (mean per infant = 11.8 hr, $SEM = 0.05$, range = 10.5–12). Observers began behavioral data coding only when interobserver reliability reached Cohen's $\kappa = .90$, as determined by tests of agreement on individual occurrences of maternal interactions (e.g., Caro, Roper, Young, & Dank, 1979).

Female dominance ranks on Cayo Santiago are maternally inherited; these ranks are recorded in a database maintained by the Caribbean Primate Research Center. We collected additional data on the outcome of dyadic agonistic interactions between mothers in Cohort 2 to determine group- and sex-specific dominance hierarchies to control for rank effects in our statistical analyses. These dyadic interaction data were placed into a winner-loser matrix in which each individual animal was represented on both axes, and all winner-loser interactions between each dyad were indicated by a number in each square of the matrix. MatMan (de Vries, Netto, & Hanegraff, 1993) was used to analyze this matrix to generate stable, significant, linear dominance hierarchies,

which were then assessed using Landau's linearity index corrected for unknown relationships (Group R: $p = .03$, Group S: $p = .03$). Combining MatMan data with matriline data, we categorized each female as high, middle, or low ranking, separately for each social group. To conduct analyses on the possible effect of rank, we placed infants in categories based on their mother's position in the dominance hierarchy.

To investigate whether maternal style early in life affects the development of bias to threat, we collected behavioral data on maternal protectiveness for Cohort 2 only. Maternal protectiveness was quantified as the summed rate of restraint (i.e., incidents in which the mother prevented her infant from breaking contact by holding its arm, leg, or tail) and retrieval (i.e., incidents in which the mother retrieved her infant from another individual or retrieved the infant when it was alone and more than 1 meter from the mother). Hourly rates of each behavior were calculated for all observations and then averaged separately across the first 12 weeks of each infant's life to determine a mean frequency of protectiveness. Mean maternal protectiveness for each mother-infant dyad was log transformed to minimize the effect of outliers.

Results¹

To determine whether 3- and 9-month-olds displayed a bias to threat during attention capture (the 1st second following stimulus exposure) or maintenance (all 5 s following stimulus exposure), we analyzed looking-time data using Wilcoxon signed-rank tests comparing looking time at the threatening stimulus with looking time at the neutral stimulus during the 1st second and overall. Three-month-olds (Cohort 1) did not display a significant bias for threat: They failed to discriminate between the threatening and neutral faces during either attention capture ($Z = 0.529$, $p = .597$, $r = .079$) or maintenance ($Z = 0.817$, $p = .414$, $r = .122$). Nine-month-olds also did not display a significant bias for threat during attention capture ($Z = 1.016$, $p = .310$, $r = .163$); however, they did exhibit vigilance for threat, spending significantly more time throughout each trial looking at the threatening face ($M = 1,804.5$ ms, $SEM = 166.4$, 95% confidence interval, or $CI = [1,469.8, 2,139.1]$) than at the neutral face ($M = 1,305.8$ ms, $SEM = 140.8$, 95% $CI = [1,022.2, 1,589.5]$; $Z = 2.207$, $p = .027$, $r = .325$; Fig. 2).

A general linear model was used to explore the effect of test parameters (i.e., which of the seven stimulus sets were used and whether the threatening or the neutral stimulus was looked at first) on the six looking-time variables (looking time at the threatening and the neutral stimulus separately during the 1st second and overall, as well as the attention-to-threat and vigilance-to-threat

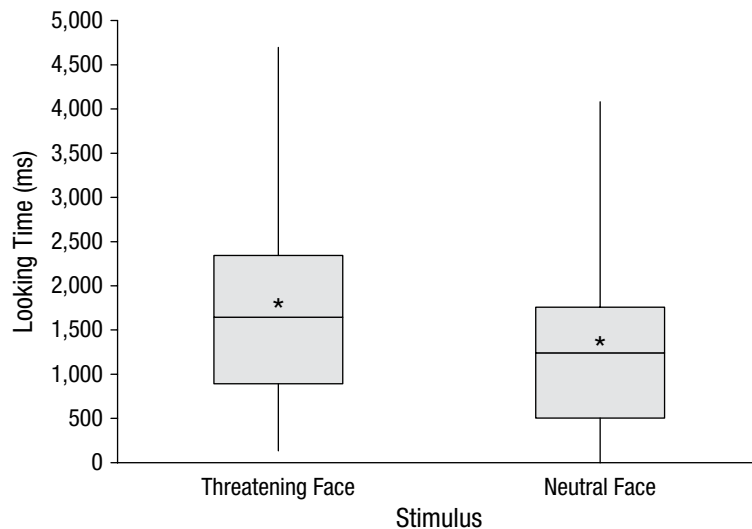


Fig. 2. Box-and-whisker plots showing mean looking time at each stimulus type in 9-month-olds. The asterisk denotes the mean, the gray box denotes the interquartile range and median, and the solid line denotes the range.

constructs). In the 1st second of testing (attention-capture period), both 3- and 9-month-olds paid more attention to whichever stimulus they happened to look at first, regardless of the nature of the stimulus. Three-month-olds exhibited increased attention to the threatening stimulus in the 1st second when they looked first at the threatening face, $F(1, 36) = 4.80, p = .035, R^2 = .11$, but increased attention to the neutral stimulus when they looked first at the neutral face, $F(1, 36) = 5.53, p = .024, R^2 = .13$. Nine-month-olds displayed the same pattern, paying increased attention to the threatening stimulus in the 1st second when the first look was to the threatening face, $F(1, 38) = 4.41, p = .042, R^2 = .07$, and paying increased attention to the neutral stimulus when the first look was to the neutral face, $F(1, 38) = 4.37, p = .043, R^2 = .07$ (Table 1). In contrast, vigilance for threat across the full 5 s was not affected by the stimulus first looked at in either age group (both $ps > .05$).

Although there was no significant relationship between attention to threat and maternal rank or maternal protectiveness (both $ps > .05$), there was a significant effect of social-experiential variables on vigilance for threat only in 9-month-olds. All subsequent analyses were therefore conducted on Cohort 2 only. A linear mixed model (LMM) was used to determine the effect of infant sex, group membership, and maternal rank on attention to threat and vigilance for threat, while controlling for any effects of test parameters. Only maternal rank was found to have a significant effect on either attention to threat or vigilance for threat; therefore, it was also incorporated in the final model as a random factor to control for its effects.

We then used an LMM to analyze the effects of maternal protectiveness, while controlling for maternal rank and test parameters, to assess the effects of early-life mother-infant interactions on attention to threat and vigilance for threat. Among these older infants, the offspring

Table 1. Attention-Capture Looking Times (in Milliseconds) for 3- and 9-Month-Olds

Stimulus looked at first	3-month-olds				9-month-olds			
	Threatening stimulus		Neutral stimulus		Threatening stimulus		Neutral stimulus	
	<i>M</i>	95% CI	<i>M</i>	95% CI	<i>M</i>	95% CI	<i>M</i>	95% CI
Threatening stimulus	557.6 (75.4)	[401.2, 714.0]	306.1 (84.2)	[130.5, 481.7]	558.7 (53.4)	[448.5, 668.8]	407.0 (64.0)	[273.5, 540.6]
Neutral stimulus	357.9 (78.0)	[196.6, 519.6]	634.8 (83.7)	[460.3, 809.3]	350.4 (49.9)	[247.3, 453.5]	492.5 (67.4)	[351.9, 633.1]

Note: Attention-capture looking time refers to looking time toward the stimulus viewed during the 1st second of a trial. Standard errors of the mean are given in parentheses. CI = confidence interval.

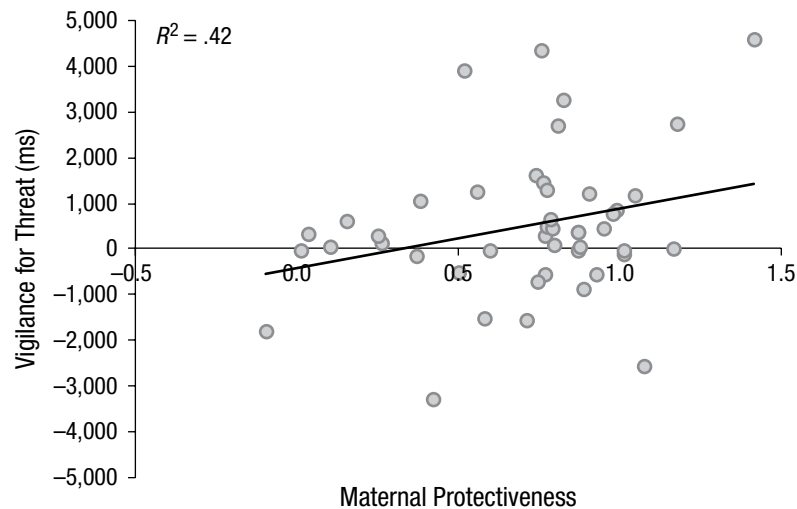


Fig. 3. Scatter plot (with best-fitting regression line) showing the relationship between vigilance for threat and log-transformed hourly rate of maternal protectiveness. Vigilance for threat was calculated by subtracting looking time at the neutral stimulus from looking time at the threatening stimulus across all 5 s of each trial.

of mothers who were more protective, $F(1, 41.8) = 5.988$, $p = .019$, $R^2 = .42$ (Fig. 3), or were higher ranking, $F(2, 36.5) = 3.42$, $p = .043$, $R^2 = .29$ (Fig. 4, Table 2), showed heightened vigilance for threat (maternal rank and protectiveness were not significantly correlated; Kruskal-Wallis test, $p > .05$). There were no rank-based differences in time spent looking at the threatening stimulus during the attention-capture period ($p > .05$; Fig. 4, Table 2) or in the attention-to-threat variable ($p > .05$; Fig. 5, Table 3).

Taken together, these results indicate that significant individual differences in looking behavior among older infants emerged after attention capture and that social-experiential variables affected the maintenance of attention toward threatening stimuli rather than initial detection of threat. Consistent with this, our results showed that infants of high-ranking mothers looked significantly more at the threatening stimulus than did infants of middle- or low-ranking mothers in the 4 s following attention capture (Kruskal-Wallis test: $Z = 2.207$, $p = .027$, $r = .325$; Fig. 5, Table 3). There was a difference in the expected direction when examining the relationship between maternal protectiveness and looking behavior after attention capture, but it failed to reach significance ($p > .05$).

Discussion

Our study documented the early development of cognitive bias to threat for the first time in a nonhuman species, the rhesus macaque. Three-month-old rhesus

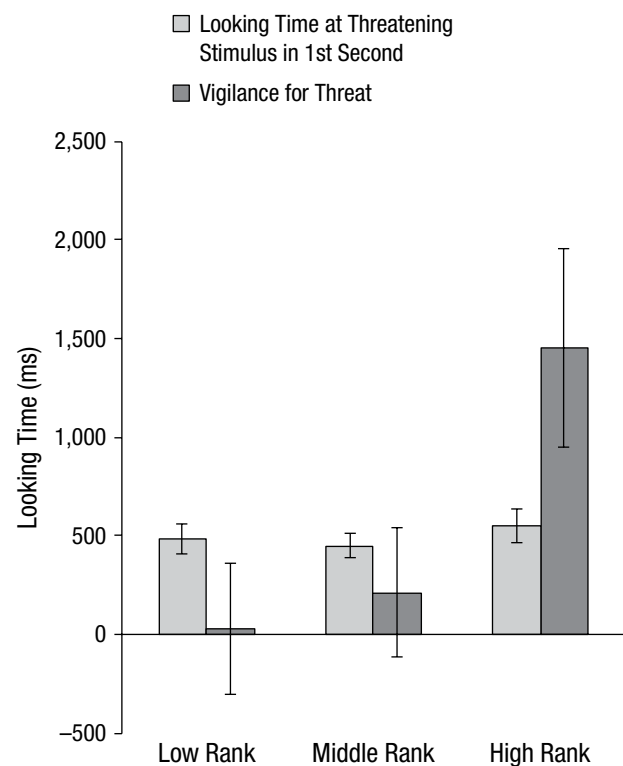


Fig. 4. Mean infant looking time in the 9-month-old group as a function of mother's dominance rank, separately for the threatening stimulus during the 1st second of a trial and for the vigilance-for-threat variable. Vigilance for threat was calculated by subtracting looking time at the neutral stimulus from looking time at the threatening stimulus across all 5 s of each trial. Error bars show standard errors of the mean.

Table 2. Mean Looking Time at the Threatening Stimulus (in Milliseconds) During the 1st Second and Vigilance for Threat for 9-Month-Olds of Mothers of Each Rank

Maternal rank	1st second of trial		Vigilance for threat	
	<i>M</i>	95% CI	<i>M</i>	95% CI
Low	480.8 (78.2)	[327.5, 634.1]	28.9 (335.1)	[-627.9, 685.7]
Middle	449.8 (64.7)	[323.0, 576.6]	209.8 (327.0)	[-431.1, 850.7]
High	551.9 (86.5)	[382.4, 721.4]	1,454.5 (501.0)	[472.5, 2,436.5]

Note: Vigilance for threat was calculated by subtracting looking time at the neutral stimulus from looking time at the threatening stimulus across all 5 s of each trial. Standard errors of the mean are given in parentheses. CI = confidence interval.

monkeys did not show evidence of vigilance for threat, but 9-month-olds did. In the latter sample, both maternal rank and the frequency of maternal protectiveness in the first 12 weeks of life affected the expression of vigilance for threat. Infants raised by high-ranking mothers or by protective mothers displayed stronger vigilance for threat than infants raised by lower ranking mothers or by less protective mothers.

Cognitive bias to threat in 9-month-olds was not the result of preferential attention capture by the threatening stimulus; there was no significant attention to threat in 3- or 9-month-olds, and no significant effect of experience

on attention to threat in 9-month-olds. In the 1st second of testing, both 3- and 9-month-olds paid more attention to the stimulus they happened to look at first, which suggests that infants find it difficult to disengage quickly from social stimuli regardless of their emotional content (e.g., Amir, Elias, Klumpp, & Przeworski, 2003).

After the 1st second of a trial, 9-month-olds of high-ranking or protective mothers continued to look at the threatening stimulus more than at the neutral stimulus for the duration of the test, whereas infants of lower ranking or less protective mothers looked at the threatening stimulus less frequently. Both the overall bias for threat and the effects of socio-experiential variables emerged during attention maintenance (i.e., the period in which infants exhibited vigilance for threat).

These results suggest that both direct and indirect maternal regulation of the infant's social environment (as expressed by the mother's protectiveness and her rank) are important to the development of cognitive bias to threat, possibly by altering infant exposure to threatening or dangerous interactions. However, these effects were opposite to what we predicted. We expected that a higher probability of exposure to threats early in life would lead to a stronger bias for threat, but found instead that threat bias was stronger in infants who were less likely to be exposed to threats.

There are several nonmutually exclusive explanations for how low exposure of infants to threatening situations could result in increased vigilance for threat. First, it is possible that infants who display increased vigilance for threat do so because the threatening stimulus is novel and salient, as a result of these infants having been less exposed to threatening faces during development than low-ranked or less protected infants. Second, if these same infants receive less aggression from other individuals, their social expectations are positively skewed, subsequent negativity is unexpected, and they may display increased attention to threat (e.g., as predicted by range-frequency theory; Vaish et al., 2008). Third, lower ranked and less maternally protected infants exposed to more threatening stimuli early in life learn to avoid such stimuli

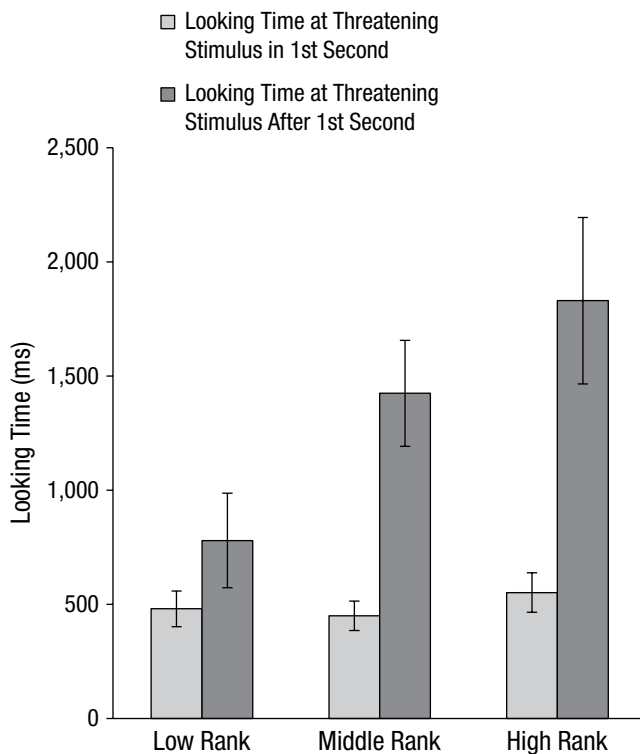


Fig. 5. Mean time infants in the 9-month-old group looked at the threatening stimulus as a function of mother's dominance rank, separately for the 1st second of a trial and the remaining 4 s. Error bars show standard errors of the mean.

Table 3. Mean Looking Time at the Threatening Stimulus (in Milliseconds) for 9-Month-Olds of Mothers of Each Rank

Maternal rank	1st second of trial		Remaining 4 s of trial	
	<i>M</i>	95% CI	<i>M</i>	95% CI
Low	480.8 (78.2)	[327.5, 634.1]	779.8 (206.8)	[374.5, 1,185.1]
Middle	449.8 (64.7)	[323.0, 576.6]	1,424.7 (232.1)	[969.8, 1,879.6]
High	551.9 (86.5)	[382.4, 721.4]	1,830.2 (364.6)	[1,150.9, 2,509.5]

Note: Standard errors of the mean are given in parentheses. CI = confidence interval.

to diminish the effects of an aversive environment (for evidence in humans, see Stirling, Eley, & Clark, 2006).

Finally, although our study was not designed to assess genetic influences on behavior, it is possible that variation in infant experience and in the expression of bias to threat may have a genetic basis. In rhesus macaques, it has been shown that maternal genotype can affect maternal behavior. For example, abusive mothers tend to carry a different variant of the serotonin-linked polymorphic region (5-HTTLPR) allele than nonabusive mothers (McCormack, Newman, Higley, Maestriperi, & Sanchez, 2009). Infants who possess this same variant often demonstrate impaired emotion regulation and heightened anxiety, but only when exposed to early life adversity (e.g., McCormack et al., 2009; Spinelli et al., 2012). In humans, the serotonin transporter gene polymorphism has been linked to variation in temperament and anxiety (Lakatos et al., 2003), in attentional responses to positive and negative emotional expressions (Pérez-Edgar et al., 2010), and in threat detection (Miu, Vultur, Chis, & Ungureanu, 2012), which is consistent with the notion that this polymorphism alters an individual's sensitivity to his or her environment (e.g., Caspi, Hariri, Holmes, Uher, & Moffitt, 2010). Therefore, although our results are consistent with an explanation emphasizing the effects of early experience on the development of vigilance for threat, we cannot rule out the possibility that variation in vigilance for threat is primarily, or even solely, due to genetic factors (e.g., maternal genotype acting via maternal behavior or genetic similarities between mothers and infants leading to correlations between maternal characteristics and infant biases in vigilance for threat).

Further research on the development of bias to threat in monkeys could address the role of genetic factors (e.g., with data on maternal and infant genotype or with cross-fostering experiments) as well as further explore the importance of social experience in the development of this cognitive bias. Further work should also address how variation in the development of cognitive biases affects both typical and pathological cognitive and social development, and whether similar processes and outcomes occur in human and nonhuman primates.

Author Contributions

T. M. Mandalaywala developed the study concept and design, and carried out data collection, testing, coding, and data analysis under the supervision of D. Maestriperi. T. M. Mandalaywala, D. Maestriperi, and K. J. Parker drafted the manuscript and provided critical revisions. All authors approved the final version of the manuscript for submission.

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Declaration of Conflicting Interests

The authors declared that they had no conflicts of interest with respect to their authorship or the publication of this article.

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Note

1. Tests were two-tailed, with $p < .05$ considered significant, and all analyses were performed in SPSS Version 22.0.

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