

# Emotion-Cognition Interaction in Nonhuman Primates: Cognitive Avoidance of Negative Stimuli in Baboons (*Papio papio*)



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## Abstract

It is well established that emotion and cognition interact in humans, but such an interaction has not been extensively studied in nonhuman primates. We investigated whether emotional value can affect nonhuman primates' processing of stimuli that are only mentally represented, not visually available. In a short-term memory task, baboons memorized the location of two target squares of the same color, which were presented with a distractor of a different color. Through prior long-term conditioning, one of the two colors had acquired a negative valence. Subjects were slower and less accurate on the memory task when the targets were negative than when they were neutral. In contrast, subjects were faster and more accurate when the distractors were negative than when they were neutral. Some of these effects were modulated by individual differences in emotional disposition. Overall, the results reveal a pattern of cognitive avoidance of negative stimuli, and show that emotional value alters cognitive processing in baboons even when the stimuli are not physically present. This suggests that emotional influences on cognition are deeply rooted in evolutionary continuity.

## Keywords

avoidance, negative stimuli, emotion-cognition interaction, short-term memory, baboons, open data

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There are important interactions between emotion and cognition in humans. Most cognitive processes, from perception and attention to reasoning and decision making, have been shown to be affected by emotion, including the emotional value of stimuli (for an overview, see De Houwer & Hermans, 2010). Little is known about the evolutionary origins of this interaction and whether it is unique to humans. Though it has been established that negative stimuli that are perceptually available, such as images of snakes or angry expressions, affect primate behavior (e.g., Lacreuse, Schatz, Strazzullo, King, & Ready, 2013), it is not known whether the emotional value of mentally represented stimuli that are not physically present can modulate cognitive processing in nonhuman animals. In this article, we consider the answer to this question, which will generally

inform understanding of the evolutionary origins of cognition-emotion interactions.

The impact of emotional stimuli on cognition has been extensively documented in humans for a wide range of cognitive functions, notably attention and memory. For example, performance on a working memory task is better when the images to be maintained in memory are emotional (positive or negative), compared with when they are neutral (Linderstrom & Bohlin, 2011). In addition, when the color in which words or images are presented must be identified, emotional stimuli, including

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faces and other biologically relevant stimuli, can cause more interference than neutral stimuli, as indexed by longer reaction times (RTs). This phenomenon, termed the emotional Stroop effect, suggests that emotional stimuli capture attentional resources to a greater extent than neutral stimuli do (Yiend & Mathews, 2001).

There are indications that cognitive processes can be modulated by the emotional value of stimuli in nonhuman primates as well, at least when stimuli are visually available. For example, studies have shown that nonhuman primates are faster to detect threatening stimuli than neutral stimuli in a visual search task (Shibasaki & Kawai, 2009). Moreover, in a dot-probe task, rhesus monkeys detected targets presented in the same locations as preceding face stimuli more rapidly when the faces had been threatening, rather than neutral (Lacreuse et al., 2013). An analogue of the emotional Stroop effect has recently been demonstrated in chimpanzees (Allritz, Call, & Borkenau, 2015). In this study, two identical images were presented to subjects, who had to select one on the basis of the frame color. Subjects took longer to respond when the content of the images was negative than when it was neutral, which suggests that the level of attention allocated to processing the content of the images (which was irrelevant to the task) changed depending on their emotional value. The modulation of cognitive processes by emotion has also been confirmed using eye tracking (Bethell, Holmes, Maclarnon, & Semple, 2012). When shown a neutral and a threatening picture side by side, rhesus monkeys were faster to orient a first gaze toward the threatening picture. Together, these studies show that cognitive processing in nonhuman primates can be modulated by the emotional value of stimuli, at least when the stimuli are visually available.

It is not known whether the emotional value of mental representations, in the absence of the physical stimuli, can have an impact on cognitive processing in nonhuman primates. The answer to this question is important, as it would inform current understanding of the origin of emotion-cognition interaction. This is the issue we investigated in this study, focusing particularly on stimuli of negative valence.

Our hypotheses were based on the basic action tendencies evoked by stimuli of positive and negative valence. Positive stimuli evoke approach tendencies, and negative stimuli evoke avoidance tendencies (Rutherford & Lindell, 2011). This has been verified in overt behavioral responses to negative and positive stimuli both in humans (Maxwell & Davidson, 2007; Onal-Hartmann, Pauli, Ocklenburg, & Güntürkün, 2012; Solarz, 1960) and in nonhuman primates (Amemori & Graybiel, 2012; Lacreuse, Gore, Chang, & Kaplan, 2012; Machado, Kazama, & Bachevalier, 2009; Sinnott, Speaker, Powell, & Mosteller, 2012; Thompson, 1954). These results suggest

evolutionary continuity. A typical way of measuring approach and avoidance tendencies in nonhuman primates is to place an object in the cage along with a desired food reward (e.g., a grape). Avoidance is indicated by longer latencies to retrieve the coveted food reward or greater time spent at the back of the cage when the object with the food reward is a negative stimulus, rather than a positive stimulus. Avoidance has been shown for both stimuli that elicit innate fears (e.g., snakes) and conditioned negative stimuli (Lacreuse et al., 2012; Machado et al., 2009).

Previous experiments with nonhuman primates have demonstrated avoidance behaviors in response to emotional stimuli that were visually available. The main originality of our approach was to use a task requiring the processing of emotional stimuli stored in short-term memory. This allowed us to investigate whether cognitive operations performed on mental representations, rather than percepts, can be affected by the emotional valence of the stimuli. On each trial, two targets (squares of the same color) and a distractor (a single square of a different color) were briefly presented in three of four possible locations on a touch screen. Subjects had to maintain this representation in short-term memory and indicate the location of the two targets by touching the screen. To manipulate the emotional valence of the stimuli, we took advantage of naturally occurring long-term negative conditioning in the subject population. The troop of baboons included in this study had been participating in experimental studies of cognition for 6 years. In all of these experiments, correct responses were associated with a reward (dry wheat). Following incorrect responses, there was instead a 3-s timeout before the animal could proceed to the next trial. During this delay, a green square was displayed, occupying the majority of the screen. In the current study, we capitalized on this long-term conditioning and compared the cognitive processing of green (negatively valenced) and nongreen (neutral) stimuli in the short-term memory task.

We reasoned that if the emotional value of stimuli has an impact on cognitive processing, accuracy and RTs in the short-term memory task would differ according to whether the targets and distractors were negative or neutral. If the avoidance tendencies observed in overt behavior have a cognitive equivalent, subjects would tend to avoid processing negative stimuli. We therefore hypothesized that we would observe longer RTs and lower accuracy when targets were negative, compared with when they were neutral. In addition, we hypothesized that negative distractors would be associated with shorter RTs and higher accuracy, compared with neutral distractors, because avoidance of these negative stimuli would result in less interference with target processing. These patterns of results would be consistent with cognitive avoidance of mentally represented negative stimuli.

Inherent to our manipulation of emotional valence is the fact that color conditioning could not be counterbalanced. The negative stimuli were always green. Because this conditioning had occurred over a number of years, we could not easily condition another color to acquire a negative valence. Consequently, it would be difficult to unequivocally ascribe effects to the negative value of the color, rather than idiosyncratic features of processing the color green. To eliminate this possible ambiguity, we examined whether the effects of valence were related to individual differences in emotional traits, which is often the case in humans (Bar-Haim, Lamy, Pergamin, Bakermans-Kranenburg, & van IJzendoorn, 2007). We inferred emotional traits from the proportions of negative and positive social behaviors expressed by the individual baboons. To do this, we used an ethological screening technique previously used with the same troop (Marzouki, Gullstrand, Goujon, & Fagot, 2014) to identify naturally occurring positive and negative behaviors. This allowed us to assess individual differences in the proportion of negative behaviors expressed. If emotional valence resulting from the history of conditioning was the dimension that affected cognitive processing, this effect would be modulated by individual differences in negative emotional traits. These individual differences would not modulate the effect, however, if it arose from idiosyncratic features of the color green. Thus, we used differences in negative emotional traits to make sure that the observed effects were related to the emotional valence of the stimuli.

## Method

### Subjects

A total of 5 male and 9 female guinea baboons (*Papio papio*) at the CNRS Primate Center of Rousset-sur-Arc were tested in this study. They belong to a social group of 24 individuals living in a 25-m  $\times$  30-m outdoor enclosure connected to a 6-m  $\times$  4-m indoor enclosure. At the time of this experiment, these subjects had had several years of exposure to computerized testing procedures involving touch screens, including procedures focusing on same/different relations among items (e.g., Fagot & Thompson, 2011), but had never been tested with the current procedure. This research followed national guidelines for animal care and was approved by the Comité d'Éthique CE14 pour l'Expérimentation Animale.

### Equipment and materials

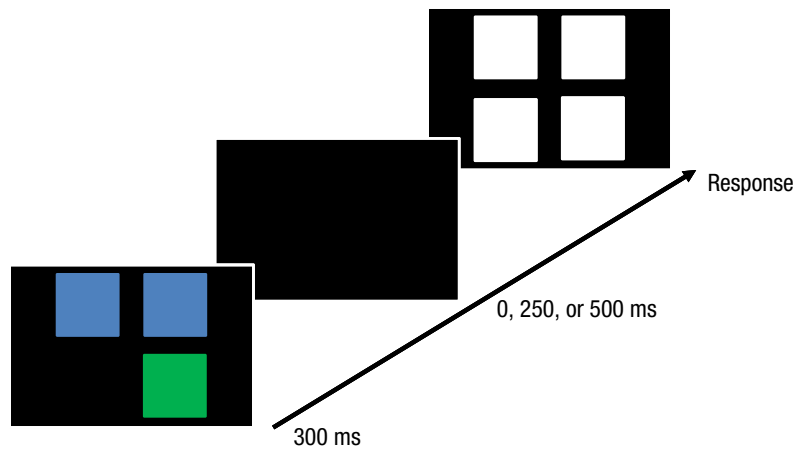
The experimental task was presented using 10 automatic learning devices (see Fagot & Bonté, 2010; Fagot & Paleressompoulle, 2009; and the Supplemental Material

available online), which were freely accessible from the baboons' enclosures. An automated radio-frequency procedure identified the subjects when they were within the automatic learning devices, so we could test the individuals without capturing them (i.e., when they reentered a device, the task resumed at the point where they had left it on the previous occasion). Each test system comprised a 19-in. touch screen and a food dispenser that delivered dry wheat when a correct response was given.

### Procedure and stimuli

**The cognitive task.** We manipulated both the valence of the targets and distractors, via their color, and the delay between their presentation and the response screen, to see if the effect of valence would attenuate with increasing delay. The trial procedure is illustrated in Figure 1. Each trial began with a display of three squares (350  $\times$  350 pixels) on a black background; each square was randomly located in the center of one of the screen quadrants. Two squares (targets) were the same color, and one (distractor) had a different color. After 300 ms, this first display was replaced by a black screen lasting 0 ms, 250 ms, or 500 ms. The black screen was followed by the response display, which contained four white squares (350  $\times$  350 pixels), one in the center of each screen quadrant. We selected the presentation time for the initial display on the basis of the durations used in previous studies (Claidière, Kirby, Smith, & Fagot, 2014; Pope, Meguerditchian, Hopkins, & Fagot, 2015). To be sure that we would be able to observe an effect of emotion on representations in short-term memory, we were careful that our longest delay interval was in the range within which baboons have been shown to retain and recall information (Sakurai, 2001). The task was to touch the two white squares in the response display that were located where the two squares of the same color had been presented in the first display. Note an important feature of our design: The target stimuli had disappeared from the screen when the choice array was presented. Correct responses therefore required that subjects maintain representations of targets (and distractors) in short-term memory. A correct response was rewarded with food, and an incorrect response gave rise to a 3-s time-out during which the screen turned green. Touching the screen during the first display or the delay period aborted the trial.

The experiment was organized in sessions of 120 randomly ordered test trials. Three colors were used during the test. In 96 trials (80%) of each session, the targets were blue. In 12 (10%) trials, the targets were pink, and in the remaining 12 (10%) trials, the targets were green. The distractor in each trial was equally likely to be either of the two colors not used for the targets. Note that the blue and pink colors had been commonly used



**Fig. 1.** Timeline of the trial procedure. The initial display consisted of two squares of the same color (targets) and a square of a different color (distractor). Following a blank screen of varying duration, the task was to touch the two white squares corresponding to the locations of the targets.

in previous experiments, and the green color had been systematically used for the 3-s time-out screen following an erroneous response. We computed that the baboons had been previously exposed to 144,520 green time-out screens on average (range: 45,619–211,502) during their experimental history. Thus, we confidently concluded that the baboons had been conditioned to have a negative emotional response to this color, as a consequence of its past systematic association with the absence of reward.

Prior to testing, the baboons completed three training phases, during which the number of items in the stimulus display increased. In the first training phase, only one stimulus was displayed on the screen in each trial. In the second training phase, two identical stimuli were displayed in each trial, and in the third training phase, two identical stimuli plus one distractor were displayed. In the first phase, subjects were rewarded if they touched the correct location where the single stimulus had been presented. In the latter two phases, touching the two identical items was required to obtain a reward. The three colors were presented in a balanced design during training, in 96-trial sessions (32 trials per target color). A 250-ms delay was used during training. For each phase, the block of 96 trials was repeated, with a random ordering of the trials in each block, until a subject responded correctly in at least 80% of the trials within a session. The training was available to the entire troop of 24 baboons during 1 month, but 10 did not participate in the training or failed to learn the task to criterion. The 10 subjects who did not complete the training and the 14 who did and consequently proceeded to the testing did not differ on any important features (see the Supplemental Material for a breakdown by sex and age). Learning speed varied

among the subjects. Training to criterion required 67 sessions on average ( $SD = 29.41$ ). The 14 baboons who were tested received a total of 364,418 test trials ( $M = 26,030$ ,  $SD = 15,350$ ).

**Behavioral coding.** Behavioral observations were conducted during the test period within the baboons' living enclosure. Four trained observers recorded the behavior of the group during repeated 2-hr periods using a scan-sampling method (Altmann, 1974; Marzouki et al., 2014) and coded the number of positively and negatively valenced behaviors spontaneously expressed by each subject (see the Supplemental Material for a list and description of the recorded behaviors). For each baboon, we computed the *behavioral negativity ratio* (BNR) as the sum of negative behaviors divided by the sum of positive behaviors. The higher this ratio was, the greater the baboon's tendency to exhibit a negative mood. We then submitted the BNRs of the 14 baboons to the *k*-means clustering technique and identified two groups of monkeys with different emotional dispositions (i.e., more negative vs. less negative).

### Data analysis

To test our hypotheses, we examined two primary dependent measures obtained from the cognitive task. The first was accuracy: whether the subject correctly pressed the two locations where the identically colored targets had been presented. The second was RT, which we operationalized as the time from the onset of the response display until the first location was pressed.

We present two main sets of analyses. In the first set, we compared performance (both accuracy and RTs) on

the trials featuring low-frequency negative (green) targets and the trials featuring low-frequency neutral (pink) targets, both presented with high-frequency neutral (blue) distractors. The second set of analyses examined accuracy and RTs for high-frequency neutral (blue) targets as a function of the valence of the low-frequency distractor (green vs. pink). Trials with RTs that were more than 2 *SD* from the mean were not included in any analyses.

We used mixed-effect models including delay condition, stimulus valence, and group as fixed factors (with reference levels of 250 ms, neutral valence, and more negative disposition, respectively) and subject as a random factor. Wald tests were used to determine whether the estimated regression parameters differed from 0 ( $\alpha = .05$ ). Given that accuracy was a binary outcome (accurate or inaccurate), we used binomial generalized linear mixed models with a logit link function to analyze the accuracy results. The results from these analyses can be interpreted in terms of odds ratio, specifically, as the probability of an accurate response relative to the probability of an inaccurate response. Given that RTs were continuous, the coefficients from the RT analyses provide estimates of the amount of change in RT as a function of change in the predictor variables. These coefficients more specifically correspond to the difference in RT between each level of the variable and the reference condition, for the main effects of theoretical relevance (additional details concerning the results for all variables can be found in the Supplemental Material).

## Results

### ***Comparing the processing of negative and neutral targets***

We hypothesized that if there is a mental equivalent of behavioral avoidance, negative targets, compared with neutral targets, would be associated with decreased accuracy and longer RTs. Further, we expected that this effect would be modulated by individual differences in negative emotional traits. Figure 2 (left panels) presents average accuracy and average RT as a function of target valence (negative vs. neutral) and group (more negative vs. less negative emotional disposition).

Analysis of the accuracy data revealed a significant interaction between target valence and group, Wald  $\chi^2(1) = 47.18, p < .001$ . The effect of target valence was more pronounced for subjects with more negative emotional dispositions. For these subjects, a Wald test indicated that the odds of being accurate decreased by an estimated 46% when targets were negative compared with when they were neutral,  $\beta(\text{neutral}) - \beta(\text{negative}) = -0.62, SE = 0.08, z = -7.86, p < .001$ . In comparison, for subjects with less negative dispositions, the odds of being

accurate decreased by an estimated 29% when targets were negative compared with when they were neutral,  $\beta(\text{neutral}) - \beta(\text{negative}) = -0.34, SE = 0.06, z = -5.99, p < .001$ . Thus, both groups of subjects were less accurate when targets were negative, but this effect was more pronounced for subjects with more negative dispositions, as we predicted.

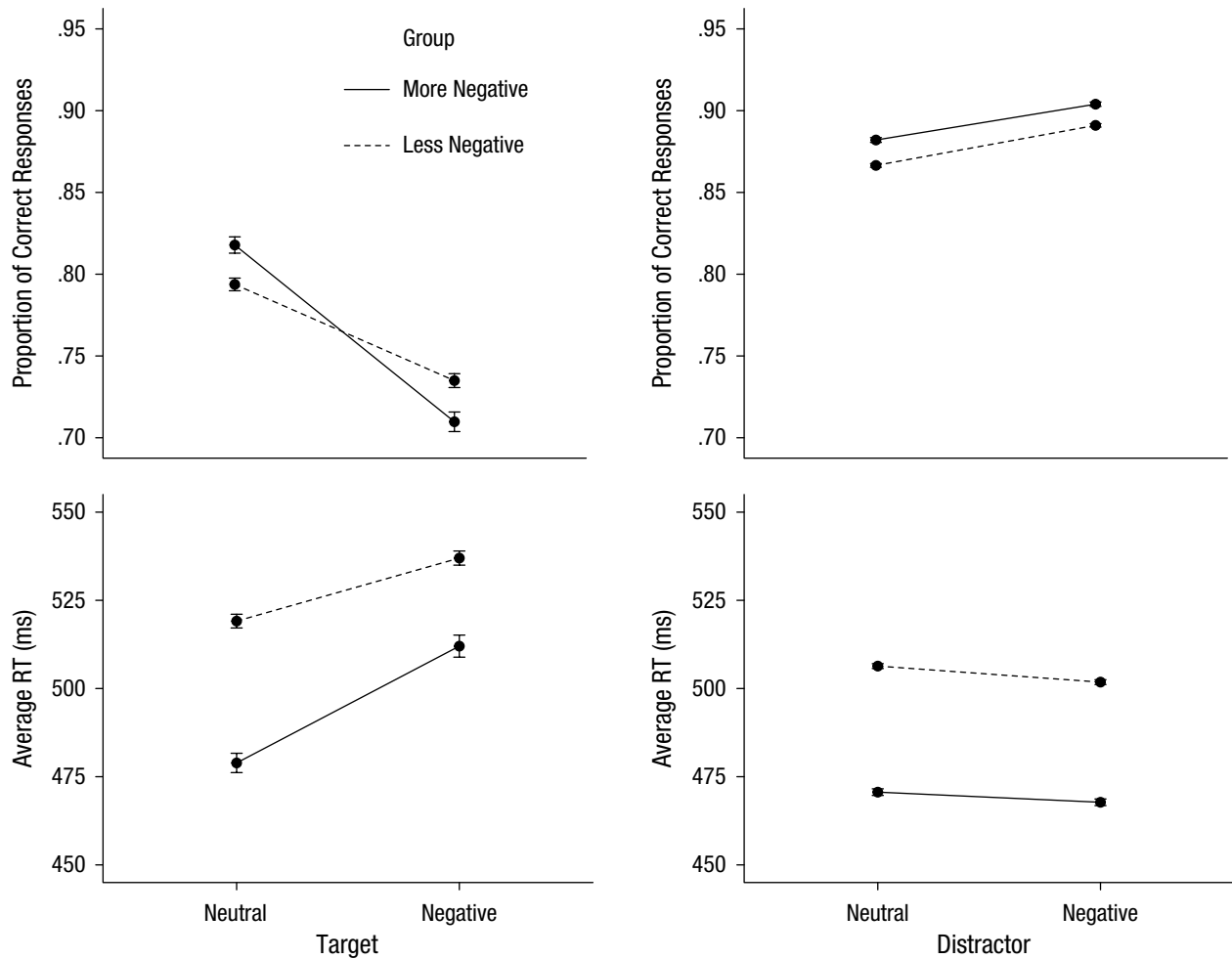
In addition to these effects, which were the most relevant to our hypotheses, the accuracy analysis revealed a main effect of delay condition, Wald  $\chi^2(2) = 119.62, p < .001$ , and an interaction between delay condition and group, Wald  $\chi^2(2) = 6.20, p < .05$  (see Table 1, top half). On average, accuracy improved with increased delays. (Because delay condition did not interact significantly with our main experimental factor, target valence, we reserve more detailed discussion regarding the effects of the delay manipulation to the Supplemental Material.)

Results for RTs also revealed a pattern consistent with our hypotheses (see Fig. 2). There was a significant interaction between target valence and group, Wald  $\chi^2(1) = 32.22, p < .001$ . For subjects with more negative dispositions, RTs were an estimated 36 ms longer when targets were negative compared with when they were neutral,  $\beta(\text{neutral}) - \beta(\text{negative}) = 35.7, SE = 5.5, t(33,616) = 6.52, p < .001$ . In comparison, for subjects with less negative dispositions, RTs increased by an estimated 22 ms when targets were negative compared with when they were neutral,  $\beta(\text{neutral}) - \beta(\text{negative}) = 21.5, SE = 4.0, t(33,616) = 5.37, p < .001$ . Thus, subjects in both groups were slower to provide responses on trials featuring negative, rather than neutral, targets, but this effect was more pronounced for subjects with more negative emotional dispositions, as we hypothesized.

In addition, delay condition had a main effect on RT, Wald  $\chi^2(2) = 14,700.54, p < .001$ , and interacted with group, Wald  $\chi^2(2) = 75.45, p < .001$  (see Table 1, top half). Overall, longer delays were associated with increased RTs. There was no reliable valence-by-delay interaction.

### ***Comparing the effects of negative and neutral distractors on target processing***

We predicted that cognitive avoidance of negative distractors would facilitate the processing of targets. Figure 2 (right panels) presents average accuracy and average RT as a function of distractor valence (negative vs. neutral) and group (more negative vs. less negative emotional disposition). The analysis of accuracy revealed a main effect of distractor valence, Wald  $\chi^2(1) = 374.07, p < .001$ , but no interaction with group, Wald  $\chi^2(1) = 0.01, p = .91$ . A Wald test revealed that for subjects with more negative tendencies, the odds of being accurate increased by an estimated



**Fig. 2.** Summary of the main results. Average accuracy and reaction time (RT) in the short-term memory task as a function of target or distractor valence (negative vs. neutral) and group (more vs. less negative emotional disposition). Note that an increase in accuracy and a decrease in RT both indicate better performance. Error bars represent  $\pm 1$  SEM.

19% when distractors were negative compared with when they were neutral,  $\beta(\text{neutral}) - \beta(\text{negative}) = 0.17$ ,  $SE = 0.04$ ,  $z = 4.55$ ,  $p < .001$ . For subjects with less negative tendencies, the odds of being accurate increased by an estimated 26% when distractors were negative compared with when they were neutral,  $\beta(\text{neutral}) - \beta(\text{negative}) = 0.23$ ,  $SE = 0.03$ ,  $z = 8.88$ ,  $p < .001$ . Thus, overall, the presence of negative distractors did facilitate accurate target processing, as we hypothesized.

On average, accuracy also improved with increasing delays, Wald  $\chi^2(2) = 401.36$ ,  $p < .001$  (see Table 1, bottom half). The effect of delay condition was modulated by group, Wald  $\chi^2(2) = 28.83$ ,  $p < .001$ , and by distractor valence, Wald  $\chi^2(2) = 7.72$ ,  $p < .05$ .

Distractor valence had a main effect on RT, Wald  $\chi^2(1) = 42.09$ ,  $p < .001$ ; subjects were faster to respond on trials with negative distractors than on trials with neutral distractors. A Wald test revealed that for subjects with

more negative dispositions, RTs were an estimated 1 ms shorter when distractors were negative compared with when they were neutral,  $\beta(\text{neutral}) - \beta(\text{negative}) = -1.20$ ,  $SE = 1.8$ ,  $t(274,017) = -0.66$ ,  $p = .51$ . For subjects with less negative tendencies, RTs were an estimated 4 ms shorter when distractors were negative compared with when they were neutral,  $\beta(\text{neutral}) - \beta(\text{negative}) = -4.06$ ,  $SE = 1.34$ ,  $t(274,017) = -3.03$ ,  $p < .05$ . These results are also consistent with our hypothesis that cognitive avoidance of negative distractors would facilitate target processing. There was no significant interaction between distractor valence and group, Wald  $\chi^2(1) = 1.34$ ,  $p = .25$ , and no main effect of group, Wald  $\chi^2(1) = 1.53$ ,  $p = .22$ .

RTs increased with increasing delays, Wald  $\chi^2(2) = 135,040.00$ ,  $p < .001$  (see Table 1, bottom half), and the effect of delay condition was modulated by group, Wald  $\chi^2(2) = 689.04$ ,  $p < .001$ . By contrast, delay condition did not interact with distractor valence.

**Table 1.** Accuracy and Reaction Times in the Three Delay Conditions, Separately for the Groups Expressing More Negative and Less Negative Emotional Dispositions

Group and delay condition	Reaction time (ms)		Accuracy	
	<i>M</i>	<i>SD</i>	<i>M</i>	<i>SD</i>
Negative and neutral targets (neutral distractors)				
More negative disposition				
0-ms delay	370	187	.73	.44
250-ms delay	456	192	.76	.43
500-ms delay	663	187	.80	.40
Less negative disposition				
0-ms delay	413	170	.73	.44
250-ms delay	499	180	.78	.42
500-ms delay	671	178	.79	.41
Negative and neutral distractors (neutral targets)				
More negative disposition				
0-ms delay	342	160	.87	.34
250-ms delay	426	158	.90	.29
500-ms delay	640	173	.90	.29
Less negative disposition				
0-ms delay	388	166	.86	.34
250-ms delay	474	173	.89	.32
500-ms delay	650	174	.88	.32

## Discussion

Our goal was to examine whether the emotional valence of mentally represented stimuli affects cognitive performance in baboons. In the task we used, subjects maintained representations of target and distractor stimuli in short-term memory. The emotional valence of these stimuli affected accuracy and RTs. When targets were negative, rather than neutral, the baboons were less accurate and slower to provide a response. When distractors were negative, rather than neutral, the baboons were more accurate and more rapid to respond. In short, relative to neutral stimuli, negative targets impaired performance and negative distractors improved performance. The fact that emotional valence had an impact on performance in a context in which the stimuli were not visually available but only mentally represented suggests a genuine emotion-cognition interaction.

The difference in processing negative and neutral targets was modulated by individual differences in emotional traits. Individuals who displayed a greater proportion of negative behaviors tended to show a greater effect of emotional value. This suggests that the effect of our valence manipulation did not result from idiosyncratic features of the color green, but rather was indeed related to the emotional valence the stimuli acquired through conditioning. The fact that the

interaction between stimulus valence and emotional disposition was significant for targets but not for distractors shows that cognitive avoidance had a greater impact when negative stimuli had to be processed to perform the task than when they were task irrelevant.

Negative targets and negative distractors did not lead to the same outcome. Thus, we can rule out the possibility that our results were due to a simple association between the color green and inhibition of behavioral response. The long-term conditioning these baboons had undergone included a 3-s time-out associated with the presentation of a green screen when incorrect responses occurred, along with the absence of a food reward. Simple behavioral conditioning could have led the baboons to merely inhibit or delay behavioral responses when the color green was presented. This would have meant slower responses whenever a green stimulus was presented or represented. Similarly, if negative stimuli had simply evoked a freezing response, an effect that has been documented in the primate literature (Bethell, Holmes, Maclarnon, & Semple, 2016), subjects would have been slower whenever a negative, rather than a neutral, stimulus was presented. This is not what we observed. The effects of negative stimuli differed depending on whether they were targets or distractors. Negative distractors actually sped up processing. Thus, our results are not consistent with conditioned inhibition of behavioral response or with a freezing reaction.

The differential effects of negative targets and negative distractors also allow us to rule out the possibility that the baboons' behavior was entirely driven by arousal. Negative stimuli could have increased arousal and thereby sped up RTs. If this were the case, however, subjects would have been faster to respond to negative than to neutral targets. This is not what we observed. Subjects were actually slower when targets were negative than when they were neutral. Thus, it is unlikely that the observed effects were simply due to arousal.

Prior research has shown that emotional valence can have an impact on cognitive processing in nonhuman primates when stimuli are visually available (Lacreuse et al., 2013; Shibasaki & Kawai, 2009). Our results add to this literature by showing that the emotional value of mentally represented stimuli can alter cognitive processing in nonhuman primates even when the stimuli are not perceptually available. Our results suggesting that negative information is avoided are consistent with a prior eye-tracking study that documented sustained avoidance of negative images in stressed rhesus macaques (Bethell et al., 2012).

Overall, the pattern of results we observed is consistent with avoidance. This suggests that the cognitive effects of negative stimuli are analogous to the behavioral avoidance they typically evoke. This parallel between cognitive

and behavioral effects is consistent with the idea that mental processes closely mirror overt behavior, as proposed by theories of embodied emotion (Niedenthal & Maringer, 2009; Winkielman, Niedenthal, & Oberman, 2008). Our results are also consistent with the idea that there is an important link between emotion and motion (Davidson, Jackson, & Kalin, 2000; Maxwell & Davidson, 2007).

To our knowledge, this study is the first to demonstrate an impact of emotional value on the cognitive processing of mentally represented stimuli in nonhuman primates. Our results suggest that negative stimuli are cognitively avoided, an effect that parallels the basic behavioral propensity to avoid negative stimuli. In general, the results of this study provide important evidence for the evolutionary continuity of emotion-cognition interactions.

### Action Editor

Steven W. Gangestad served as action editor for this article.

### Author Contributions

All the authors developed the experimental paradigm and formulated the hypotheses and the theoretical framework together. I. Blanchette was primarily responsible for writing the manuscript. N. Claidière had primary responsibility for the statistical analyses. All the authors reviewed and edited the manuscript.

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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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### Supplemental Material

Additional supporting information can be found at <http://pss.sagepub.com/content/by/supplemental-data>

### Open Practices



All data have been made publicly available via the Open Science Framework and can be accessed at <https://osf.io/9bsa7/>.

The complete Open Practices Disclosure for this article can be found at <http://pss.sagepub.com/content/by/supplemental-data>. This article has received the badge for Open Data. More information about the Open Practices badges can be found at <https://osf.io/tvyxz/wiki/1.%20View%20the%20Badges/> and <http://pss.sagepub.com/content/25/1/3.full>.

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