ABC 2025, 12(4):583-606
DOI: https://doi.org/10.26451/abc.12.04.07.2025

Animal Behavior and Cognition

A Comparative Perspective on Attentional Bias Toward Social Threat

Olivia T. Reilly[1,2,3,*] **and Sarah F. Brosnan**[1,2,4,5]

[1]Department of Psychology, Georgia State University, Atlanta, GA 30302 USA
[2]Language Research Center, Georgia State University, Atlanta, GA 30302 USA
[3]Department of Human Evolutionary Biology, Harvard University, Cambridge, MA 02138 USA
[4]Center for Behavioral Neuroscience, Georgia State University, Atlanta, GA 30302 USA
[5]Neuroscience Institute, Georgia State University, Atlanta, GA 30302 USA

*Corresponding author (Email: reillyoliviat@gmail.com)

Citation – Reilly, O. T., & Brosnan, S. F. (2025). A comparative perspective on attentional bias toward social threat. *Animal Behavior and Cognition, 12*(4), 583-606. https://doi.org/10.26451/abc.12.04.07.2025

Abstract – For group-living species, including humans and nonhuman primates, the ability to navigate social encounters and quickly process threats from others is a critical skill. Rapid detection of threatening stimuli, referred to as an attentional bias toward threat, is adaptive in that fast threat detection can lead to improved survival outcomes. Despite this fitness benefit, the evolutionary roots of attentional bias formation are not well understood, and attentional bias toward social threat is not well studied across the primate phylogeny, particularly across more phylogenetically distant species such as the platyrrhine primates. The present review proposes the use of a comparative perspective to explore the evolutionary origins of this bias, to determine how far back in the primate phylogeny attentional bias toward social threat may have emerged. We discuss the methods that have been used to study attentional bias in humans, and then focus on a popular method for measuring attentional bias in nonhuman primates, the dot probe task. Evidence suggests that humans are not unique in their propensity for showing an attentional bias toward socially threatening stimuli when evaluated with a dot probe task, but there are some nonhuman primate species in need of further study to clarify their susceptibility to this bias. We suggest that the prevalence of attentional bias toward social threat in nonhuman primates can be understood in the context of their respective socioecologies and conclude by discussing future directions that can be taken to explore attentional bias toward social threat in other species.

Keywords – Attentional bias, Dot probe task, Nonhuman primate, Facial expression, Cortisol, Oxytocin

Threatening stimuli are perhaps the most salient features of any animals' environment, and the preferential allocation of attention toward threatening, rather than neutral or non-threatening, stimuli is referred to as an attentional bias toward threat (Bar-Haim et al., 2007; Cisler & Koster, 2010; MacLeod et al., 1986; Mogg & Bradley, 1998). This bias can form toward nonsocial, biological threats in the environment as well as toward social threats from other individuals. Attentional biases are adaptive, as individuals that are quicker to respond to the presence of a threat are more likely to survive to reproduce (Isbell, 2006). For example, adult humans detect a snake stimulus among neutral stimuli more quickly than they find a neutral stimulus among threatening distractor images (Öhman et al., 2001). Children show an attentional bias toward threat as well; adults and three- to five-year-old children show a faster reaction towards snakes than flowers in a visual search task (LoBue & DeLoache, 2008), suggesting that extensive previous experience with such stimuli is not required for this bias to form in humans. Humans are not alone in this; there is evidence that nonhuman primates show an attentional bias toward snakes in both a natural field setting (Boinski, 1988; Mineka et al., 1980; Seyfarth et al., 1980) and in a laboratory setting, even with no prior exposure to snakes (Shibasaki & Kawai, 2009). This hints that the evolutionary roots of attentional bias toward threat may precede the human species, warranting further investigation of this bias formation across the primate phylogeny.

While the expression of attentional bias toward nonsocial threat is not unique to humans, this cognitive bias has not been well examined with socially threatening stimuli, which are as important and perhaps even more prevalent than nonsocial threats for the socially living primates. Little is known about how other nonhuman primate species, particularly platyrrhine primate species, allocate attention to such threats. Here, we argue that using a comparative approach to study attentional bias formation toward social threats will provide valuable insight about the origins of attentional bias toward social threat. For instance, the various social and feeding ecologies across primate species may be a predictor of the prevalence of attentional bias toward social threat. Socially, despotic species that are highly sensitive to facial expressions or direct gaze/eye contact from conspecifics, and who are generally less socially tolerant (Matsumura, 1999; Thierry, 1985), such as rhesus macaques (*Macaca mulatta*), might be more likely to show an attentional bias toward socially threatening stimuli than other species for whom direct gaze is less threatening. On the other hand, species that are more tolerant or affiliative in social or food-sharing contexts, such as bonobos (*Pan paniscus;* De Petrillo & Rosati, 2019; Hare et al., 2007; Malenky & Wrangham, 1994; Rosati, 2017) might show less evidence of attentional bias toward threatening social stimuli. In less tolerant species, showing an attentional bias toward threatening conspecifics could have adaptive survival value in a group setting, while in more tolerant species this bias toward threat may be less meaningful from a survival standpoint.

Additionally, using a comparative approach allows us to explore the mechanisms of attentional bias formation in model species that are not influenced by the socio-cultural norms that confound human populations, such as the wide within-species cultural variation of humans, which shapes our perceptual and attentional processes in comparison to other nonhuman primate species (Han & Northoff, 2008). It can be challenging to study the evolutionary origins of certain behaviors in nonhuman primate species due to both the nature of working with non-lingual primates and the challenge of maintaining consistent paradigms across species to reduce methodological confounds. Nonetheless, it is useful to adapt human cognitive tasks to assess parallels in nonhuman primate behavior and cognition, and it is possible to do so effectively with the right methodological paradigm.

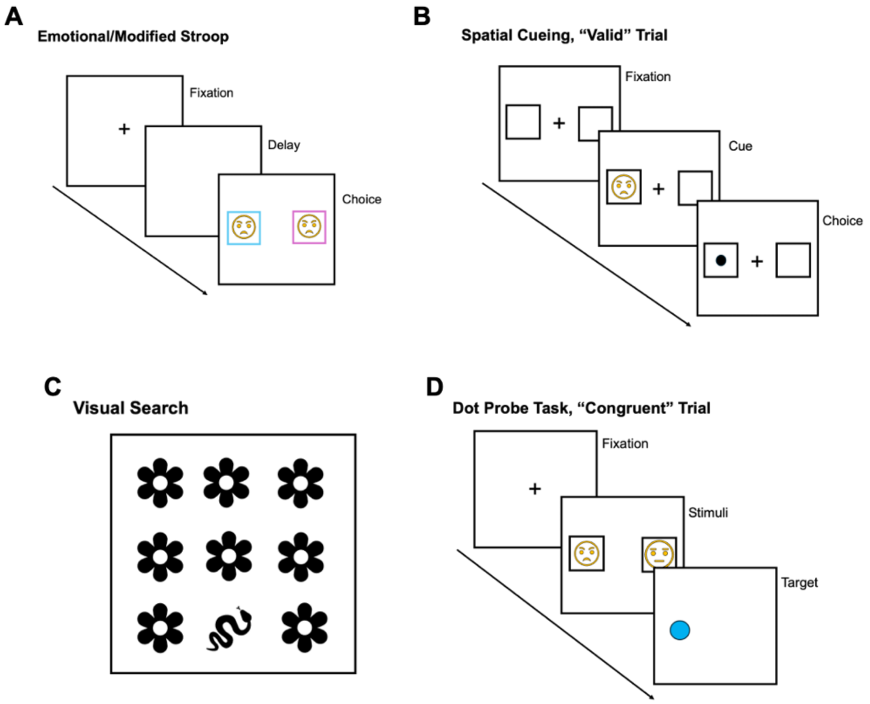
The aim of this narrative review is to highlight the importance of using a comparative approach to the study of attentional bias toward threat, with an emphasis on attentional bias toward social threats. We will discuss the most commonly used methods for studying attentional bias in humans and how these methods have been modified for use with nonhuman primates, with emphasis on the most commonly used comparative paradigm, the dot probe task. We discuss the importance of using social stimuli, such as faces and facial expressions in the study of attentional bias, as well as the hormonal factors that may be involved in attentional bias formation, including cortisol and oxytocin. Lastly, we suggest broadening the investigation of attentional bias toward social threat to include platyrrhine primate species in order to create a more complete picture of the evolutionary trajectory of attentional bias formation across the primate phylogeny.

Measuring Attentional Bias

The study of attentional bias in humans has gained considerable interest over the past few decades, and recently in nonhuman primates as well (van Rooijen et al., 2017). Not surprisingly, many methods have been developed to study attentional biases, some of which are better suited for comparative contexts than others. While the primary focus of this review is the dot probe task, we consider three other primary methods that have also been used to study attentional bias to threat, including the emotional/modified Stroop task, the spatial cueing task, and the visual search task (Cisler & Koster, 2010). We focus on the dot probe task because it is most commonly used to assess attentional bias specifically toward social threat in humans. We begin with a description of each of these methods, followed by an in-depth discussion of the current state of the comparative literature of the dot probe task.

Figure 1

Examples of the Four Different Methods Discussed in This Article, including A) the Emotional/Modified Stroop task, B) the Spatial Cueing Task, C) the Visual Search Task, and D) the Dot Probe Task



Emotional/Modified Stroop Task

The emotional Stroop task is based on the original Stroop test paradigm (Stroop, 1935) in which subjects are asked to name the font color of a string of letters while ignoring the semantic meaning of the color word itself. In the original task, if the subject saw the word "blue" written in black font, they had to name the font color (black) rather than the word itself (blue). The original Stroop task has been modified and presented to nonhuman primates, supporting that a Stroop-like interference effect is not unique to humans (Beran et al., 2010; Lauwereyns et al., 2000; Washburn, 1994). An "emotional" version of the task has also been used to study this effect in nonhuman primates. In the emotional version of the Stroop task, words with *emotional* content are used instead of words with *color* content (i.e., the word "sickness" has an emotionally negative content, instead of the word "tree," which has a neutral content), and participants must name the color of the word as quickly as they can, while ignoring the emotional content of the word (Mathews & Macleod, 1985). Typically, participants are slower to name the color of negative words (sickness) compared to the color of neutral words (tree), indicating an effect of the negative connotation of the word itself, or an attentional bias toward the negative word compared to the neutral word (Macleod, 1991). Individuals with anxiety tend to show an attentional bias toward threat on the emotional Stroop task, demonstrated by the interference effect that occurs when naming the color of threatening words in comparison to naming the color of neutral words (Bar-Haim et al., 2007; Chew, 2015; Williams et al., 1996).

From a comparative perspective, neither version of this task can be used directly to test attentional bias in nonhuman primates. However, Allritz and colleagues (2016) modified the emotional Stroop task for use with chimpanzees (*Pan troglodytes*) to assess attentional prioritization in the context of stressful social and nonsocial images. They combined stressful pictorial stimuli and neutral stimuli to assess whether the emotional content of the stimuli had an effect on chimpanzees' cognitive performance. This paradigm required training: chimpanzees were initially presented with two otherwise identical images with differently colored frames on a computer screen. The chimpanzees were trained to select the image framed by only one of the colors in each trial. After this training, the first part of the study investigated whether the content within the colored frame affected discrimination performance when the stimuli were no longer identical. As predicted, this did impact performance, despite chimpanzees having been trained to only make selections based on stimulus frame color. The second part of the study examined whether the *emotional* content of the images influenced the discrimination task. There was an interference effect for aversive stimuli (pictures of the veterinarian) compared to neutral control images (Allritz et al., 2016), such that subjects were slower to make a response on correct trials for aversive compared to neutral stimuli in the first session, prior to habituation of these stimuli. Despite demonstrating an effect of the emotional and social content of stimuli on attention, the task could not determine *how* the emotional content of the stimuli interrupted performance (attentional avoidance v. difficulty disengaging from the aversive stimulus), nor was it clear whether the chimpanzees were more affected by the perceptual features of the aversive stimuli (such as the color and contrast of the image itself) or the content itself (recognition of the veterinarian or the veterinary tools in the photograph). The potential impact of the physical features of stimuli is not unique to this particular study; future studies should be mindful of these confounds through the incorporation of control images, such as scrambled stimuli. Nonetheless, this modified emotional Stroop task is useful in assessing the presence of attentional bias in nonhuman primates.

Two additional studies have employed this modified paradigm with nonhuman primates (Hopper et al., 2021; Laméris, Verspeek, et al., 2022), one of which specifically evaluated the effect of socially distressing stimuli on bonobo performance (Laméris, Verspeek, et al., 2022). Laméris and colleagues conducted three experiments. The first tested the classic color-interference Stroop effect, the second used social emotional stimuli, including positive, neutral, and negative or distressing facial expressions from bonobos unfamiliar to the subjects, and the third used nonsocial emotional objects as stimuli, such as images of predators, food, and flowers. Ultimately, the positively valenced social stimuli interfered with bonobo attention more than the negative facial expressions did, contrary to what has been found in other primate species using different attention paradigms (see below), but this aligns with previous evidence that bonobos show an attentional bias toward positive social stimuli (Kret et al., 2016).

Spatial Cueing Task

In the classic spatial cueing task (Posner, 1980), participants are presented with a cue that appears in one of two locations, followed by a target that is presented at the cue location in the majority of trials, called a "valid-cue condition." For a small number of trials, the target appears in an alternative location, called an "invalid-cue condition." In the emotional version of the task (Fox et al., 2001; Stormark et al., 1995), threatening and neutral stimuli are used on valid-cue or invalid-cue trials. The attentional bias to threat is indicated by slower responses to the invalid-cue trials and faster responses to the valid-cue trials when the cue is threatening rather than neutral in content. This task presents one stimulus instead of two different emotionally valenced stimuli, as in the Stroop tasks, which may reduce competition for the participant's attention. Studies of humans have found evidence of robust attentional bias using this task (Bar-Haim et al., 2007; Cisler et al., 2009).

This method has been employed to assess attention in nonhuman primates (Eckstein et al., 2013; Tomonaga & Imura, 2009). Tomonaga & Imura (2009) tested chimpanzees using neutral familiar chimpanzee face stimuli, neutral familiar human face stimuli, banana stimuli because of the chimpanzees' preference for that food, and other object category stimuli. Chimpanzees showed attentional bias toward the face stimuli *versus* other stimuli, compared to the banana *versus* object and the object *versus* object stimuli. This result generalized to human faces as well (Tomonaga & Imura, 2009). An important future consideration would be to determine whether chimpanzees would show an attentional bias toward threatening facial expressions in comparison to these neutral faces.

Visual Search Task

The visual search task (Öhman et al., 2001; Rinck et al., 2003) assesses attentional bias via spatial attentional allocation (Cisler & Koster, 2010). In the visual search task, the participant must locate a target threatening stimulus from a matrix of neutral stimuli. There may also be a reverse condition, in which the participant must locate the neutral target stimulus from an array of threatening stimuli. For example, the participant might see a 3 x 3 display of words, and they must locate the word "spider" from within the matrix of distractor neutral words (Cisler & Koster, 2010). A faster response time to locate the threatening target from an array of neutral stimuli compared to response times to locate a neutral stimulus from an array of threatening stimuli is evidence of an attentional bias towards threat. Likewise, slower response times to locate a neutral target from a matrix of threatening distractor stimuli also provides evidence of an attentional bias to threat. This task has yielded somewhat inconsistent evidence of attentional bias toward threat in several studies via facilitated attention towards threat (Lipp & Waters, 2007; Rinck et al., 2003), difficulty disengaging from threatening stimulus distractors (Öhman et al., 2001; Pflugshaupt et al., 2005), and sometimes both (Byrne & Eysenck, 1995; Miltner et al., 2004), suggesting that facilitated attention to threat and difficulty disengaging from threat are not necessarily competing processes as was once thought based on previous studies that found evidence for just one of the two processes (Cisler et al., 2009).

The visual search task can be modified for use with nonhuman animals by using threatening and neutral pictural stimuli instead of words (Shibasaki & Kawai, 2009). However, in the visual search task there is less control over stimulus presentation time, due to the nature of the task presenting both neutral and threatening stimuli simultaneously. It also presents additional training requirements for animals compared to humans (Shibasaki & Kawai, 2009), because nonhuman subjects must learn which image type to identify from the matrix. A few studies have used this task to evaluate attentional bias in nonhuman primates (Matsuno & Tomonaga, 2006; Shibasaki & Kawai, 2009; Tomonaga, 1995; Tomonaga & Imura, 2015). Chimpanzees are more efficient at detecting faces than non-face objects using a visual search paradigm (Tomonaga & Imura, 2015), though no studies to date have determined how socially threatening stimuli influences nonhuman primate attention using this paradigm.

Dot Probe Task

The dot probe task is a commonly used task to assess attentional bias toward threat in humans (Bar-Haim et al., 2007) that was originally developed by MacLeod and colleagues (1986). In this paradigm, participants are simultaneously presented with a threatening cue and a neutral cue for a short interval of time. After this time interval, the threatening and neutral cue disappear and a target appears in the place of one of the cues. In a congruent trial, the target appears in place of the threatening cue. In an incongruent trial, the target appears in the place of the neutral cue. Typically, each trial contains one neutral stimulus and one threatening stimulus, and the participant is instructed to respond to the target as quickly as they can. Faster reaction times to reach the target on congruent trials compared to incongruent trials are considered to indicate an "attentional bias" toward threat (Waechter et al., 2014). Generally, this is reported as an attentional bias "score," in which the average reaction time from congruent trials is subtracted from the average reaction time of incongruent trials. If the bias score is positive, that indicates an attentional bias toward threat. If the attentional bias score is negative, that indicates an attentional bias away from threat. In this review, we focus on this dot probe task to consider the methodological advantages and disadvantages associated with it in the field of comparative psychology.

Dot Probe Task: Methodological Considerations

Attention Strategies

The dot probe task is thought to measure attentional allocation rather than response inhibition and allows the researcher to control for stimulus onset asynchrony so that the time course of attentional allocation can be investigated. However, the dot probe task alone cannot always distinguish attentional strategies, namely, vigilance toward threat, difficulty or delayed disengaging from threat, and attentional/vigilance-avoidance. The delayed disengagement hypothesis suggests that individuals struggle to shift attention away from threatening stimuli, while the vigilance-avoidance hypothesis suggests that individuals will initially orient attention toward the threatening stimulus, and then shift attention away. Thus, both vigilance toward threat and difficulty disengaging from threat will result in a positive attentional bias score. Other methods, such as the use of eye-tracking systems or varying stimulus presentation times, are necessary to make this distinction with certainty. Eye tracking allows for the determination of the location on which the eye fixates, which is important because unless we know exactly where the eye fixates, we cannot know for certain whether an individual is avoiding a threatening stimulus or fixating on the threatening stimulus from the very first fixation (Garner et al., 2006; Liang et al., 2016). Varying stimulus presentation time can also aid in this differentiation: attentional vigilance toward threat is likely to occur in early stages of attentional processing, captured with stimuli presented for a short period of time (100ms or less), while attentional avoidance is more likely to be captured using stimuli presented for a longer period of time ($\geq$ 1250 ms), though this is not always the case (Cisler & Koster, 2010). Finally, the inclusion of baseline stimulus pairs of trials that present two neutral stimuli in addition to the threatening-neutral stimulus pairing would help to make the distinction between difficulty disengaging from threat and attentional avoidance of threat. Using baseline reaction time from neutral-neutral trial types to compare to threat-neutral trials, Koster et al (2004) found evidence in human subjects in support of difficulty disengaging from threat instead of attentional vigilance toward threat, as there was a delay in the response to incongruent threat trials (Koster et al., 2004). Future studies that use the dot probe task, particularly nonhuman animal studies, should consider incorporating these neutral-neutral trial types in order to disentangle the two possible mechanisms.

Reliability Challenges

There are reports of reliability challenges with the dot probe task. Reliability has repeatedly been found to be low across studies that use an attentional bias score as the measure of attention on the dot probe task, particularly in non-clinical populations (Chapman et al., 2019; Schmukle, 2005; Staugaard, 2009). Broadbent and Broadbent (1988) tested low, moderate, and high anxiety participants on the dot probe task, and found that only the high trait anxiety individuals showed an attentional bias toward the threatening words used as stimuli. However, other studies failed to replicate this finding in high trait anxiety participants (Mogg et al., 1997, 2000). Schmukle (2005) suggested that the dot probe task might be most appropriate for studies that compare attentional bias scores between groups rather than on an individual level. Reliability issues may be due to the differences in methodology used across studies. Different studies vary in stimuli (faces *versus* words), presentation time, participants (clinical *versus* nonclinical), and trial numbers (Bögels & Mansell, 2004; van Rooijen et al., 2017; Waechter et al., 2014). In studies that use faces as stimuli, longer presentation times with an anxiety induction manipulation tend to find threat *avoidance*, but studies that use shorter presentation times without an anxiety induction manipulation tend to find attentional bias *toward* threat (Bögels & Mansell, 2004).

Daily repetition of the dot probe task over the span of several weeks improves attentional bias score reliability (Enock et al., 2014), which is important to consider for studies that use repeated measures within-subject experimental designs, as many comparative studies do. Enock and colleagues tested participants three times daily across four weeks using a smartphone dot-probe task. They used neutral faces and disgust faces that were presented on the screen for 500 ms and found moderate to strong test-retest reliability of attentional bias scores between weeks (Enock et al., 2014). This is particularly encouraging for nonhuman primate studies that use this task, because of the repeated-measures design that these studies typically use. Using raw reaction times to assess attentional bias in place of the traditional attentional bias scores also improves dot probe reliability (Waechter et al., 2014). The benefit to using raw reaction time data is that it allows for more data points to work with, rather than collapsing incongruent and congruent raw reaction times into one difference score (van Rooijen et al., 2017). Yet the use of raw reaction time data instead of attentional bias scores can lead to other statistical challenges when comparing group-level performance across different trial types and stimulus blocks (van Rooijen et al., 2017). This is particularly relevant when testing for interaction effects with small sample sizes, as is frequently the case in nonhuman primate research, thus investigators should take this into account when deciding which measure is most appropriate for their study.

Stimulus Color and Presentation Time

Another issue raised by previous studies is the degree to which faces vs full bodies are key for eliciting attention-based responses. The stimuli discussed in the studies above focused on the entire body of the individual, not just the face, so it is possible that the bias found was related to body posture and not simply facial expression, as is the case in other studies. Instead of using whole-body stimuli, one dot-probe study tested chimpanzees on conspecific threatening and neutral facial expressions. Faces are one of the most salient types of socially communicative stimuli (Parr et al., 2000) and serve as social identifiers within a group and to convey information about an individual's internal state or the focus of their attention. This allows the interactor to predict future behavior based on the information portrayed by the face (Leopold & Rhodes, 2010). Aggressive or threatening facial expressions could indicate to an individual that they are the target of aggression (Hoffman et al., 2007), so competency in rapidly attending to and interpreting facial expressions, or showing an attentional bias toward threatening facial expressions, offers social advantages and could result in severe fitness consequences if ignored (Schmidt & Cohn, 2001). Wilson and Tomonaga (2018) used unfamiliar conspecific facial expressions presented in greyscale and scrambled stimuli to control for perceptual aspects of the images, such as color, contrast, luminance, and brightness, and included both high and low intensity threat faces to measure salience. In order to capture early attention, they used a short stimulus onset asynchrony of 150 ms to prevent attention switching from one stimulus to the other, which can occur as rapidly as within 200 ms (Bourne, 2006). Chimpanzees showed no difference in reaction time following congruent trials and incongruent trials when threatening faces were paired with neutral faces or in response to low intensity threat compared to high intensity threat across trials (Wilson & Tomonaga, 2018), suggesting that chimpanzees do not show an attentional bias toward threat when viewing facial expressions from unfamiliar conspecifics, at least when using a short stimulus presentation time of 150ms. The authors suggested that time may have been too limiting on exposure to the images presented (Wilson & Tomonaga, 2018), and indeed, other studies that have found effects have used longer presentation times (300ms; Kret et al., 2016, 1000ms, King et al., 2012). Yet to confirm this effect of presentation time, it is important that future work compares different presentation time durations within the same study.

Emotional Expressions

Nonhuman primates can discriminate facial expressions (Calcutt et al., 2017; Micheletta et al., 2015; Parr & Heintz, 2009), yet the ability to recognize different facial expressions does not necessarily indicate that there should be an attentional bias toward specific kinds of expressions. Indeed, responses to threatening facial expressions have not been found consistently in nonhuman primates, possibly because threat detection is influenced by a variety of factors in addition to facial expressions. One such factor could be individual facial identity – an individual may only respond to a threatening facial expression if it comes from a higher-ranking individual than themselves, or a lower-ranking individual who is a threat to one's current rank. For instance, chimpanzees and rhesus macaques are both able to identify individuals by their facial identity, even unfamiliar individuals (Parr et al., 2000) and even across the span of decades (Lewis et al., 2023). Capuchin monkeys (*Sapajus [Cebus] apella*), too, can generalize the identity of specific individuals across multiple different angles (Pokorny & de Waal, 2009) and are able to discriminate familiar ingroup and familiar outgroup members, although not unfamiliar individuals (Talbot et al., 2016).

Stimulus presentation time may also influence attentional bias expression, as noted above, though evidence for this is mixed. Kret and colleagues (2018) explored the effect of using different stimulus presentation durations on attentional bias toward emotions with a touch screen dot probe task in humans and chimpanzees. In their first experiment, they presented chimpanzees with image pairs for either 33 ms (subliminal) or 300 ms (supraliminal) and then immediately masked them with neutral images. Stimuli were full-body photographs of male chimpanzees showing either an aggressive display, a submissive display, or a neutral whole-body posture and were presented in luminance-controlled greyscale. All stimuli were also scrambled to control for other low-level features that could influence attention. Chimpanzees did not show an attentional bias toward the emotional stimuli at either presentation duration (Kret et al., 2018), indicating that presentation time of the stimuli did not modulate attention in this context for chimpanzees. The authors suggested that the stimulus set used in this study might not have been ecologically valid enough to evoke an attentional bias in chimpanzees, because the stimuli were not in color and did not depict scenes, but instead depicted body expressions. Additionally, positive emotional scenes were not used in this study, yet positive emotional scenes were the drivers of the attentional bias to emotional compared to neutral stimuli in bonobos (Kret et al., 2016). The authors emphasize that chimpanzees are sensitive to the emotional expressions of conspecifics (Buttelmann et al., 2009; Kano et al., 2008; Kano & Tomonaga, 2010; Parr, 2003; Parr et al., 2008), but again, the ability to differentiate emotional expressions does not equate to demonstrating an attentional bias toward threatening expressions specifically.

From an evolutionary perspective, emotional expressions should be salient signals to chimpanzees, bonobos, and orangutans, yet there has not been strong evidence of attentional bias toward threatening facial expressions in chimpanzees or orangutans, and only evidence of attentional bias toward emotional expressions that are driven by positive expressions in bonobos. One possibility is that the methodological differences between the current set of studies explain this difference. In both of the chimpanzee studies discussed above, all stimuli were in greyscale, and in the Wilson and Tomonaga study (2018) the stimuli were cropped to only show the facial expression, compared to the two bonobo studies that showed full-body in-color photographic scenes. Color images are presumably more ecologically valid and salient to the viewer, as they appear more realistic and "natural." Cropping images to just the face may have a similar effect on ecological validity. However, the orangutan study did use color images for full-body stimuli, and still found no evidence of attentional bias toward emotional stimuli (Laméris et al., 2022). Another important factor to note is that eye gaze may be influential in attentional bias outcomes, due to the important role that it plays in communicating social information (Lewis & Krupenye, 2022). There is evidence in tufted capuchin monkeys that eye gaze influences approach behavior: capuchins are slower to approach food located in front of images of conspecifics with a direct gaze compared to an averted gaze (Morton et al., 2016). Parr and colleagues (2013) investigated the influence of gaze on attentional bias with and without intranasal oxytocin administration in rhesus macaques. They did not find a significant difference in attentional bias score between the placebo and oxytocin conditions, suggesting that eye gaze may not be as aversive as threat expression (the direct and averted gazes during this condition were all of neutral expression; Parr et al. 2013).

Comparative Dot Probe Studies with Apes

The dot-probe offers another useful method for the comparative assessment of nonhuman primate attentional bias because of its implicit nature and minimal training requirements. Participants need only learn to touch or respond in some way to a target when it appears, instead of learning to select specific types of stimuli (as required for a visual search task) or rules about selecting stimuli based on specific characteristics of the stimuli (as required for an emotional Stroop task). Finally, and unlike the other tasks, the dot-probe allows for the control of stimulus presentation time, which may be a moderator of attentional bias. There have been a handful of attempts at measuring attentional bias toward social threat in nonhuman primates, most of which use a version of the dot probe task paradigm. Each of the studies we discuss has contributed to our understanding of how nonhuman primates allocate their attention, though there are gaps that remain to be filled (Table 1).

Table 1

Dot Probe Studies that Investigate Attentional Bias toward Social Threat in Nonhuman Primates

Study	Species	System	Stimuli	Valence	Faces/ Full Body	Stimuli Color	Presen-tation Time	Manipulation	Evaluation	Results
Parr et al., 2013	*Macaca mulatta*	Touchscreen	Unfamiliar monkey faces, nonsocial object images	neutral, negative, direct gaze, averted gaze, scrambled	Faces	color images	500ms	Oxytocin, placebo	Attention bias score	Bias away from negative faces with oxytocin; bias toward direct gaze over averted gaze increased with oxytocin; no effect on objects with oxytocin
King et al., 2012	*Macaca mulatta*	Touchscreen	Unfamiliar monkey faces, nonsocial object images	neutral, positive, negative	Faces	grayscale images	1000ms	Baseline, testosterone, placebo	Attention bias score	Bias toward negative faces but not objects at baseline; No bias with placebo; bias toward positive faces and away from negative objects with testosterone
Reilly et al., 2024	*Sapajus [Cebus] apella*	Joystick	Familiar and unfamiliar monkey faces, nonsocial objects	neutral, negative, scrambled	Faces	color images	500ms	Baseline, oxytocin, placebo	Attention bias score	Bias away from scrambled
Morin et al., 2019	*Macaca mulatta*	Touchscreen	Unfamiliar monkey faces, nonsocial objects	neutral, negative	Faces	color images	500ms	Maternal maltreatment group, control group	Attention bias score; reaction time	No group differences reported using attentional bias scores; slower reaction times in social threat v. neutral trials compared to controls and independent of trial congruency; higher hair cortisol levels at birth were predictive of slower reaction time in social threat v. neutral trials
Lacreuse et al., 2019	*Macaca mulatta*	Touchscreen	Unfamiliar monkey faces, nonsocial objects	negative, neutral, positive	Faces	grayscale images	1000ms	Baseline	Attention bias score	Monkeys showed attentional bias toward threat faces, but not toward other stimuli
Kret et al., 2018	*Pan troglodytes*	Touchscreen	a) Unfamiliar male chimpanzees,	a) submission, display, neutral,	Full body	grayscale images	300ms or 33ms	Baseline	Reaction time	a) No attentional bias for either presentation time across stimulus type;

			whole-body images; b) Unfamiliar male human body expressions	scrambled (chimpanzee); b) anger, fear, neutral, scrambled, (human) and submission, display, neutral, scrambled (chimpanzee)						b) No attentional bias for either presentation time across chimpanzee and human stimulus categories
Kret et al., 2016	*Pan paniscus*	Touchscreen	Unfamiliar bonobo social scenes and non-bonobo control animals	emotional (positive & negative), neutral, control	Full body	color images	300ms	Baseline	Reaction time	Bias toward emotional stimuli compared to neutral stimuli, with stimulus categories of sex, grooming, and yawning driving this bias
van Berlo et al., 2023	*Pan paniscus*	Touchscreen	Familiar and unfamiliar bonobo whole-body images	neutral or emotional scenes	Full body	color images	300ms	Baseline	Reaction time	Bias toward emotional scenes compared to neutral scenes if they involved unfamiliar but not familiar individuals
Wilson & Tomonaga, 2018	*Pan troglodytes*	Touchscreen	a) color; b) objects; c) Unfamiliar chimpanzee, orangutan, and baboon faces; d) Unfamiliar chimpanzee faces	a) two shades of red; b) neutral and scrambled; c) neutral and scrambled; d) negative and scrambled	Faces	grayscale images	150ms	Baseline	Reaction time	a) no difference in response time between light and dark red; b) faster response time toward chairs compared to scrambled images; c) faster response time toward chimpanzee faces compared to scrambled images, and toward chimpanzee faces compared to baboon faces; d) no difference in response time between emotional faces and scrambled faces
Laméris et al., 2022	*Pongo pygmaeus*	Touchscreen	Unfamiliar orangutan face and whole-body images	neutral or emotional scenes	Full body	color images	300ms	Baseline	Reaction time	No bias toward emotion stimuli over neutral scenes

Prevalence of attentional bias toward social stimuli has been explored using a dot-probe task in some of our closest phylogenetic relatives, the apes, in this case including chimpanzees, bonobos, and orangutans (*Pongo pygmaeus*), although results have been inconsistent. Orangutans do not show evidence of attentional bias toward emotional whole-body scenes (Laméris et al., 2022). The orangutans in the study were presented with images from emotional behavioral categories consisting of yawning, sex, play, grooming, and aggression postures matched with neutral emotional stimuli, and these stimuli pairs were presented for 300 ms. They showed no attentional bias toward or away from any of the stimulus categories, which the authors suggest could be due to a lack of stimuli salience (Laméris et al., 2022). However, there is evidence that bonobos show an attentional bias toward emotional scenes in a touch-screen dot probe task using similar stimuli (Kret et al., 2016), though these scenes were not threatening in nature. Specifically, emotional scenes consisted of whole-body images and they were either in distress, playing, grooming, yawning, engaging in sex, feeding, or pant-hooting, the latter of which is a behavior expressed when bonobos are excited (Kret et al., 2016). Neutral or emotional scenes were presented in color to view for 300 ms, which is the same amount of time that the orangutans viewed their stimuli for (Laméris et al., 2022). Unlike orangutans, bonobos showed an attentional bias toward the emotional scenes over the neutral scenes, and the more emotional the scene (as rated by humans, at least), the faster the bonobos responded to the target. This result seems to have been driven by a few specific categories, including grooming, engaging in sex, and yawning, which the authors suggested could have been due the fact that all three are thought to increase social bonding and affiliation or, in the case of yawning, increase empathy and social affinity (Demuru & Palagi, 2012; Palagi et al., 2014), and therefore are important in bonobo social organization (Kret et al., 2016). Notably, these three stimuli categories were non-threatening in nature, which leaves the question of how socially threatening stimuli influences attentional bias in bonobos unanswered. These studies demonstrate that socially relevant, non-threatening emotional stimuli can result in an attentional bias toward conspecific social emotional information in bonobos, but has not been found in orangutans so far.

In a follow up touch-screen study, van Berlo et al. (2023) assessed bonobo attention toward familiar or unfamiliar individuals with emotional (distress, play, grooming, sex, yawning, scratching) or neutral expressions. Similar to the previous study, stimuli used in Experiment 1 included the whole body of the bonobo, not just the face. Using the same stimulus presentation time of 300 ms, the researchers found that bonobos showed an attentional bias toward unfamiliar conspecific emotional scenes, but not toward familiar conspecific emotional scenes, suggesting that attention to emotional expressions is modulated by familiarity of the expressor. In a second study, researchers further explored the role of familiarity by using color photos of facial expressions (angry, fearful, happy, sad) of familiar and unfamiliar humans. In this case, the bonobos did not show an attentional bias toward either familiar or unfamiliar humans. However, several issues make it difficult to interpret these results. It is possible – and indeed likely – that the human stimuli were less salient to the bonobos than the (conspecific) bonobo stimuli (van Berlo et al., 2023). However, the researchers also switched from full body stimuli to face stimuli, and there may be differences in how faces are interpreted and/or bonobos' responses to them as compared to full bodies. Of course, a third possibility is that the bonobos found them salient and interpreted them perfectly well, but do not show a response to human faces, which might suggest that this would be the case for any heterospecific, as humans are similar in form and are a familiar species to these bonobos. Overall, these experiments suggest that social information is most relevant from conspecifics, although more work is needed before we can conclude this. More importantly, they suggest that the familiarity of the individual being observed is important (at least for conspecifics).

Comparative Dot Probe Studies with Monkeys

Interestingly, the evidence for attentional bias toward threat specifically has been more consistent in rhesus monkeys than in ape species. King and colleagues (2012) tested a group of adult male rhesus macaques on a touch screen dot probe task to determine what effect testosterone administration had on this attentional bias. In this study, stimuli were presented for a longer duration – 1000 ms – before the target appeared. Stimuli were presented in pairs of one neutral image and one positive or negative image. All images were faces of unfamiliar macaques cropped to just show the face, and all images were presented in greyscale, suggesting that color and whether the image is restricted to the face may not influence attentional bias in these tasks, at least in rhesus macaques. As an additional manipulation, nonsocial objects that were threatening (e.g., gloves, syringes), neutral (e.g., shoes, cage locks), and positive (e.g., bananas, grapes) were presented to assess whether the attentional bias to threat was exclusively to social threat, or if it included nonsocial threat as well. At baseline, rhesus macaques showed an attentional bias toward negative social stimuli, but not towards positive social stimuli, negative nonsocial stimuli, nor positive nonsocial stimuli (King et al., 2012). The authors also noted that this initial attentional bias diminished between the first month of testing and the fourth month of testing, likely due to repeated exposure to the stimuli over time.

Interestingly, when testosterone was administered, rhesus monkeys showed a general decrease in reaction time in response to the target. They also showed an attentional bias away from negative nonsocial stimuli (avoidance), and an attentional bias toward positive social stimuli, which is the opposite of what was observed at baseline (King et al., 2012). However, all reaction times to respond to the target were reduced in the testosterone treatment condition, including the placebo sessions, which indicates that this result could have occurred due to repeated exposure to the stimuli over the course of four months rather than due to the hormone manipulation. Habituation to stimuli is an issue that can be circumvented with careful planning when using the dot probe task. For instance, when possible, researchers should use large sets of stimuli instead of small sets that then require multiple repetitions of the same images, which could lead to faster habituation. Oftentimes this is challenging to do, such as when working with images that are difficult to obtain, in which case it is critical that researchers incorporate statistical analyses that account for the possibility of habituation to stimuli. Lastly, researchers should be mindful of proportion-congruent effects through careful consideration of what proportion of trials presented will be those of statistical interest compared to “filler” trials within each block of trials (Bugg & Crump, 2012). Future studies should take the issue of habituation of stimuli into account when using the dot probe task.

In a direct comparison of humans and nonhuman primates, male rhesus macaque performance on the dot probe task was compared to human male performance on the task using both face and nonsocial threatening, positive, and neutral stimuli. Humans viewed unfamiliar human faces and macaques viewed unfamiliar macaque faces. Both versions of the task presented stimuli in emotional-neutral pairs for 1000ms. Humans showed a significant attentional bias toward negative human faces, but attentional avoidance of negative objects (Lacreuse et al., 2013), while rhesus macaques also showed an attentional bias toward threat faces but neither a bias toward or avoidance of nonsocial stimuli. Due to the long stimulus presentation time, this bias was not explained by early attentional orienting and vigilance, but instead measured difficulty in disengaging from threatening stimuli or attentional capture (Lacreuse et al., 2013). The lack of attentional bias toward positive stimuli in the Lacreuse (2013) study contrasts what was found in bonobos (Kret et al., 2016). However, there were several methodological differences that could account for these differences in results, including the use of face stimuli instead of whole-body stimuli, and the use of colored stimuli instead of greyscale stimuli, so more work is needed before we conclude that there is a species difference in their responses. Also of note is that some of these studies only tested male animals (King et al., 2012; Lacreuse et al., 2013). It is equally important to consider female primates in the response to threatening social stimuli, as it is possible that females, who have very different ecological and social constraints, will respond differently than males.

Another study compared attentional bias toward threatening facial expressions in both male and female macaques that experienced early maternal maltreatment compared to subjects that experienced competent maternal treatment (Morin et al., 2019). These subjects were tested on a touch screen dot probe task using color stimuli of pairs of conspecific threat faces and neutral faces presented for 500 ms. In a separate task, subjects were also presented with threatening nonsocial objects and neutral nonsocial objects as a comparison to the social stimuli. The authors reported a main effect of maternal treatment group on reaction time during the dot probe task such that subjects with a history of maltreatment reacted more slowly on the social task during threat/neutral trials compared to controls on both congruent and incongruent trials, but they did not react more slowly on the nonsocial task. In the nonsocial task, control subjects showed faster reaction times over the span of the testing days, but the maltreated subjects did not show this change over time. Interestingly, this effect was not seen when using the attentional bias score, but only the raw reaction time data (Morin et al., 2019). Elevated levels of prenatal cortisol exposure were associated with threat avoidance (slower reaction times) in both competent and maltreated groups, which suggests that cortisol plays an important role in the development of emotional attention in rhesus macaques.

A related study evaluated the influence of a stressful intervention on attention to social stimuli in rhesus macaques, though not with a dot probe paradigm. Bethell and colleagues (2012) found that male macaques were more likely to show an attention bias toward a threatening conspecific face stimulus compared to a neutral conspecific face stimulus following a stress-inducing health evaluation, as measured by the proportion of time the subject spent gazing at each stimulus (Bethell et al., 2012). This study quantified the stressful experience by conducting focal observations on each subject for behavioral indicators of stress, but did not provide additional biological indicators of stress, such as change in cortisol level. These results do not align with the results of the study presented above, which found a slower reaction time in subjects with a stressful rearing history of maternal maltreatment when viewing social trials (Morin et al., 2019). These differences could reflect a difference in the influence of long-term versus short-term stress on attention, although this will need to be repeated using the same task in both contexts. Few studies have investigated the hormonal mechanisms of attentional bias toward threat in nonhuman primates, leaving a future avenue for exploration.

Hormonal Mechanisms of Attentional Bias toward Social Threat

Cortisol and Attentional Bias toward Threat

Stress is an important yet largely unexplored factor that may influence attentional bias toward social threat in nonhuman primates. Cortisol, the main output hormone of the hypothalamic-pituitary-adrenocortical (HPA) axis, is known to increase in response to both physical and psychological stressors in primates (Sapolsky, 2005), though these stressors may disproportionately extend towards subordinate individuals compared to dominant individuals within a social group (Abbott et al., 2003; Dettmer et al., 2017; Feng et al., 2016). As a result, subordinate individuals might pay attention to threatening social signals differently than dominant individuals do. Some primates can distinguish between threatening and neutral interactions better than others in a social setting, regardless of social rank. As an example, some male olive baboons (“cluster E”; Ray & Sapolsky, 1992) are better at distinguishing between threatening and neutral interactions with competitive rivals than others, making them highly adept at navigating their social groups (Ray & Sapolsky, 1992; Sapolsky & Ray, 1989). These males also had lower basal cortisol concentrations than males that were not as adept at distinguishing threatening versus neutral interactions (Ray & Sapolsky, 1992), making basal cortisol level a better correlate of behavioral profile than of dominance rank. Male olive baboons that had lower basal cortisol concentrations were also more likely to initiate a fight if the interaction was deemed threatening, win the fight against a competitor, and displace aggression to a third-party individual if they lost the fight to a competitor compared to males with different behavioral profiles (Sapolsky & Ray, 1989). Unlike these low-cortisol males, the dominant males in the same group of baboons did not show these behavioral styles and had basal cortisol levels as high as that of subordinate individuals (Sapolsky & Ray, 1989). Thus, one might predict that individuals with low levels of cortisol would be more adept at discerning mild threat from non-threatening situations by showing an attentional bias toward these social threats compared to individuals with high levels of cortisol, regardless of dominance.

One study has investigated the relationship between cortisol and attentional bias toward socially threatening stimuli in a platyrrhine species, the tufted capuchin monkey (Reilly et al., 2024). Capuchins viewed pairs of threatening and neutral color images of familiar or unfamiliar conspecific faces and non-face stimuli for 500 ms in a dot probe task. Stimuli were also presented in scrambled form as a control. Interestingly, capuchins showed no evidence of attentional bias in any of the face or non-face categories of stimuli. They did, however, show attentional avoidance of scrambled familiar face stimuli. Individuals with higher attentional bias scores (indicative of attention toward threat) also had higher levels of baseline fecal cortisol, though the authors suggest that the biological effect of this relationship is likely small, based on the small effect size (Reilly et al., 2024).

Oxytocin and Attentional Bias toward Threat

It would also be insightful to further investigate the hormonal mechanisms involved in social affiliation via oxytocin because exogenously administered oxytocin has been found to mediate attention to socially threatening signals in primates. There is evidence that oxytocin, administered intranasally, suppresses the vigilance response of rhesus monkeys towards socially threatening faces (Ebitz et al., 2013), but the way in which it does this is unclear. There are two hypotheses: the first hypothesis attributes this reduction in reactivity towards social threats to the stress-reducing properties of oxytocin (Bartz & Hollander, 2006; Heinrichs et al., 2003), specifically by reducing HPA axis activity (Neumann, 2002). Much of the evidence in support of the anxiolytic hypothesis has been focused on lactation in animals and humans because lactation leads to a release of oxytocin in response to suckling behavior (Uvnäs-Moberg et al., 1990), and lactating rats show reduced cortisol secretion in response to physical and psychosocial stressors (Neumann et al., 1998). Moreover, injection administration of oxytocin leads to decreased cortisol levels in female rats (Uvnäs-Moberg, 1998) and humans (Chiodera & Coiro, 1987). Social support also suppresses salivary cortisol levels. In chimpanzees, grooming with preferred social partners led to an increase in urinary oxytocin levels (Crockford et al., 2013) and a decrease in cortisol levels (Wittig et al., 2016), though whether this is the mechanism that leads to a reduction in reactivity toward social threat has yet to be explored.

A second hypothesis is the social-salience hypothesis (Shamay-Tsoory et al., 2009; Shamay-Tsoory & Abu-Akel, 2016), which posits that oxytocin increases the salience of social signals, and thereby leads to increased attentional processing of these signals (Harari-Dahan & Bernstein, 2014). Evidence in support of this hypothesis is seen in studies in which intranasal oxytocin administration increases gaze to the eye region of conspecific faces in both humans (Gamer et al., 2010; Guastella et al., 2008) and monkeys (Dal Monte et al., 2014; Ebitz et al., 2013). Not only does this hypothesis account for the positive effects of oxytocin by increasing individual attention to social signals, such as increased prosocial behavior, it also accounts for the negative effects, such as decreased prosociality during competitive situations (De Dreu et al., 2010) or when interacting with outgroup members (Shamay-Tsoory et al., 2009). For this reason, we might also expect that intranasally administered oxytocin directs attention to social signals more than would be attended to at baseline (Bartz et al., 2010). In the case of individuals who are already hyper-alert towards social signals, negative stimuli may exacerbate their negative interpretation of social cues (Bartz et al., 2010).

Taubert and colleagues (2019) distinguished between these hypotheses by determining whether intranasal oxytocin administration had a general anxiolytic effect, or whether intranasal oxytocin had a selective effect on stimulus salience for negative-valence face stimuli. Rhesus macaques performed an identity matching-to-sample task and an expression matching-to-sample task. In the identity matching-to-sample task, monkeys had to match the identity of a sample conspecific face, and in the expression matching-to-sample, the monkeys were tasked with matching the facial expression. If oxytocin had a general anxiolytic effect on performance, then we would expect that these effects would generalize to both the identity task and the expression task. Instead, the results of this study showed that oxytocin only had an effect on performance in the expression matching task, not the identity matching task, suggesting that oxytocin's effect was specific to behavior (Taubert et al., 2019).

Stress Buffering Effects of Oxtocin on Attentional Bias

Although cortisol is a measure of stress in nonhuman primate species (Novak et al., 2013), and oxytocin may serve as a buffer to stress, few studies have investigated the possible stress-buffering effects of intranasal oxytocin administration on attention to emotional stimuli in male and female rhesus macaques using the dot probe task (Parr et al., 2013). The task presented images for 500 ms in the following pairs: one neutral face paired with its scrambled equivalent, one bared-teeth display facial expression and its scrambled equivalent, or one open mouth threat face and its scrambled equivalent. 48 IU of intranasal oxytocin or placebo was administered before completing the task. Subjects could begin the task 60 min after placebo or oxytocin administration in an effort to maximize the peak uptake of oxytocin into cerebrospinal fluid (Parr et al., 2013). oxytocin led to an attentional bias away from negative facial expressions but did not affect attention toward neutral faces. Moreover, reaction times were slower on emotionally congruent trials and faster on emotionally incongruent trials, suggesting that intranasal oxytocin did not just reduce the salience of social stimuli, but led to the active avoidance of those stimuli. One would not expect any increase in reaction time on incongruent trials if oxytocin acted to simply reduce salience, because a reduction in salience should only reflect a change in response to the emotional stimuli (congruent trials). These results show that oxytocin may act specifically on the most aversive social signals, rather than on social signals compared to nonsocial signals in general, making it a good candidate to investigate as a moderator of attentional bias toward social threats, particularly in other primate species.

One such species is the tufted capuchin monkey. Reilly and colleagues (2024) investigated the influence of oxytocin on attentional bias toward threat in tufted capuchin monkeys using a dot probe task. Capuchins were treated with two different oxytocin manipulations: an exogenous intranasal oxytocin manipulation in which 15 IU of intranasal oxytocin was administered, or an endogenously induced oxytocin manipulation, in which oxytocin increase was induced through eliciting a species-typical fur-rubbing behavior that has been shown to reliably increase capuchin urinary oxytocin levels (Benítez et al., 2018; Sosnowski et al., 2023). Subjects also completed an intranasal saline control condition and a non-fur-rub-inducing control condition. Thirty minutes post-oxytocin manipulation, subjects were given a dot probe task and were presented with image pairs of threatening and neutral conspecific familiar and unfamiliar color face images as well as scrambled pairs of each image for 500 ms. Interestingly, in the manipulated oxytocin conditions, monkeys only showed attentional avoidance of the scrambled threatening face stimuli. Specifically, monkeys showed attentional avoidance of the scrambled familiar face category in the intranasal oxytocin manipulation compared to the intranasal saline control, and they showed attentional avoidance of the scrambled unfamiliar face category in the fur-rubbing condition compared to the non-fur-rubbing control. They showed no bias toward or away from any of the other categories of stimuli (Reilly et al., 2024). The authors suggest that this may have been due to the ambiguous nature of the scrambled images, as several face features were perceptible (i.e., teeth) despite the scrambled appearance of the image as a whole, which could have drawn more attention than an unscrambled image. Nonetheless, future work would benefit from clarifying the role of oxytocin in the modulation of attentional bias toward social threat in other species.

Discussion

Studying the presence of attentional bias toward social threat in other nonhuman primate species, particularly more phylogenetically distant species such as platyrrhine primates, allows us to determine whether this bias is unique to humans and, if not, when it might have emerged across evolutionary history. Current evidence suggests that exhibiting an attentional bias toward threatening social stimuli may not be a cognitive trait unique to humans. However, the literature is not entirely conclusive, and still little is known about the mechanisms that underlie this cognitive bias in nonhuman primates, particularly the hormonal mechanisms involved. The dot probe task is a particularly useful tool among others to evaluate this attentional bias in nonhuman primates through the use of neutral and threatening images. In fact, the dot probe task may be the best available task for assessing attentional bias toward social threat in a comparative context (King et al., 2012; Kret et al., 2018; Lacreuse et al., 2013; Laméris, van Berlo, et al., 2022; van Berlo et al., 2023; van Rooijen et al., 2017; Wilson & Tomonaga, 2018) due in part to its minimal training requirements, ease of administration, and to the implicit nature of the task itself. This is not to say that the task is without flaws; aside from the abovementioned concerns, there are tradeoffs that come with tasks that do not require more attentional demand on the subject. For instance, it is possible that subjects completing a more complex task, such as an emotional Stroop task, may also maintain stronger focus than when they complete a dot probe task simply due to the lower task demands of the dot probe task. However, more demanding tasks also tend to be more time intensive with training requirements, and therefore more limiting in the species that can be evaluated.

There has been a growing number of studies that investigate attentional bias toward social threat in great ape species and in rhesus macaques using a dot probe task, yet contradictory results indicate that there are open questions about the presence of this bias in chimpanzees and bonobos that might be clarified with methodological adjustments. Evidence suggests that although bonobos are sensitive to positive emotional social stimuli over neutral stimuli, and they do not appear to be as sensitive to threatening social stimuli, though they have not been specifically evaluated on their attention to threatening conspecific facial expressions. Conversely, chimpanzees have been evaluated with stimuli of threatening and neutral conspecific facial expressions, yet there is no evidence that chimpanzees show an attentional bias toward threatening facial expressions, despite the social information that they are able to extrapolate from faces. Because of the methodological differences across studies, however, it is premature to conclude that other ape species besides humans do not show an attentional bias toward social threat; it will be important to repeat some of these studies using more consistent methodologies, and to assess this bias in gorillas using comparable methodology, in order to broadly comprehend the prevalence of attentional bias toward socially threatening stimuli. The dot probe task has been successfully implemented with gorillas, though not in the context of socially threatening stimuli (Leinwand et al., 2022), leaving an opportunity for future investigation. Preliminarily, the current results from chimpanzee, orangutan, and bonobo research might be explained by differences in behavioral ecology between the species (Kret et al., 2016; Laméris, et al., 2022; Wilson & Tomonaga, 2018).

Differences in the prevalence of attentional bias toward social threat that have been observed across the primate phylogeny may also be understood in the context of differences in species social and feeding ecologies. For instance, chimpanzees and capuchins inhabit similar niches in their natural environments (De Petrillo & Rosati, 2019) and also share commonalities across their foraging ecologies: both species are omnivorous and engage in extractive foraging (Fragaszy et al., 2004; Sanz & Morgan, 2009). Importantly, chimpanzees (Wilson & Tomonaga, 2018) and capuchins do not show an attentional bias toward or away from social threat (Reilly et al., 2024), unlike bonobos, who do show an attentional bias toward positive emotional stimuli expressions and affiliative social scenes (Kret et al., 2016). Bonobos differ in their social and feeding ecologies from other apes in that they experience more homogenous food resources that are less seasonally dependent, exerting less time and effort to acquire their diets. They are also more affiliative (De Petrillo & Rosati, 2019; Malenky & Wrangham, 1994; Rosati, 2017) and tolerant food-sharers than chimpanzees (Hare et al., 2007; but see Jaeggi et al., 2010 for zoo-housed apes). Orangutan feeding ecology resembles that of capuchins and chimpanzees (Knott, 1999) in that they feed on seasonal, dispersed fruits. Their social ecology differs from other apes in that they tend to be more solitary (Roth et al., 2020; Van Schaik, 1999) with variation between subspecies (van Schaik et al., 2009), but they do use facial expressions to communicate, and may do so intentionally (Waller et al., 2015). Even so, orangutans do not show an attentional bias toward emotional expressions (Laméris, et al., 2022). In comparison to apes, rhesus macaques show a robust bias toward threatening facial expressions (King et al., 2012; Lacreuse et al., 2013; Parr et al., 2013), and this aligns with their behavioral ecology, as they are a less tolerant, despotic species (Matsumura, 1999; Thierry, 1985). Future studies should investigate the prevalence of an attentional bias toward socially threatening stimuli in gorillas. Based on evidence from gorilla social and feeding ecology, which, like bonobos, focuses on a fairly homogenous, herbaceous diet (Rogers et al., 2004), one might predict that gorillas would show an attentional bias toward emotional conspecific faces similar to bonobos. A large part of the gorilla diet consists of herbaceous vegetation over fruit, similar to bonobos, which may result in less competition within groups for a more plentiful food source. This may also contribute to a more tolerant social ecology in gorillas, again like bonobos (although they are different in other socioecological ways, for instance because bonobos are a female-dominant species). Thus, there is reason to believe that gorillas might show a similar level of attention toward an emotional conspecific facial expression as has been found in bonobos. This would not be the first instance of this sort of phylogenetic split in a cognitive process relating to species foraging ecology: gorillas and bonobos have been found to be risk averse, while orangutans and chimpanzees (and capuchins; De Petrillo & Rosati, 2019) have been found to be risk-seeking (Pelé et al., 2014), as their respective foraging ecologies would predict.

To fully characterize the emergence of attentional bias toward socially threatening stimuli, we argue that it is important to evaluate other, more distantly related primate species that also rely on faces to communicate social information, such as other platyrrhines, as well as the ape species that has not yet been evaluated, namely, gorillas. Additionally, there is a need to go beyond the primate taxa to investigate other non-primate species in order to better understand how differences in behavioral ecology between species influence attentional biases more broadly. Lastly, there is evidence to suggest that there may be shared hormonal mechanisms that are associated with attentional bias formation specific to socially threatening stimuli, yet few studies have explored this relationship. Future studies should evaluate the relationship between cortisol, oxytocin, and attentional bias toward social threat in these additional species to help form a clearer picture of when this bias emerged across the primate phylogeny and beyond.

Author Contributions: OTR: Conceptualization, Writing – Original Draft, Writing – Review & Editing, Funding Acquisition. SFB: Supervision, Writing – Review & Editing, Funding Acquisition

Funding: SFB was supported during the writing of this paper by NSF SES 1919305 and NSF BCS 2127375. OTR was supported by the Georgia State University Provost's Dissertation Fellowship.

Conflict of Interest: The authors have no competing interests to declare.

Data Availability: This dataset

References

Abbott, D. H., Keverne, E. B., Bercovitch, F. B., Shively, C. A., Mendoza, S. P., Saltzman, W., Snowdon, C. T., Ziegler, T. E., Banjevic, M., Garland, T., & Sapolsky, R. M. (2003). Are subordinates always stressed? A comparative analysis of rank differences in cortisol levels among primates. *Hormones and Behavior*, *43*(1), 67–82. https://doi.org/10.1016/S0018-506X(02)00037-5

Allritz, M., Call, J., & Borkenau, P. (2016). How chimpanzees (*Pan troglodytes*) perform in a modified emotional Stroop task. *Animal Cognition*, *19*, 435–449. https://doi.org/DOI 10.1007/s10071-015-0944-3

Bar-Haim, Y., Lamy, D., Pergamin, L., Bakermans-Kranenburg, M. J., & Van Ijzendoorn, M. H. (2007). Threat-related attentional bias in anxious and nonanxious individuals: A meta-analytic study. *Psychological Bulletin*, *133*(1), 1–24. https://doi.org/10.1037/0033-2909.133.1.1

Bartz, J. A., & Hollander, E. (2006). The neuroscience of affiliation: Forging links between basic and clinical research on neuropeptides and social behavior. *Hormones and Behavior*, *50*(4), 518–528. https://doi.org/10.1016/j.yhbeh.2006.06.018

Bartz, J. A., Zaki, J., Bolger, N., Hollander, E., Ludwig, N. N., Kolevzon, A., & Ochsner, K. N. (2010). Oxytocin selectively improves empathic accuracy. *Psychological Science*, *21*(10), 1426–1428. https://doi.org/10.1177/0956797610383439

Bartz, J., Simeon, D., Hamilton, H., Kim, S., Crystal, S., Braun, A., Vicens, V., & Hollander, E. (2010). Oxytocin can hinder trust and cooperation in borderline personality disorder. *Social Cognitive and Affective Neuroscience*, *6*(5), 556–563. https://doi.org/10.1093/scan/nsq085

Benítez, M. E., Sosnowski, M. J., Tomeo, O. B., & Brosnan, S. F. (2018). Urinary oxytocin in capuchin monkeys: Validation and the influence of social behavior. *American Journal of Primatology*, *80*(10), e22877. https://doi.org/10.1002/ajp.22877

Beran, M. J., Washburn, D. A., & Rumbaugh, D. M. (2010). A Stroop-like effect in color-naming of color-word lexigrams by a chimpanzee (Pan Troglodyte). *The Journal of General Psychology*, *134*(2), 217–228. https://doi.org/10.3200/GENP.134.2.217-228

Bethell, E. J., Holmes, A., MacLarnon, A., & Semple, S. (2012). Evidence that emotion mediates social attention in rhesus macaques. *PLoS One*, *7*(8), e44387. https://doi.org/10.1371/journal.pone.0044387

Bögels, S. M., & Mansell, W. (2004). Attention processes in the maintenance and treatment of social phobia: Hypervigilance, avoidance and self-focused attention. *Clinical Psychology Review*, *24*(7), 827–856. https://doi.org/10.1016/j.cpr.2004.06.005

Boinski, S. (1988). Use of a club by a wild white-faced capuchin (*Cebus capucinus*) to attack a venomous snake (*Bothrops asper*). *American Journal of Primatology*, *14*(2), 177–179. https://doi.org/10.1002/ajp.1350140208

Bourne, V. J. (2006). The divided visual field paradigm: Methodological considerations. *Laterality*, *11*(4), 373–393. https://doi.org/https://doi.org/10.1080/13576500600633982

Bugg, J. M., & Crump, M. J. C. (2012). In support of a distinction between voluntary and stimulus-driven control: A review of the literature on proportion congruent effects. *Frontiers in Psychology*, *3*, 367, 1-16. https://doi.org/10.3389/fpsyg.2012.00367

Buttelmann, D., Call, J., & Tomasello, M. (2009). Do great apes use emotional expressions to infer desires? *Developmental Science*, *12*(5), 688–698. https://doi.org/10.1111/J.1467-7687.2008.00802.X

Byrne, A., & Eysenck, M. W. (1995). Trait anxiety, anxious mood, and threat detection. *Cognition & Emotion*, *9*(6), 549–562. https://doi.org/10.1080/02699939508408982

Calcutt, S. E., Rubin, T. L., Pokorny, J. J., & de Waal, F. B. M. (2017). Discrimination of emotional facial expressions by tufted capuchin monkeys (*Sapajus apella*). *Journal of Comparative Psychology*, *131*(1), 40–49. https://doi.org/10.1037/com0000055

Chapman, A., Devue, C., & Grimshaw, G. M. (2019). Fleeting reliability in the dot-probe task. *Psychological Research*, *83*(2), 308–320. https://doi.org/10.1007/s00426-017-0947-6

Chew, P. (2015). Attentional bias: A methodological review. *GESJ: Education Science and Psychology*, *5*(37), 1521–1801.

Chiodera, P., & Coiro, V. (1987). Oxytocin reduces metyrapone-induced ACTH secretion in human subjects. *Brain Research*, *420*(1), 178–181. https://doi.org/10.1016/0006-8993(87)90257-5

Cisler, J. M., Bacon, A. K., & Williams, N. L. (2009). Phenomenological characteristics of attentional biases towards threat: A critical review. *Cognitive Therapy and Research*, *33*(2), 221–234. https://doi.org/10.1007/s10608-007-9161-y

Cisler, J. M., & Koster, E. H. W. (2010). Mechanisms of attentional biases towards threat in anxiety disorders: An integrative review. *Clinical Psychology Review*, *30*(2), 203–216. https://doi.org/10.1016/j.cpr.2009.11.003

Crockford, C., Wittig, R. M., Langergraber, K., Ziegler, T. E., Zuberbühler, K., & Deschner, T. (2013). Urinary oxytocin and social bonding in related and unrelated wild chimpanzees. *Proceedings of the Royal Society B: Biological Sciences*, *280*(1755), 20122765. https://doi.org/10.1098/rspb.2012.2765

Dal Monte, O., Noble, P. L., Costa, V. D., & Averbeck, B. B. (2014). Oxytocin enhances attention to the eye region in rhesus monkeys. *Frontiers in Neuroscience*, *8*(8), 41. https://doi.org/10.3389/fnins.2014.00041

De Dreu, C. K. W., Greer, L. L., Handgraaf, M. J. J., Shalvi, S., Van Kleef, G. A., Baas, M., Ten Velden, F. S., Van Dijk, E., & Feith, S. W. W. (2010). The neuropeptide oxytocin regulates parochial altruism in intergroup conflict among humans. *Science*, *328*(5984), 1408–1411. https://doi.org/10.1126/science.1189047

De Petrillo, F., & Rosati, A. G. (2019). Ecological rationality: Convergent decision-making in apes and capuchins. *Behavioural Processes*, *164*, 201–213. https://doi.org/10.1016/J.BEPROC.2019.05.010

Demuru, E., & Palagi, E. (2012). In bonobos yawn contagion is higher among kin and friends. *PLoS One*, *7*(11), e49613. https://doi.org/10.1371/journal.pone.0049613

Dettmer, A. M., Wooddell, L. J., Rosenberg, K. L., Kaburu, S. S. K., Novak, M. A., Meyer, J. S., & Suomi, S. J. (2017). Associations between early life experience, chronic HPA axis activity, and adult social rank in rhesus monkeys. *Social Neuroscience*, *12*(1), 92–101. https://doi.org/10.1080/17470919.2016.1176952

Ebitz, R. B., Watson, K. K., & Platt, M. L. (2013). Oxytocin blunts social vigilance in the rhesus macaque. *Proceedings of the National Academy of Sciences of the United States of America*, *110*(28), 11630–11635. https://doi.org/10.1073/pnas.1305230110

Eckstein, M. P., Mack, S. C., Liston, D. B., Bogush, L., Menzel, R., & Krauzlis, R. J. (2013). Rethinking human visual attention: Spatial cueing effects and optimality of decisions by honeybees, monkeys and humans. *Vision Research*, *85*, 5–19. https://doi.org/10.1016/J.VISRES.2012.12.011

Enock, P. M., Hofmann, S. G., & McNally, R. J. (2014). Attention bias modification training via smartphone to reduce social anxiety: A randomized, controlled multi-session experiment. *Cognitive Therapy and Research*, *38*(2), 200–216. https://doi.org/10.1007/s10608-014-9606-z

Feng, X., Wu, X., Morrill, R. J., Li, Z., Li, C., Yang, S., Li, Z., Cui, D., Lv, L., Hu, Z., Zhang, B., Yin, Y., Guo, L., Qin, D., & Hu, X. (2016). Social correlates of the dominance rank and long-term cortisol levels in adolescent and adult male rhesus macaques (*Macaca mulatta*). *Scientific Reports*, *6*(1), 1–9. https://doi.org/10.1038/srep25431

Fox, E., Russo, R., Bowles, R., & Dutton, K. (2001). Do threatening stimuli draw or hold visual attention in subclinical anxiety? *Journal of Experimental Psychology: General*, *130*(4), 681–700. https://doi.org/10.1037/0096-3445.130.4.681

Fragaszy, D., Visalberghi, E. & Fedigan, L. M. (2004). *The Complete Capuchin: The Biology of the Genus Cebus.* Cambridge University Press.

Gamer, M., Zurowski, B., & Büchel, C. (2010). Different amygdala subregions mediate valence-related and attentional effects of oxytocin in humans. *Proceedings of the National Academy of Sciences of the United States of America*, *107*(20), 9400–9405. https://doi.org/10.1073/pnas.1000985107

Garner, M., Mogg, K., & Bradley, B. P. (2006). Orienting and maintenance of gaze to facial expressions in social anxiety. *Journal of Abnormal Psychology*, *115*(4), 760–770. https://doi.org/10.1037/0021-843X.115.4.760

Guastella, A. J., Mitchell, P. B., & Dadds, M. R. (2008). Oxytocin increases gaze to the eye region of human faces. *Biological Psychiatry*, *63*(1), 3–5. https://doi.org/10.1016/j.biopsych.2007.06.026

Han, S., & Northoff, G. (2008). Culture-sensitive neural substrates of human cognition: A transcultural neuroimaging approach. *Nature Reviews Neuroscience*, *9*(8), 646–654. https://doi.org/10.1038/NRN2456;KWRD=BIOMEDICINE

Harari-Dahan, O., & Bernstein, A. (2014). A general approach - avoidance hypothesis of oxytocin: Accounting for social and non-social effects of oxytocin. *Neuroscience and Biobehavioral Reviews*, *47*, 506–519. https://doi.org/10.1016/j.neubiorev.2014.10.007

Hare, B., Melis, A. P., Woods, V., Hastings, S., & Wrangham, R. (2007). Tolerance Allows Bonobos to Outperform Chimpanzees on a Cooperative Task. *Current Biology*, *17*(7), 619–623. https://doi.org/10.1016/J.CUB.2007.02.040

Heinrichs, M., Baumgartner, T., Kirschbaum, C., & Ehlert, U. (2003). Social support and oxytocin interact to suppress cortisol and subjective responses to psychosocial stress. *Biological Psychiatry*, *54*(12), 1389–1398. https://doi.org/10.1016/S0006-3223(03)00465-7

Hoffman, K. L., Gothard, K. M., Schmid, M. C. C., & Logothetis, N. K. (2007). Facial-expression and gaze-selective responses in the monkey amygdala. *Current Biology*, *17*(9), 766–772. https://doi.org/10.1016/j.cub.2007.03.040

Hopper, L. M., Allritz, M., Egelkamp, C. L., Huskisson, S. M., Jacobson, S. L., Leinwand, J. G., & Ross, S. R. (2021). A comparative perspective on three primate species' responses to a pictorial emotional Stroop task. *Animals 11,* 588. https://doi.org/10.3390/ani11030588

Isbell, L. A. (2006). Snakes as agents of evolutionary change in primate brains. *Journal of Human Evolution*, *51*(1), 1–35. https://doi.org/10.1016/j.jhevol.2005.12.012

Jaeggi, A. V., Stevens, J. M. G., & Van Schaik, C. P. (2010). Tolerant food sharing and reciprocity is precluded by despotism among bonobos but not chimpanzees. *American Journal of Physical Anthropology*, *143*(1), 41–51. https://doi.org/10.1002/ajpa.21288

Kano, F., Tanaka, M., & Tomonaga, M. (2008). Enhanced recognition of emotional stimuli in the chimpanzee (*Pan troglodytes*). *Animal Cognition*, *11*(3), 517–524. https://doi.org/10.1007/S10071-008-0142-7/FIGURES/4

Kano, F., & Tomonaga, M. (2010). Attention to emotional scenes including whole-body expressions in chimpanzees (Pan troglodytes). *Journal of Comparative Psychology*, *124*(3), 287–294. https://doi.org/10.1037/A0019146

King, H. M., Kurdziel, L. B., Meyer, J. S., & Lacreuse, A. (2012). Effects of testosterone on attention and memory for emotional stimuli in male rhesus monkeys. *Psychoneuroendocrinology*, *37*(3), 396–409. https://doi.org/10.1016/j.psyneuen.2011.07.010

Knott, C. D. (1999). Orangutan behavior and ecology. In P. Dolhinow & A. Fuentes (Eds.), *The Nonhuman Primates. Mountain View.* Mayfield Publishing p.50-57.

Koster, E. H. W., Crombez, G., Verschuere, B., & De Houwer, J. (2004). Selective attention to threat in the dot probe paradigm: Differentiating vigilance and difficulty to disengage. *Behaviour Research and Therapy*, *42*(10), 1183–1192. https://doi.org/10.1016/j.brat.2003.08.001

Kret, M. E., Jaasma, L., Bionda, T., & Wijnen, J. G. (2016). Bonobos (*Pan paniscus*) show an attentional bias toward conspecifics' emotions. *Proceedings of the National Academy of Sciences of the United States of America*, *113*(14), 3761–3766. https://doi.org/10.1073/pnas.1522060113

Kret, M. E., Muramatsu, A., & Matsuzawa, T. (2018). Emotion processing across and within species: A comparison between humans (*Homo sapiens*) and chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, *132*(4), 395–409. https://doi.org/10.1037/com0000108

Lacreuse, A., Schatz, K., Strazzullo, S., King, H. M., & Ready, R. (2013). Attentional biases and memory for emotional stimuli in men and male rhesus monkeys. *Animal Cognition*, *16*(6), 861–871. https://doi.org/10.1007/s10071-013-0618-y

Laméris, D., Van Berlo, E., Roth, T., & Kret, M. (2022). No evidence for biased attention towards emotional scenes in Bornean orangutans (*Pongo pygmaeus*). *Affective Science, 3*(4), 772–782. https://doi.org/10.1007/S42761-022-00158-X

Laméris, D., Verspeek, J., Eens, M., & Stevens, J. (2022). Social and nonsocial stimuli alter the performance of bonobos during a pictorial emotional Stroop task. *American Journal of Primatology*, *84*(2). https://doi.org/10.1002/AJP.23356

Lauwereyns, J., Koizumi, M., Sakagami, M., Hikosaka, O., Kobayashi, S., & Tsutsui, K. (2000). Interference from irrelevant features on visual discrimination by macaques (*Macaca fuscata*): A behavioral analogue of the human Stroop effect. *Journal of Experimental Psychology: Animal Behavior Processes*, *23*(6), 352–357. doi: 10.1037/0097-7403.26.3.352

Leinwand, J. G., Fidino, M., Ross, S. R., & Hopper, L. M. (2022). Familiarity mediates apes' attentional biases toward human faces. *Proceedings of the Royal Society B: Biological Sciences*, *289*(1973). 20212599 https://doi.org/10.1098/RSPB.2021.2599

Leopold, D. A., & Rhodes, G. (2010). A comparative view of face perception. *Journal of Comparative Psychology*, *124*(3), 233–251. https://doi.org/10.1037/a0019460

Lewis, L. S., & Krupenye, C. (2022). Eye-tracking as a window into primate social cognition. *American Journal of Primatology*, *84*(10), e23393. https://doi.org/10.1002/AJP.23393;SUBPAGE:STRING:FULL

Lewis, L. S., Wessling, E. G., Kano, F., Stevens, J. M. G., Call, J., & Krupenye, C. (2023). Bonobos and chimpanzees remember familiar conspecifics for decades. *Proceedings of the National Academy of Sciences of the United States of America*, *120*(52), e2304903120. https://doi.org/10.1073/PNAS.2304903120/SUPPL_FILE/PNAS.2304903120.SD03.XLSX

Liang, C.-W., Tsai, J.-L., & Hsu, W.-Y. (2016). Sustained visual attention for competing emotional stimuli in social anxiety: An eye tracking study. *Journal of Behavior Therapy and Experimental Psychiatry, 54*, 178-185. https://doi.org/10.1016/j.jbtep.2016.08.009

Lipp, O. V, & Waters, A. M. (2007). When danger lurks in the background: Attentional capture by animal fear-relevant distractors is specific and selectively enhanced by animal fear. *Psychological Association*, *7*(1), 192–200. https://doi.org/10.1037/1528-3542.7.1.192

LoBue, V., & DeLoache, J. S. (2008). Detecting the snake in the grass: Attention to fear-relevant stimuli by adults and young children: Research article. *Psychological Science*, *19*(3), 284–289. https://doi.org/10.1111/j.1467-9280.2008.02081.x

Macleod, C. M. (1991). Half a century of research on the Stroop effect: an integrative review. *Psychological Bulletin*, *109*(2), 163–203. https://doi.org/https://doi.org/10.1037/0033-2909.109.2.163

MacLeod, C., Mathews, A., & Tata, P. (1986). Attentional bias in emotional disorders. *Journal of Abnormal Psychology*, *95*(1), 15–20. https://doi.org/10.1037/0021-843X.95.1.15

Malenky, R. K., & Wrangham, R. W. (1994). A quantitative comparison of terrestrial herbaceous food consumption by Pan paniscus in the Lomako Forest, Zaire, and Pan troglodytes in the Kibale Forest, Uganda. *American Journal of Primatology*, *32*(1), 1–12. https://doi.org/10.1002/AJP.1350320102

Mathews, A., & Macleod, C. (1985). Selective processing of threat cues in anxiety states. *Behaviour Research and Therapy*, *23*(5), 563–569. https://doi.org/10.1016/0005-7967(85)90104-4

Matsumura, S. (1999). The evolution of 'Egalitarian' and 'Despotic' social systems among macaques. *Primates*, *40*(1), 23–31. https://doi.org/10.1007/BF02557699/METRICS

Matsuno, T., & Tomonaga, M. (2006). Visual search for moving and stationary items in chimpanzees (*Pan troglodytes*) and humans (*Homo sapiens*). *Behavioural Brain Research*, *172*(2), 219–232. https://doi.org/10.1016/J.BBR.2006.05.004

Micheletta, J., Whitehouse, J., Parr, L. A., & Waller, B. M. (2015). Facial expression recognition in crested macaques (*Macaca nigra*). *Animal Cognition*, *18*(4), 985–990. https://doi.org/10.1007/s10071-015-0867-z

Miltner, W. H. R., Krieschel, S., Hecht, H., Trippe, R., & Weiss, T. (2004). Eye movements and behavioral responses to threatening and nonthreatening stimuli during visual search in phobic and nonphobic subjects. *Emotion*, *4*(4), 323–339. https://doi.org/10.1037/1528-3542.4.4.323

Mineka, S., Keir, R., & Price, V. (1980). Fear of snakes in wild- and laboratory-reared rhesus monkeys (*Macaca mulatta*). *Animal Learning & Behavior*, *8*(4), 653–663. https://doi.org/10.3758/BF03197783

Mogg, K., & Bradley, B. P. (1998). A cognitive-motivational analysis of anxiety. *Behaviour Research and Therapy*, *36*(9), 809–848. https://doi.org/10.1016/S0005-7967(98)00063-1

Mogg, K., Bradley, B. P., De Bono, J., & Painter, M. (1997). Time course of attentional bias for threat information in non-clinical anxiety. *Behaviour Research and Therapy*, *35*(4), 297–303. https://doi.org/10.1016/S0005-7967(96)00109-X

Mogg, K., Bradley, B. P., Dixon, C., Fisher, S., Twelftree, H., & McWilliams, A. (2000). Trait anxiety, defensiveness and selective processing of threat: An investigation using two measures of attentional bias. *Personality and Individual Differences*, *28*(6), 1063–1077. https://doi.org/10.1016/S0191-8869(99)00157-9

Morin, E. L., Howell, B. R., Meyer, J. S., & Sanchez, M. M. (2019). Effects of early maternal care on adolescent attention bias to threat in nonhuman primates. *Developmental Cognitive Neuroscience*, *38*, e100643. https://doi.org/10.1016/j.dcn.2019.100643

Morton, F. B., Brosnan, S. F., Prétôt, L., Buchanan-Smith, H. M., O'Sullivan, E., Stocker, M., D'Mello, D., & Wilson, V. A. D. (2016). Using photographs to study animal social cognition and behaviour: Do capuchins' responses to photos reflect reality? *Behavioural Processes*, *124*, 38–46. https://doi.org/10.1016/j.beproc.2015.10.005

Neumann, I. D. (2002). Involvement of the brain oxytocin system in stress coping: Interactions with the hypothalamo-pituitary-adrenal axis. *Progress in Brain Research*, *139*, 147–162. https://doi.org/10.1016/S0079-6123(02)39014-9

Neumann, I. D., Johnstone, H. A., Hatzinger, M., Liebsch, G., Shipston, M., Russell, J. A., Landgraf, R., & Douglas, A. J. (1998). Attenuated neuroendocrine responses to emotional and physical stressors in pregnant rats involve adenohypophysial changes. *Journal of Physiology*, *508*(1), 289–300. https://doi.org/10.1111/j.1469-7793.1998.289br.x

Novak, M. A., Hamel, A. F., Kelly, B. J., Dettmer, A. M., & Meyer, J. S. (2013). Stress, the HPA axis, and nonhuman primate well-being: A review. *Applied Animal Behaviour Science*, *143*, 135–149. https://doi.org/10.1016/j.applanim.2012.10.012

Öhman, A., Flykt, A., Esteves, F., & Institute, K. (2001). Emotion drives attention: Detecting the snake in the grass. *Journal of Experimental Psychology: General*, *130*(3), 466–478. https://doi.org/10.1037/AXJ96-3445.130.3.466

Palagi, E., Norscia, I., & Demuru, E. (2014). Yawn contagion in humans and bonobos: Emotional affinity matters more than species. *PeerJ*, *2014*(1), e519. https://doi.org/10.7717/peerj.519

Parr, L. A. (2003). The discrimination of faces and their emotional content by chimpanzees (*Pan troglodytes*). *Annals of the New York Academy of Sciences*, *1000*(1), 56–78. https://doi.org/10.1196/ANNALS.1280.005

Parr, L. A., & Heintz, M. (2009). Facial expression recognition in rhesus monkeys, *Macaca mulatta*. *Animal Behaviour*, *77*(6), 1507–1513. https://doi.org/10.1016/j.anbehav.2009.02.024

Parr, L. A., Modi, M., Siebert, E., & Young, L. J. (2013). Intranasal oxytocin selectively attenuates rhesus monkeys' attention to negative facial expressions. *Psychoneuroendocrinology*, *38*(9), 1748–1756. https://doi.org/10.1016/j.psyneuen.2013.02.011

Parr, L. A., Waller, B. M., & Heintz, M. (2008). Facial expression categorization by chimpanzees using standardized stimuli. *Emotion*, *8*(2), 216–231. https://doi.org/10.1037/1528-3542.8.2.216

Parr, L. A., Winslow, J. T., Hopkins, W. D., & de Waal, F. B. M. (2000). Recognizing facial cues: Individual discrimination by chimpanzees (*Pan troglodytes*) and rhesus monkeys (*Macaca mulatto*). *Journal of Comparative Psychology*, *114*(1), 47–60. https://doi.org/10.1037/0735-7036.114.1.47

Pelé, M., Broihanne, M. H., Thierry, B., Call, J., & Dufour, V. (2014). To bet or not to bet? Decision-making under risk in non-human primates. *Journal of Risk and Uncertainty*, *49*(2), 141–166. https://doi.org/10.1007/s11166-014-9202-3

Pflugshaupt, T., Mosimann, U. P., Von Wartburg, R., Schmitt, W., Nyffeler, T., & Müri, R. M. (2005). Hypervigilance-avoidance pattern in spider phobia. *Journal of Anxiety Disorders*, *19*(1), 105–116. https://doi.org/10.1016/j.janxdis.2003.12.002

Pokorny, J. J., & De Waal, F. B. M. (2009). Face recognition in capuchin monkeys (*Cebus apella*). *Journal of Comparative Psychology*, *123*(2), 151–160. https://doi.org/10.1037/a0014073

Posner, M. I. (1980). Orienting of attention. *Quarterly Journal of Experimental Psychology*, *32*(1), 3–25. https://doi.org/10.1080/00335558008248231

Ray, J. C., & Sapolsky, R. M. (1992). Styles of male social behavior and their endocrine correlates among high-ranking wild baboons. *American Journal of Primatology*, *28*(4), 231–250. https://doi.org/10.1002/ajp.1350280402

Reilly, O. T., Benítez, M. E., Beran, M. J., Barber, S. J., & Brosnan, S. F. (2024). No evidence of attentional bias toward threatening conspecific and allospecific faces in capuchin monkeys (*Sapajus* [*Cebus*] *apella*) using a dot-probe task. *Journal of Comparative Psychology*. https://doi.org/10.1037/com0000381

Rinck, M., Becker, E. S., Kellermann, J., & Roth, W. T. (2003). Selective attention in anxiety: Distraction and enhancement in visual search. *Depression and Anxiety*, *18*(1), 18–28. https://doi.org/10.1002/da.10105

Rogers, M. E., Abernethy, K., Bermejo, M., Cipolletta, C., Doran, D., Mcfarland, K., Nishihara, T., Remis, M., & Tutin, C. E. G. (2004). Western gorilla diet: A synthesis from six sites. *American Journal of Primatology*, *64*(2), 173–192. https://doi.org/10.1002/AJP.20071

Rosati, A. G. (2017). Ecological variation in cognition: Insights from bonobos and chimpanzees. In Hare, B., Yammamoto, S. (Eds.), Bonobos: Unique in Mind, Brain, and Behavior. Oxford University Press, Oxford, pp157-170. https://doi.org/10.1093/oso/9780198728511.003.0011

Roth, T. S., Rianti, P., Fredriksson, G. M., Wich, S. A., & Nowak, M. G. (2020). Grouping behavior of Sumatran orangutans (Pongo abelii) and Tapanuli orangutans (*Pongo tapanuliensis*) living in forest with low fruit abundance. *American Journal of Primatology*, *82,* e23123. https://doi.org/10.1002/ajp.23123

Sanz, C. M., & Morgan, D. B. (2009). Flexible and persistent tool-using strategies in honey-gathering by wild chimpanzees. *International Journal of Primatology*, *30*(3), 411–427. https://doi.org/10.1007/s10764-009-9350-5

Sapolsky, R. M. (2005). The influence of social hierarchy on primate health. *Science*, *308*(5722), 648–652. https://doi.org/10.1126/science.1106477

Sapolsky, R. M., & Ray, J. C. (1989). Styles of dominance and their endocrine correlates among wild olive baboons (Papio anubis). *American Journal of Primatology*, *18*(1), 1–13. https://doi.org/10.1002/ajp.1350180102

Schmidt, K. L., & Cohn, J. F. (2001). Human facial expressions as adaptations: Evolutionary questions in facial expression research. *American Journal of Physical Anthropology*, *116*(S33), 3–24. https://doi.org/10.1002/ajpa.20001

Schmukle, S. C. (2005). Unreliability of the dot probe task. *European Journal of Personality*, *19*(7), 595–605. https://doi.org/10.1002/per.554

Seyfarth, R. M., Cheney, D. L., & Marler, P. (1980). Vervet monkey alarm calls: Semantic communication in a free-ranging primate. *Animal Behaviour*, *28*, 1070–1094. https://doi.org/https://doi.org/10.1016/S0003-3472(80)80097-2

Shamay-Tsoory, S. G., & Abu-Akel, A. (2016). The social salience hypothesis of oxytocin. *Biological Psychiatry*, *79*(3), 194–202. https://doi.org/10.1016/j.biopsych.2015.07.020

Shamay-Tsoory, S. G., Fischer, M., Dvash, J., Harari, H., Perach-Bloom, N., & Levkovitz, Y. (2009). Intranasal administration of oxytocin increases envy and schadenfreude (gloating). *Biological Psychiatry*, *66*, 864–870. https://doi.org/10.1016/j.biopsych.2009.06.009

Shibasaki, M., & Kawai, N. (2009). Rapid detection of snakes by Japanese monkeys (Macaca fuscata): An evolutionarily predisposed visual system. *Journal of Comparative Psychology*, *123*(2), 131–135. https://doi.org/10.1037/a0015095

Sosnowski, M. J., Reilly, O. T., Brosnan, S. F., & Benítez, M. E. (2023). Oxytocin increases during fur-rubbing regardless of level of social contact in tufted capuchin monkeys. *American Journal of Primatology*, e23490. https://doi.org/10.1002/AJP.23490

Staugaard, S. R. (2009). Reliability of two versions of the dot-probe task using photographic faces. *Psychology Science Quarterly*, *51*(3), 339–350.

Stormark, K. M., Nordby, H., & Hugdahl, K. (1995). Attentional shifts to emotionally charged cues: Behavioural and erp data. *Cognition and Emotion*, *9*(5), 507–523. https://doi.org/10.1080/02699939508408978

Stroop, J. R. (1935). Studies of interference in serial verbal reactions. *Journal of Experimental Psychology*, *18*(6), 643–662. https://doi.org/https://doi.org/10.1037/h0054651

Talbot, C. F., Leverett, K. L., & Brosnan, S. F. (2016). Capuchins recognize familiar faces. *Animal Behaviour*, *122*, 37–45. https://doi.org/10.1016/j.anbehav.2016.09.017

Taubert, J., Flessert, M., Liu, N., & Ungerleider, L. G. (2019). Intranasal oxytocin selectively modulates the behavior of rhesus monkeys in an expression matching task. *Scientific Reports*, *9*(1) 15187. https://doi.org/10.1038/s41598-019-51422-3

Thierry, B. (1985). Patterns of agonistic interactions in three species of macaque *(Macaca mulatta, M fascicularis, M tonkeana) Aggress Behav 11 (3)*, 223-233. https://doi.org/10.1002/1098-2337(1985)11:33.0.CO;2-A

Tomonaga, M. (1995). Visual search by chimpanzees (*Pan*): Assessment of controlling relations. *Journal of the Experimental Analysis of Behavior*, *63*, 175–186. https://doi.org/https://doi.org/10.1901/jeab.1995.63-175

Tomonaga, M., & Imura, T. (2009). Faces capture the visuospatial attention of chimpanzees (*Pan troglodytes*): evidence from a cueing experiment. *Frontiers in Zoology*, *6*(1), 1–7. https://doi.org/10.1186/1742-9994-6-14

Tomonaga, M., & Imura, T. (2015). Efficient search for a face by chimpanzees (*Pan troglodytes*). *Scientific Reports*, *5*, 11437. https://doi.org/10.1038/srep11437

Uvnäs-Moberg, K. (1998). Oxytocin may mediate the benefits of positive social interaction and emotions. *Psychoneuroendocrinology*, *23*(8), 819–835. https://doi.org/10.1016/S0306-4530(98)00056-0

Uvnäs-Moberg, K., Widström, A. M., Nissen, E., & Björvell, H. (1990). Personality traits in women 4 days postpartum and their correlation with plasma levels of oxytocin and prolactin. *Journal of Psychosomatic Obstetrics and Gynecology*, *11*(4), 261–273. https://doi.org/10.3109/01674829009084422

van Berlo, E., Bionda, T., & Kret, M. E. (2023). Attention toward emotions is modulated by familiarity with the expressor: A comparison between bonobos and humans. *Emotion*. https://doi.org/10.1037/emo0000882

van Rooijen, R., Ploeger, A., & Kret, M. E. (2017). The dot-probe task to measure emotional attention: A suitable measure in comparative studies? *Psychonomic Bulletin and Review*, *24*(6), 1686–1717. https://doi.org/10.3758/s13423-016-1224-1

Van Schaik, C. P. (1999). The socioecology of fission-fusion sociality in Orangutans. *Primates*, *40*(1), 69–86. https://doi.org/10.1007/BF02557703/METRICS

van Schaik, C. P., Marshall, A. J., & Wich, S. A. (2009). Geographic variation in orangutan behavior and biology. Its functional interpretation and its mechanistic basis. In *Orangutans: Geographic Variation in Behavioral Ecology and Conservation* (eds S. A. Wich, S. S. Utami Atmoko, T. M. Setia and C. P. Schaik), pp. 351–361. Oxford University Press, New York..

Waechter, S., Nelson, A. L., Wright, C., Hyatt, A., & Oakman, J. (2014). Measuring attentional bias to threat: Reliability of dot probe and eye movement indices. *Cognitive Therapy and Research*, *38*(3), 313–333. https://doi.org/10.1007/s10608-013-9588-2

Waller, B. M., Caeiro, C. C., & Davila-Ross, M. (2015). Orangutans modify facial displays depending on recipient attention. *PeerJ*, *2015*(3), e827. https://doi.org/10.7717/PEERJ.827/SUPP-1

Washburn, D. A. (1994). Stroop-like effects for monkeys and humans: Processing Speed or Strength of Association? *Psychological Science*, *5*(6), 375–379. https://doi.org/10.1111/j.1467-9280.1994.tb00288.x

Williams, J. M. G., Mathews, A., & Macleod, C. (1996). The emotional stroop task and psychopathology. *Psychological Bulletin*, *120*(1), 3–24. https://doi.org/https://doi.org/10.1037/0033-2909.120.1.3

Wilson, D. A., & Tomonaga, M. (2018). Exploring attentional bias towards threatening faces in chimpanzees using the dot probe task. *PLoS One*, *13*(11), e0207378. https://doi.org/10.1371/journal.pone.0207378

Wittig, R. M., Crockford, C., Weltring, A., Langergraber, K. E., Deschner, T., & Zuberbühler, K. (2016). Social support reduces stress hormone levels in wild chimpanzees across stressful events and everyday affiliations. *Nature Communications*, *7*(1), 1–8. https://doi.org/10.1038/ncomms13361