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Original Article

Dangerous Animals Capture and Maintain Attention in Humans

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Abstract: Predation is a major source of natural selection on primates and may have shaped attentional processes that allow primates to rapidly detect dangerous animals. Because ancestral humans were subjected to predation, a process that continues at very low frequencies, we examined the visual processes by which men and women detect dangerous animals (snakes and lions). We recorded the eye movements of participants as they detected images of a dangerous animal (target) among arrays of nondangerous animals (distractors) as well as detected images of a nondangerous animal (target) among arrays of dangerous animals (distractors). We found that participants were quicker to locate targets when the targets were dangerous animals compared with nondangerous animals, even when spatial frequency and luminance were controlled. The participants were slower to locate nondangerous targets because they spent more time looking at dangerous distractors, a process known as delayed disengagement, and looked at a larger number of dangerous distractors. These results indicate that dangerous animals capture and maintain attention in humans, suggesting that historical predation has shaped some facets of visual orienting and its underlying neural architecture in modern humans.

Keywords: attention, humans, delayed disengagement, eye-tracking, predation, predator detection

Introduction

Predation has been an important source of natural selection on primates. A variety of predators, such as snakes and felids (Hart and Sussman, 2005; Isbell, 2006; Stanford, 2002), have preyed upon primates for millions of years. Humans are no exception, as their

hominin ancestors also suffered from predation, and they continue to experience predation from large-bodied felids and snakes in rural areas (Coss, Fitzhugh, Schmid-Holmes, Kenyon, and Etling, 2009; Coss and Moore, 2002; Hart and Sussman, 2005; Headland and Greene, 2011; Treves and Palmqvist, 2007). The ability of primates to rapidly respond to potential danger is critical to their survival (Caro, 2005). Before individuals can respond to potential danger and engage in defensive action, they must first detect the threat by directing their attention (covertly or overtly) toward it (Cronin, 2005; Dukas and Kamil, 2000; Huijding, Mayer, and Koster, 2011; Yorzinski, Patricelli, Babcock, Pearson, and Platt, 2013; Yorzinski and Platt, 2014).

It is possible that our long evolutionary history with predators has shaped our visual system to quickly detect dangerous animals (Coss, 2003; Isbell, 2006). Visual-search experiments have found that children, including infants as young as 8-months, and adults, are faster to detect threatening animals, including snakes, spiders, and lions, compared with nonthreatening animals (Blanchette, 2006; Brosch and Sharma, 2005; Flykt, 2005; LoBue and DeLoache, 2008, 2010; Öhman, Flykt, and Esteves, 2001; Penkunas and Coss, 2013a,b; Rosa, Gamito, Oliveira, Morais, and Saraiva, 2011; Waters, Lipp, and Spence, 2004). Ontogenetic experiences with threats also influence detection performance (Blanchette, 2006; Fox, Griggs, and Mouchlianitis, 2007). People are faster to detect contemporary threats (such as guns and syringes) compared to neutral stimuli even though these contemporary threats are too recent to have influenced our evolutionary history. The perceptual processes responsible for this rapid detection of threats are largely unknown.

Based on studies that directly measure visual attention (using eye-trackers to monitor eye movements), threatening stimuli are often better at attracting and holding attention compared to nonthreatening stimuli. Humans are faster at detecting images of dangerous people and people experiencing threat than people who are not threatened (Nummenmaa, Hyona, and Calvo, 2006). Furthermore, humans, especially high-anxious individuals, are slower to disengage their attention when viewing angry faces compared with happy or neutral faces (Belopolsky, Devue, and Theeuwes, 2012; Reinholdt-Dunne et al., 2012). Similarly, people often detect spider and snake images faster than neutral images (Gerdes, Pauli, and Alpers 2009; Rosa et al., 2011).

The purpose of this study was to examine the processes of visual scanning that guide humans' abilities to detect dangerous animals rapidly. The eye movements of adult participants were recorded as they located a single image of a dangerous animal (target) embedded in an array of nondangerous animals (distractors) or detected a nondangerous animal (target) embedded in an array of dangerous animals (distractors). The participants were presented with color images and images in which low-level features were minimized (spatial frequency and luminance were controlled). We tested whether dangerous animals: (i) maintain attention or "delay disengagement" during visual search (Fox, Russo, and Dutton, 2002) and/or (ii) exogenously attract attention through low-level features (e.g., luminance or contrast; Simons, 2000). If dangerous animals are effective at maintaining attention, we predicted that humans would spend more time looking at distractors when the distractors were dangerous animals compared with nondangerous animals. If dangerous animals capture attention through low-level features, we predicted that humans would look at a larger number of distractors when the distractors were dangerous animals compared

with nondangerous animals.

Materials and Methods

Participants

Thirty men and 30 women participated in this study at Duke University from November 2012 through March 2013. They were all of European heritage and between the ages of 18 and 30 years old (M=21.4, SE=0.33 years). Flyers and emails were used to recruit participants, and they were told that they would be participating in a study that explored predator recognition. They earned \$15 for their participation. The Institutional Review Board of Duke University (#7646) approved this study; written consent was obtained from all participants.

Animal images

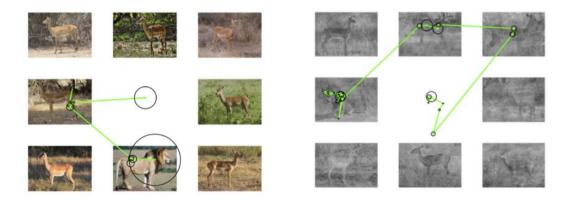
We created two sets of 96 matrices that displayed images of dangerous and nondangerous animals. One set showed images of lions (*Panthera leo*) and impalas (*Aepyceros melampus*), and the other set showed images of snakes (*Serpentes*) and lizards (*Lacertilia*). Each set included four treatment blocks of 24 matrices.

In the first set, the first treatment block (Target Lion) consisted of 24 matrices that were created from 24 images of lions and impalas. Each matrix consisted of a 3×3 array in which one lion image (target) and seven impala images (distractors) were displayed (the middle matrix position was left empty; see Figure 1a). Each matrix was 1280 × 1024 pixels (dpi = 96) and filled the entire screen. Images within the matrices were 293×208 pixels (approximately 7.4 degrees wide and 5.2 degrees high); 100 pixels separated images from each other and from the edges of the matrices. Lion images appeared three times in each of the eight possible positions across the 24 matrices, and a different lion photograph was used in each matrix. Impala images appeared in pseudo-randomized positions within each matrix such that each image appeared seven times across the 24 matrices but was never in the same matrix position more than once and only appeared one time within the same matrix. The lion and impala images consisted of adult males with manes and adult females, respectively, and displayed animals that were standing with all four legs on the ground and not looking directly at the camera. The images depicted each animal in a natural scene and none of the animals were displaying obviously threatening or defensive postures; the images were obtained from online sources.

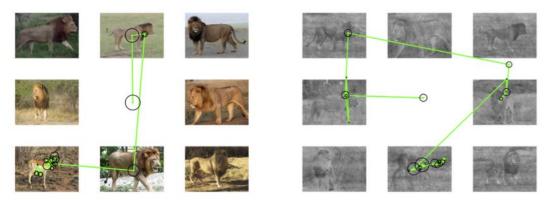
A second treatment block (Target Lion Low Level Control) was created using the 24 matrices that were generated in the first treatment block; the matrices were processed using the SHINE toolbox (default settings; Willenbockel et al., 2010) in MATLAB to minimize low-level confounds (images within a matrix were matched for luminance and spatial frequency; see Figure 1b). The SHINE toolbox first matches the Fourier amplitude spectra of the images (spatial frequency matching) and then matches the luminance histograms (Willenbockel et al., 2010); the low-level features of the resulting images are therefore minimized (because they have the same luminance and spatial frequency) but not entirely eliminated since the toolbox does not match other low-level features (such as edges or orientation).

Figure 1. Examples of scanpaths from one male participant on matrices from the four treatment blocks of the lion and impala set

a. b.



c. d.



Note. (a) Target Lion; (b) Target Lion Low Level Control; (c) Target Impala; (d) Target Impala Low Level Control. The size of the black circles indicates the amount of time the participant spent looking at each location. Gaze begins in the middle of the image and ends on the target animal.

The process used to create images in the first and second treatment blocks was repeated to generate the third and fourth treatment blocks (Target Impala and Target Impala Low Level Control) except that one impala image (target) and seven lion images (distractors) were used in each image. Therefore, there were a total of 96 matrices in the Target Lion, Target Lion Low Level Control, Target Impala, and Target Impala Low Level Control treatment blocks.

The second set of 96 matrices was created using the same procedure that we used to create the first set except that we used images of snakes and lizards. The snake and lizard images were the same as those used in previous studies (see Penkunas and Coss, 2013a,b). The images were used to create the Target Snake, Target Snake Low Level Control, Target Lizard, and Target Lizard Low Level Control blocks.

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Eye-tracker

We used a Tobii T60 eye-tracker along with Tobi Studio 3.1 and 3.2 (Tobii Technology, Inc., Sweden) to present our images and record the gaze of participants (accuracy: 0.5 degrees; data rate: 60 Hz; binocular tracking). Participants were told that we were measuring the size of their pupils but were not told that their eye movements were being monitored until after they completed the trial. The images were displayed using Tobii StudioTM software (version 3.1 or 3.2) on a 1280×1024 pixel monitor (43.18 cm diagonal). Participants were positioned approximately 60 cm from the screen and were unrestrained (i.e., no bite bar or chin rest was used). The equipment was calibrated (9 points) before each trial began. We used the Tobii Velocity-Threshold Identification filter (I-VT filter; gap fill-in: 75 ms; eye selection: average; noise reduction: median; noise reduction samples: 7; velocity calculator window: 20 ms; I-VT classifier threshold: 30 degrees/sec; merge adjacent time: 75 ms; merge adjacent angle: 0.5 degrees; discard short fixations: 60 ms) to classify fixations and saccades. This filter classifies eye movements as fixations or saccades based upon the velocity of eye movements; eye movements below and above the velocity threshold (30 degrees/sec, in this study) are classified as fixations and saccades, respectively. Eye-tracking data consisted of coordinates of where participants were known to be looking during each sampling point.

Experimental procedure

The experimenter (JLY) first asked participants to perform two practice trials so they could become familiar with the procedure. In the first practice trial, participants were asked to fixate a black dot that appeared in the center of the screen for 1 sec. They were then presented with a 3×3 matrix that consisted of one image of a dog and seven images of cats (arranged in the same manner as described above for the predator and nonpredator matrices). They were instructed to press the space bar on the keyboard as soon as they located the dog image within the matrix. Once they pressed the space bar, the matrix disappeared and the fixation dot reappeared. They repeated this process for 10 matrices. The second practice trial was similar to the first except that the 10 matrices of the dogs and cats were altered to minimize low-level confounds (see above).

After completing the two practice trials, participants were then presented with the first set of 24 matrices. As in the practice trials, they were instructed to fixate a central dot; when a matrix appeared, they were asked to press the space bar as soon as they found the target animal. Because the participants fixated this central dot, the middle position of the matrices was left empty (see animal images above) to ensure that participants had to search for the target. They performed this task for each of the four blocks of matrices within the set (the order of the blocks was randomized across participants). This process was repeated a second time with the second set of matrices (the order of the sets was randomized across participants). Therefore, a participant would perform the search task on eight blocks of matrices: Target Lion, Target Impala, Target Lion Low Level Control, Target Impala Low Level Control, Target Snake, Target Lizard, Target Snake Low Level Control, and Target Lizard Low Level Control, with the order of the blocks and sets randomized across participants.

Measurements and statistical analysis

Using a customized MATLAB program, we drew rectangular regions of interest (ROI) around each target and distractor. All target and distractor images were the same size (293 × 208 pixels; see Animal Images above) and their ROIs included the entire rectangular region of each image. For each fixation coordinate, we determined which ROI it fell within to determine whether the participant was looking at the target image, distractor images, or neither the target nor distractor images. We calculated four metrics: the amount of time that elapsed before participants fixated on the target (Latency to Fixate Target Animal), the amount of time that elapsed before participants manually responded by pressing the space bar to indicate they detected the target (Latency to Manual Response), the number of different distractors the participants fixated (No. of Different Distractors Fixated), and the average time that participants spent looking at each distractor, only including distractors that were fixated (Time Viewing Distractors). For each participant, we calculated the mean value of the metrics within each of the eight treatment blocks (Target Lion, Target Impala, Target Lion Low Level Control, Target Impala Low Level Control, Target Snake, Target Lizard, Target Snake Low Level Control, and Target Lizard Low Level Control). In matrices where the data indicated a participant never fixated the target, it was not possible to determine whether (i) participants did not fixate the target (and therefore did not correctly perform the task) or (ii) whether the eye-tracker failed to record the participants' gaze when they were fixating the target. We therefore excluded a given matrix from the analysis if a participant's fixations never fell within the target or if more than 10% of the gaze data was missing; only 4.6% of the matrices were discarded due to this restriction.

We analyzed our data using linear mixed-effects models with repeated measures and an unstructured covariance structure (PROC MIXED) in SAS (SAS Institute Inc., Cary, NC). We examined whether the latency to fixate the target animal, latency to manually respond, number of different distractor images fixated, and time viewing each distractor image were influenced by the sex of the participant (male or female), animal class of the target (mammal vs. reptile), danger level of the target (dangerous vs. not dangerous), type of image (natural image vs. image that controlled for low-level features), and their interactions; we included participant identity as a random effect. Because sex of the participant was nonsignificant in all models (ps > 0.2), we dropped this term from the models. We made *a priori* predictions regarding differences among treatment blocks and created contrasts to evaluate these differences; we performed eight comparisons and used a Bonferroni correction to evaluate significance. Means \pm SEs are provided in the Results section to illustrate effect sizes.

Results

The latency to locate the target image (fixate and manual response), number of different distractor images fixated, and time viewing each distractor image varied depending on the animal class (see Table 1A), danger level (see Table 1B), image type (see Table 1C), and some of the interactions among these variables (see Table 1D-G). Participants were faster to fixate the target when the target was a dangerous animal (lion and snake) compared to when it was a nondangerous animal (impala and lizard) in both the

natural matrices (lion: 621 ± 11 ms; impala: 773 ± 15 ms; snake: 733 ± 18 ms; lizard: 836 ± 20 ms; see Latency to Fixate Target Animal, Table 1H and J) and matrices that minimized low-level features (lion: 801 ± 16 ms; impala: 969 ± 23 ms; snake: 941 ± 24 ms; lizard: 1071 ± 18 ms; see Latency to Fixate Target Animal, Table 1I and K); however, participants were slower to fixate a given target in the low-level matrices compared with the natural matrices (see Latency to Fixate Target Animal, Table 1L-O; see Figure 2a).

Participants were also faster to detect the target via manual response when the target was a dangerous animal (lion and snake) compared to when it was a nondangerous animal (impala and lizard) in both the natural matrices (lion: 980 ± 22 ms; impala: 1182 ± 25 ms; snake: 1174 ± 32 ms; lizard: 1381 ± 44 ms; see Latency to Manual Response, Table 1H and J) and matrices that minimized low-level features (lion: 1250 ± 27 ms; impala: 1511 ± 34 ms; snake: 1608 ± 60 ms; lizard: 1868 ± 56 ms; see Latency to Manual Response, Table 1I and K); however, participants were slower to detect a given target in the low-level matrices compared with the natural matrices (see Latency to Manual Response, Table 1L-O; see Figure 2b). Participants were faster to visually fixate the target than indicate they had detected the target via a manual response (paired t-test: t = 44.1, p < 0.0001).

In both the natural matrices and the matrices that minimized low-level features, participants looked at a greater number of distractor images (see No. of Different Distractors Fixated, Table 1H-K; see Figure 3) and spent more time looking at each distractor image (see Time Viewing Distractors, Table 1H-K; see Figure 4) when the distractors were dangerous animals compared with nondangerous animals. Participants looked at fewer distractors (see No. of Different Distractors Fixated, Table 1L-O; see Figure 3) and spent less time looking at each distractor (see Time Viewing Distractors, Table 1L-O; see Figure 4) for a given target in the natural matrices compared with the matrices matched for luminance and spatial frequency.

Table 1. The effect of animal class, danger level, and image type on the latency to locate the target (via fixations and manual responses), number of different distractors fixated, and

time viewing each distractor

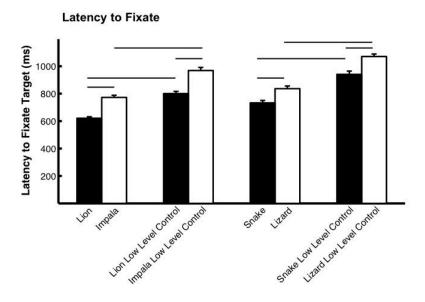
		Latency to Fixate Target Animal	Latency to Manual Response	No. of Different Distractors Fixated	Time Viewing Distractors
Overall Model			•		
A	Animal Class	52.1*	74.9*	44.1*	68.2*
В	Danger Level	207.9*	284.6*	222.4*	135.7*
С	Image Type	474.5*	353.5*	464.9*	458.2*
D	Animal Class × Danger Level	4.5 (0.04)	0.01 (0.93)	0.39 (0.53)	1.5 (0.23)
Е	Animal Class × Image Type	3.3 (0.08)	33.2*	0.70 (0.41)	15.2 (0.0003)
F	Danger Level × Image Type	1.4 (0.24)	3.6 (0.06)	0.02 (0.89)	7.27 (0.009
G	Animal Class × Danger Level × Image Type	0.09 (0.76)	0.01 (0.94)	0.01 (0.92)	0.15 (0.70)
Comparisons H	Lion vs. Impala	10.5* [1.49]	12.4* [1.12]	9.0* [0.96]	6.0* [0.48]
I	Lion Low Level Control vs. Impala Low Level Control	8.2* [1.10]	11.1* [1.08]	8.1* [0.96]	6.0* [0.76]
J	Snake vs. Lizard	5.7* [0.70]	6.7* [0.70]	7.5* [0.92]	6.9* [0.68]
K	Snake Low Level Control vs. Lizard Low Level Control	6.3* [0.79]	6.8* [0.58]	6.5* [0.91]	6.9* [0.73]
L	Lion vs. Lion Low Level Control	11.8* [1.70]	13.7* [1.41]	11.4* [1.40]	8.5* [1.10]
M	Impala vs. Impala Low Level Control	10.5* [1.30]	13.3* [1.41]	13.0* [1.25]	13.6* [1.29
N	Snake vs. Snake Low Level Control	12.3* [1.27]	10.8* [1.17]	10.3* [1.26]	12.7* [1.37
O	Lizard vs. Lizard Low Level Control	11.1* [1.57]	12.4* [1.25]	9.9* [1.21]	16.2* [1.65

Note. F values are displayed; p-values are indicated in parentheses unless the result is highly statistically significant (p < 0.0001) and thus indicated with an asterisk. Effect size (Cohen's d) is reported in brackets. The numerator degrees of freedom is 1 and the denominator degrees of freedom is 59 in all tests.

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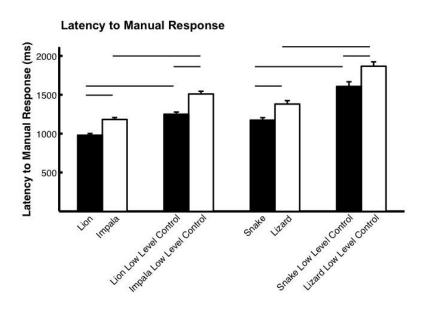
Figure 2. The latency to (a) first fixate the target animal and (b) manually respond (key press) after detecting the target animal

a.



Target

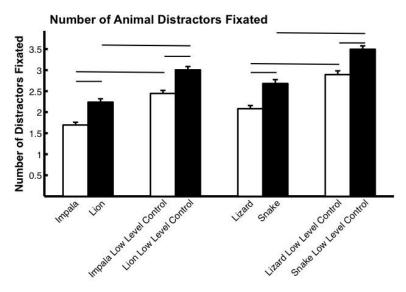
b.



Target

Note. Means and standard-error bars are shown; horizontal lines indicate planned comparisons and all comparisons were statistically significant (p < 0.0001).

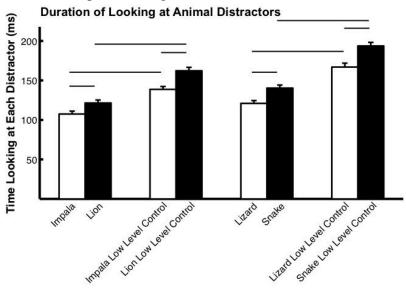
Figure 3. Number of dangerous and nondangerous animal distractors fixated



Distractor

Note. The number of different distractors fixated with respect to the treatment block is displayed. Means and standard-error bars are shown; horizontal lines indicate planned comparisons and all comparisons were statistically significant (p < 0.0001).

Figure 4. Duration of time spent looking at animal distractors



Distractor

Note. The amount of time spent looking at each distractor with respect to the treatment block is displayed. Means and standard-error bars are shown; horizontal lines indicate planned comparisons and all comparisons were statistically significant (p < 0.0001).

Discussion

We found that participants visually detected dangerous animals (snakes and lions) faster than nondangerous animals (lizards and impalas). These results are consistent with previous studies showing that humans (including infants, children, and adults) are quicker to detect dangerous compared with nondangerous animals (Blanchette, 2006; Brosch and Sharma, 2005; Flykt, 2005; LoBue and DeLoache, 2008, 2010; Öhman et al., 2001; Penkunas and Coss, 2013a,b; Rosa et al., 2011; Waters et al., 2004). Unlike these previous studies (but see LoBue and DeLoache, 2010; Rosa et al., 2011), we quantified detection based on eye movements as well as manual responses (a key press). Eye movements are a more ecologically valid method of assessing attention than manual responses. When humans detect potentially dangerous situations, they orient their eyes to the danger before they respond manually (Bannerman, Milders, de Gelder, and Sahraie, 2009). Indeed, the latency to detect animals, both dangerous and nondangerous, in our study was at least 52% faster based on eye movement patterns compared to manual responses.

In addition, we found that adults were quicker to detect dangerous animals even when some low-level features of the images (spatial frequency and luminance) were controlled. Low-level features can influence attention through bottom-up processing, in which properties of the image exogenously capture attention (James, 1890). For example, spatial frequency (large changes in intensity; Mannan, Ruddock, and Wooding, 1997), color, form, and luminance (Turatto and Galfano, 2000) can automatically attract attention. Because the participants in our study were faster to detect dangerous animals compared with nondangerous animals, even after controlling for spatial frequency and luminance, these low-level features were not driving the ability of humans to detect danger rapidly. Similarly, previous studies also reported that adults and children detected dangerous animals faster than nondangerous animals even when the images were gray-scale (Flykt, 2005; Hayakawa, Kawai, and Masataka, 2011). Importantly, we found that humans were slower to detect both dangerous and nondangerous animals when these low-level features were controlled, suggesting that these low-level features can generally aid in detection but are not specific to detecting dangerous animals.

The perceptual processes by which humans rapidly detect danger in natural settings are largely unexplored. One hypothesis is that dangerous objects are particularly effective at maintaining attention or "delaying disengagement" during visual search (Fox et al., 2002). In further support of this hypothesis, studies generally find that fearful and angry faces attract more attention than neutral or happy ones (Bannerman et al., 2009; Belopolsky et al., 2012). Our results provide support for the delayed-disengagement hypothesis. We found that adults detected nondangerous animals slower than dangerous animals because they spent more time looking at each of the dangerous (distractor) images (i.e., they were slower to disengage their attention from the dangerous animals). This suggests that it is critical for humans to fixate dangerous animals so that they can assess levels of threat.

A second hypothesis explaining why humans rapidly detect danger is that dangerous animals exogenously attract attention based on their low-level features (Öhman, 1986; Simons, 2000). Although our results indicated that some low-level features (spatial frequency and luminance) do not affect humans' ability to detect dangerous animals (see

above), additional low-level features may influence detection. For example, the shape of some dangerous animals may exogenously draw attention. LoBue and DeLoache (2011) found that the coiled shape of snakes facilitated detection. Our results are in agreement with this attentional-capture hypothesis because participants looked at a larger number of dangerous (distractor) animals when searching for nondangerous animals, indicating that the dangerous animals drew attention even though the participants were searching for nondangerous animals. Therefore, in the context of the current study presenting animal images, humans appear to assess levels of danger rapidly in their surroundings because they (i) spend more time looking at dangerous animals (delayed disengagement) and (ii) detect dangerous animals through salient visual features.

Because primates, including humans, have experienced predation for millions of years, selection has likely shaped their antipredator behaviors (Coss and Ramakrishnan, 2000; Hart and Sussman, 2005; Isbell, 2006; Stanford, 2002). Primates exhibit intense antipredator responses that involve emitting alarm calls, increasing vigilance levels, avoidance, piloerection, and mobbing or attacking predators (Caro, 2005; Isbell, 1994). Individuals sometimes display these antipredator behaviors in response to predators that they have never even seen before (reviewed in Yorzinski, 2010). In particular, humans often react with fear and increase their attention toward dangerous animals, a process that is mediated by the amygdala and hippocampus and then modulated by cortical areas for regulating action (Lovett-Barron et al., 2014; Öhman, 2005). It is likely beneficial for animals, including humans, to increase their attention toward potential threats so they can respond appropriately (Cresswell, Butler, Whittingham, and Quinn, 2008). Future eyetracking experiments could examine the relationship between visual attention and predator detection in children to better understand the development of visual biases in humans.

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References

- Bannerman, R. L., Milders, M., de Gelder, B., and Sahraie, A. (2009). Orienting to threat: Faster localization of fearful facial expressions and body postures revealed by saccadic eye movements. *Proceedings of the Royal Society B*, 276, 1635-1641.
- Belopolsky, A. V., Devue, C., and Theeuwes, J. (2012). Angry faces hold the eyes. *Visual Cognition*, 19, 27-36.
- Blanchette, I. (2006). Snakes, spiders, guns, and syringes: How specific are evolutionary constraints on the detection of threatening stimuli? *Quarterly Journal of Experimental Psychology*, 59, 1484-1504.
- Brosch, T., and Sharma, D. (2005). The role of fear-relevant stimuli in visual search: A comparison of phylogenetic and ontogenetic stimuli. *Emotion*, *5*, 360-364.

- Caro, T. (2005). Antipredator defenses in birds and mammals. Chicago: University of Chicago Press.
- Coss, R. G. (2003). The role of evolved perceptual biases in art and design. In E. Voland and K. Grammer (Eds.), *Evolutionary aesthetics* (pp. 69-130). Heidelberg: Springer-Verlag.
- Coss, R. G., Fitzhugh, E. L., Schmid-Holmes, S., Kenyon, M. W., and Etling, K. (2009). The effects of human age, group composition, and behavior on the likelihood of being injured by attacking pumas. *Anthrozoös*, 22, 77-87.
- Coss, R. G., and Moore, M. (2002). Precocious knowledge of trees as antipredator refuge in preschool children: An examination of aesthetics, attributive judgments, and relic sexual dinichism. *Ecological Psychology*, *14*, 181-222.
- Coss, R. G., and Ramakrishnan, U. (2000). Perceptual aspects of leopard recognition by wild bonnet macaques (*Macaca radiata*). *Behaviour*, 137, 315-335.
- Cresswell, W., Butler, S., Whittingham, M. J., and Quinn, J. L. (2008). Very short delays prior to escape from potential predators may function efficiently as adaptive risk-assessment periods. *Behaviour*, 146, 795-813.
- Cronin, T. W. (2005). The visual ecology of predator-prey interactions. In *Ecology of predator-prey interactions*. New York: Oxford University Press.
- Dukas, R. and Kamil, A. C. (2000). The cost of limited attention in blue jays. *Behavioral Ecology*, 11, 502-506.
- Flykt, A. (2005). Visual search with biological threat stimuli: Accuracy, reaction times, and heart rate changes. *Emotion*, *5*, 349-353.
- Fox, E., Griggs, L., and Mouchlianitis, E. (2007). The detection of fear-relevant stimuli: Are guns noticed as quickly as snakes? *Emotion*, 7, 691-696.
- Fox, E., Russo, R., and Dutton, K. (2002). Attentional basis for threat: Evidence for delayed disengagement from emotional faces. *Cognition and Emotion*, *16*, 355-379.
- Gerdes, A. B. M., Pauli, P., and Alpers, G. W. (2009). Toward and away from spiders: Eyemovements in spider-fearful participants. *Journal of Neural Transmission*, 116, 725-733.
- Hart, D., and Sussman, R. W. (2005). *Man the hunted: Primates, predators, and human evolution*. New York: Westview Press.
- Hayakawa, S., Kawai, N., and Masataka, N. (2011). The influence of color on snake detection in visual search in human children. *Scientific Reports*, 1, 1-4.
- Headland, T. N., and Greene, H. W. (2011). Hunter–gatherers and other primates as prey, predators, and competitors of snakes. *Proceedings of the National Academy of Sciences*, 108, E1470–E1474.
- Huijding, J., Mayer, B., and Koster, E. H. W. (2011). To look or not to look: An eye movement study of hypervigilance during change detection in high and low spider fearful students. *Emotion*, 11, 666-674.
- Isbell, L. A. (1994). Predation on primates: Ecological patterns and evolutionary consequences. *Evolutionary Anthropology*, *3*, 61-71.
- Isbell, L. A. (2006). Snakes as agents of evolutionary change in primate brains. *Journal of Human Evolution*, 51, 1-35.
- James, W. (1890). The principles of psychology. Cambridge: Harvard University Press.

- LoBue, V., and DeLoache, J. S. (2008). Detecting the snake in the grass: Attention to fear-relevant stimuli by adults and young children. *Psychological Science*, *19*, 284-289.
- LoBue, V., and DeLoache, J. S. (2010). Superior detection of threat-relevant stimuli in infancy. *Developmental Science*, 13, 221-228.
- LoBue, V., and DeLoache, J. S. (2011). What's so special about slithering serpents? Children and adults rapidly detect snakes based on their simple features. *Visual Cognition*, 19, 129-143.
- Lovett-Barron, M., Kaifosh, P., Kheirbek, M. A., Danielson, N., Zaremba, J. D., Reardon, T. R., . . . Losonczy, A. (2014). Dendritic inhibition in the hippocampus supports fear learning. *Science*, *343*, 857-863.
- Mannan, S. K., Ruddock, K. H., and Wooding, D. S. (1997). Fixation patterns made during brief examination of two-dimensional images. *Perception*, 26, 1059-1072.
- Nummenmaa, L., Hyona, J., and Calvo, M. G. (2006). Eye movement assessment of selective attentional capture by emotional pictures. *Emotion*, *6*, 257-268.
- Öhman, A. (1986). Face the beast and fear the face: Animal and social fears as prototypes for evolutionary analyses of emotion. *Psychophysiology*, 23, 123-145.
- Öhman, A. (2005). The role of the amygdala in human fear: Automatic detection of threat. *Psychoneuroendocrinology*, *30*, 953-958.
- Öhman, A., Flykt, A., and Esteves, F. (2001). Emotion drives attention: Detecting the snake in the grass. *Journal of Experimental Psychology: General*, 130, 466-478.
- Penkunas, M. J., and Coss, R. G. (2013a). Rapid detection of visually provocative animals by preschool children and adults. *Journal of Experimental Child Psychology*, 114, 522-536.
- Penkunas, M. J., and Coss, R. G. (2013b). A comparison of rural and urban Indian children's visual detection of threatening and nonthreatening animals. *Developmental Science*, 16, 463-475.
- Reinholdt-Dunne, M. L., Mogg, K., Benson, V., Bradley, B. P., Hardin, M. G., Liversedge, S. P., . . . Ernst, M. (2012). Anxiety and selective attention to angry faces: An antisaccade study. *Journal of Cognitive Psychology*, 24, 54-65.
- Rosa, P. J., Gamito, P., Oliveira, J., Morais, D., and Saraiva, T. (2011). Attentional orienting to biologically fear-relevant stimuli: Data from eye tracking using the continual alternation flicker paradigm. *Journal of Eyetracking, Visual Cognition and Emotion*, 1, 22-29.
- Simons, D. J. (2000). Attentional capture and inattentional blindness. *Trends in Cognitive Sciences*, *4*, 147-155.
- Stanford, C. B. (2002). Avoiding predators: Expectations and evidence in primate antipredator behavior. *International Journal of Primatology*, 23, 741-757.
- Treves, A., and Palmqvist, P. (2007). Reconstructing hominin interactions with mammalian carnivores (6.0–1.8 Ma). In K. A. I. Nekaris and S. L. Gursky (Eds.), *Primates and their predators* (pp. 355-381). New York: Springer.
- Turatto, M., and Galfano, G. (2000). Color, form, and luminance capture attention in visual search. *Vision Research*, 40, 1639-1643.
- Waters, A. M., Lipp, O. V., and Spence, S. H. (2004). Attentional bias toward fear-related stimuli: An investigation with nonselected children and adults and children with

- anxiety disorders. Journal of Experimental Child Psychology, 89, 320-337.
- Willenbockel, V., Sadr, J., Fiset, D., Horne, G. O., Gosselin, F., and Tanaka, J. W. (2010). Controlling low-level image properties: The SHINE toolbox. *Behaviour Research Methods*, 42, 671-684.
- Yorzinski, J. L. (2010). Predator recognition in the absence of selection. In S. Gursky-Doyen and J. Supriatna (Eds.), *Indonesian primates, developments in primatology: Progress and prospects*. New York: Springer.
- Yorzinski, J. L., Patricelli, G. L., Babcock, J., Pearson, J. M., and Platt, M. L. (2013). Through their eyes: Selective attention in peahens during courtship. *Journal of Experimental Biology*, 216, 3035-3046.
- Yorzinski, J. L., and Platt, M. L. (2014). Selective attention in peacocks during predator detection. *Animal Cognition*, 17, 767-777.