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Animals in Upright Postures Attract Attention in Humans

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Abstract

Individual predators differ in the level of risk they represent to prey. Because prey incur costs when responding to predators, prey can benefit by adjusting their antipredator behavior based on the level of perceived risk. Prey can potentially assess the level of risk by evaluating the posture of predators as an index of predators' motivational state. Like other prey species, humans might evaluate predator body posture as a prominent cue for assessing danger. We tested whether human participants adjusted their visual attention based on the postures of predators by presenting participants with photographic arrays of predators (lions) that varied in postures while we recorded the participants' gaze behavior. The participants searched for a standing lion (representing a high-risk target) among an array of reclining lions (representing low-risk distractors) or searched for a reclining lion among an array of standing lions. They also searched through similar arrays consisting of non-threatening prey (impalas) standing or reclining, rather than predators. Participants detected standing lions and impala faster than reclining lions and impala. Surprisingly, they detected standing lions at similar latencies as standing impala. They detected the reclining lions and impala more slowly because they spent more time looking at the standing lion and impala distractors and looked at more of those distractors. These results show that upright animals, regardless of whether they are predators or prey, attract attention in humans, and this could allow humans to rapidly evaluate predatory threats or the flight readiness of hunted game.

Keywords Attention · Humans · Delayed disengagement · Posture · Predator detection

Introduction

Individual predators vary in the degree of risk they pose to prey (Carlson et al. 2017). During much of their time, predators are not actively hunting (Baladrón et al. 2016) and they therefore represent minimal risk to prey (Griesser 2008). Even when predators are actively hunting, the level of risk to prey can vary widely. For example, prey that are farther away from predators have a lower chance of being predated while closer prey have a higher chance of being predated (Ydenberg and Dill 1986).

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Because prey incur costs (such as energy and time) when responding to predators (Preisser et al. 2005), prey can benefit by adjusting their antipredator response based on the level of risk. If the level of risk is low, prey should invest their time and energy into other behaviors, such as foraging, rather than engaging in defensive behaviors (Dugatkin and Godin 1992; Ydenberg and Dill 1986). In fact, prey are often aware of the level of risk that predators represent and adjust their behavior accordingly. Prey are sensitive to the speed and distance of approaching predators (Stankowich and Coss 2006; Fallow and Magrath 2010; Wilson and Evans 2012), where predators are directing their gaze (Hampton 1994; Kyle and Freeberg 2016; Yorzinski et al. 2018) and predators' locations (Ficken et al. 1978). Some prey even differentiate between specific behaviors of predators: Siberian jays (*Perisoreus infaustus*) emit distinct calls corresponding to the hunting stages of their predators (Griesser 2008). Many studies have also shown that threat-related stimuli, including lions and snakes (Öhman et al. 2001; Blanchette 2006; Lipp and Waters 2007; Penkunus and Coss 2013a, b; Yorzinski et al. 2014; Yorzinski et al. 2018), capture attention (reviewed in Öhman and Mineka 2001). However, we are unaware of any studies

that have examined whether prey distinguish between predator postures that often represent either resting predators (reclining postures; low risk) or active predators (standing postures; high risk).

The aim of this study was to test the hypothesis that predators exhibiting dangerous body postures attract more attention than predators exhibiting less dangerous postures. We selected predator body posture for study because anecdotal observations suggest that prey use body posture to assess danger level. For example, warthogs (*Phacochoerus aethiopicus*) will inspect resting lions at dangerously close distances (Coss, pers. obs.; see [Supplementary Material](#)). Furthermore, previous work has shown that body posture can impact attention in humans (Bannerman et al. 2009; Bannerman et al. 2010).

We tested our hypothesis using human subjects (*Homo sapiens*) because hominins were targets of a variety of large predators (Coss and Moore 2002; Treves and Palmqvist 2007). Even though modern humans often have limited experience with predators, they still perceive predators as dangerous (Penkunas and Coss 2013a, b). In fact, humans are faster at detecting predators compared to non-predators (Yorzinski et al. 2014). Furthermore, we previously found that humans do use predatory cues to assess danger levels: humans are fastest at detecting predators that are facing toward versus away from them (Yorzinski et al. 2018).

As a method for evaluating the salience of predator body postures, we recorded the eye movements of human participants as they searched for predators (lions; *Panthera leo*). They searched for an image of a lion that was standing (high-risk target) embedded in an array of reclining lions (low-risk distractors) or searched for an image of a lion that was reclining (low-risk target) embedded in an array of lions that were standing (high-risk distractors). We considered standing lions as high-risk because lions' final attack on their prey occurs when they are upright and rushing toward the prey (Scheel and Packer 1991); furthermore, lions are among the predators of humans (Yeakel et al. 2009). To determine whether their detection abilities were specific to lions or generalized to non-dangerous mammals, the participants also searched through similar arrays that displayed standing or reclining impalas (*Aepyceros melampus*), a historical (Lombard 2005) and current game species (Muposhi et al. 2016; Setsaas et al. 2007). We presented the participants with color images and images in which low-level features were minimized (spatial frequency and luminance were controlled).

If lions exhibiting dangerous postures attract more attention than lions exhibiting less dangerous postures, we expected that participants would be faster to detect high-risk lions that were standing versus low-risk lions that were reclining. If lion posture does not impact the attention of prey, we expected that participants would detect lions standing and reclining at similar speeds. It is also possible that upright animals, including but not limited to lions, attract more attention than reclining

animals; if this is the case, we expect that participants would also be faster at detecting standing impala versus reclining impala. In addition, we examined the visual-scanning process that participants used while searching through the predator and prey arrays. We tested whether high-risk lions (a) maintain attention or "delay disengagement" during visual search (Fox et al. 2002) and/or (b) exogenously attract attention through low-level features (e.g., luminance or contrast; Simons 2000). If high-risk lions are effective at maintaining attention, we predicted that humans would spend more time looking at distractors when the distractors were standing lions compared with reclining lions. If high-risk lions capture attention through low-level features, we predicted that humans would look at a larger number of distractors when the distractors were standing lions compared with reclining lions. If these effects are specific to lions and not generalizable to non-dangerous mammals, we expected that humans' attention toward the impala distractors would not differ relative to the impalas' postures.

Materials and Methods

Participants

Conducted at Texas A&M University from September 2017 to March 2018, this study examined 30 men (mean age = 20.7 years; range = 18–28 years) and 30 women (mean age = 19.7 years; range = 18–23 years) of European heritage. E-mails and posters describing the study were employed to recruit participants who gave written consent and earned \$10 for participating.

Animal Images

We employed an experimental protocol similar to our earlier study of the latency to detect images of lions and impala with facing and averted heads (see Yorzinski et al. 2018). For this study, we compared two sets of 96 images of male lions (*Panthera leo*) and impala (*Aepyceros melampus*) that were standing or reclining. The lion images consisted of adult males with manes (Fig. 1a) and adult female impala, both of which faced the photographer. These images were obtained from online sources of animals photographed in natural settings that did not exhibit hyperalert, defensive, or aggressive postures.

We also examined the perceptual effects low-level features have on image detection by controlling for differences in image color, luminance, and spatial frequency using the SHINE toolbox (Fig. 1b; default settings; Willenbockel et al. 2010) in MATLAB. The SHINE toolbox adjusts the images for consistency by first matching the Fourier amplitude spectra of the images (spatial frequency matching) and then matching the luminance histograms (Willenbockel et al. 2010); thus, the low-level features

Fig. 1 Examples of scan paths from one participant on matrices from the four treatment blocks of the lion set (**a**, **b** target standing; **c**, **d** target reclining). The participant begins looking at the middle of the images and ends by looking at the target animals. The size of the black circles corresponds to the amount of time the participant spent looking at a given location

are more equivalent across the sets except for some low-level features (such as contour edges and orientation).

The lion set of images consisted of four treatment blocks comprised of 24 matrices: Standing, Standing Control, Reclining, and Reclining Control. The first treatment block (Target Lion Standing) consisted of 24 matrices created from 24 images of lions presented in 3×3 arrays with one lion standing as the target and seven lions reclining as distractors. The center matrix was empty (Fig. 1a). Each matrix filled the entire 63.5-cm diagonal computer screen (Dell UltraSharp UP2516D: 2560×1440 pixels overall; dpi = 96). Each animal image within the matrices was 293×208 pixels, yielding from the participant's perspective a field of view of approximately 7.4° wide and 5.2° high; 100 pixels separated images from each other.

Within the first treatment block of lion photographs, the images within the 24 matrices were organized spatially. For example, a standing lion target appeared once within each matrix and only three times in each of the eight possible positions in all matrices. For all 24 matrices within this block, the reclining lion distractor images were arranged in pseudo-randomized positions within each matrix such that each image appeared only once and seven times across all matrices. The second lion-treatment block (Target Lion Standing Control) employed the same spatial arrangement as the first treatment block. Similarly, the third and fourth treatment blocks of lion images consisted of 96 matrices of a Target Lion Reclining

and a Target Lion Reclining Control (see Fig. 1 c and d) using the same spatial arrangement format.

The second set of 96 matrices consisted of four impala treatment blocks of 24 matrices (Target Impala Standing, Target Impala Standing Control, Target Impala Reclining, and Target Impala Reclining Control). This impala set employed the same spatial arrangement format as was done for the lion images.

Eye-Tracking Measurement

Our study of target detection used a Tobii X2-60 eye-tracker (Tobii Technology, Inc., Sweden) to record participant gaze and Tobii Studio 3.4 software to present our images and record the gaze of participants (accuracy 0.4° ; data rate 60 Hz; binocular tracking). Participants were told initially that their pupil size would be recorded as they looked at the images; they were told after the experiment that their eye movements were also recorded. From the participant's perspective, the white-background luminance of the Dell monitor was 185 cd/m^2 at approximately 60 cm from the participant and room illuminance was 30 lx (Spectra Cine PhoRad Meter, SC-820). To minimize participant head movements, we used a chin cup (UHCOTech HeadSpot). We calibrated the equipment (5 points) before starting each trial. To classify visual fixations and scanning saccades, we used the Tobii Velocity-Threshold Identification filter (I-VT filter; gap fill-in 75 ms; eye selection

average; velocity calculator window 20 ms; I-VT classifier threshold 30°/s; merge adjacent time 75 ms; merge adjacent angle 0.5°). This filter incorporates a velocity threshold to classify whether an eye movement is a visual fixation or saccade; eye movements below and above the velocity threshold (30°/s, in this study) are classified as fixations and saccades, respectively. To measure the position of participant gaze, the Tobii eye-tracker records the coordinates of where participants are looking during each sampling point.

Eye-Tracking Procedure

After participants were resting their chin in the cup, the experimenter first asked participants to perform two practice trials so they could become familiar with the procedure. In the first practice trial, participants fixated a black dot for 1 s that was centered on the screen. Next, they were instructed to press the space bar on a keyboard as soon as they detected a standing cat (*Felis catus*) among seven images of reclining cats in a 3 × 3 matrix (the center matrix position was empty). After pressing the space bar, the matrix disappeared and the fixation dot reappeared, a process that was repeated for five matrices. In the second practice trials, participants searched for reclining cat targets among images of standing cat distractors.

Following completion of the two practice trials, participants were then presented with the first set of 24 matrices of lions or impala using the same spacebar procedure and initial fixation of the black dot prior to matrix presentation. Participants were presented each of the four blocks of matrices within the set followed by four blocks of matrices within the second set. The lion and impala sets were randomized across participants as was the order of the blocks for a total search task of eight blocks of matrices.

Eye-Tracking Statistical Analyses

To measure visual fixation, we drew a rectangular region of interest (ROI) of the same size around each target and distractor (293 × 208 pixels) using a customized MATLAB script. For each fixation coordinate, the script determined which target or distractor ROI images were fixated or not fixated. We calculated four gaze-behavior metrics: the latency of initial target fixation (Latency to Fixate Target), the latency of space-bar pressing after target detection (Latency to Manual Response), the number of different distractors the participants fixated (No. of Different Distractors Fixated), and the average time participants spent looking at each distractor (Time Viewing Distractors). We calculated for each participant the mean values of these metrics within each of the eight treatment blocks (Target Lion Standing, Target Lion Standing Control, Target Lion Reclining, Target Lion Reclining Control, Target Impala Standing, Target Impala Standing Control, Target Impala Reclining, and Target Impala

Reclining Control). We had evidence in several matrices that participants never fixated the target. As such, we were unsure whether participants failed to perform the target-identification task or whether the eye tracker failed to record target fixation. Matrices were excluded from statistical analyses if targets were not fixated or if more than 10% of the gaze data was missing; it must be noted that only 4.8% of the matrices were discarded due to this restriction. Data associated with the study are available online (Yorzinski 2019).

We analyzed our data using linear mixed effects models with repeated measures (PROC MIXED) in SAS (version 9.4; SAS Institute Inc., Cary, NC). Our statistical analyses consisted of one between-subject factor (gender) and four within-subject factors: target standing vs. reclining, animal type (lion vs. impala), type of image (natural image vs. image controlled for low-level features), and trial order (the order in which the eight treatment blocks were presented). Four dependent variables were examined: latency to fixate the target, latency to respond manually, number of different distractor images fixated, and time viewing each distractor image. Since these independent variables were highly correlated, we condensed our analyses by performing a factor analysis on the four dependent variables to extract a single principal-component factor (“search performance”) derived from varimax rotation that explained 73.6% of the variance using Minitab version 18.1 (Minitab Inc., State College, PA); the four variables were loaded positively on the single factor. We examined this principal-component factor as a dependent variable using the aforementioned mixed effects statistical model with repeated measures. We made eight simple-effect comparisons and used the false discovery rate correction (Benjamini and Hochberg 1995) to evaluate statistical significance.

Finally, we calculated Weber contrast using custom MATLAB scripts to determine the contrast between the animals (lions or impalas) and their backgrounds in the natural images. It was calculated as the difference between the mean pixel intensity of the animals and the mean pixel intensity of the environments surrounding the animals and then divided by the mean pixel intensity of the environments surrounding the animals (Rieucan et al. 2014). We measured Weber contrast between each animal and its surrounding environment and then calculated the absolute value of the Weber contrast to determine the magnitude of the contrast. We performed a linear mixed effects model to test whether the magnitude of Weber contrast varied depending on the animal type (lion or impala), posture (standing or reclining), or their interaction.

Results

Posture impacted predator detection (Table 1; Fig. 2; $F(1,58) = 123.94, p < 0.0001$). Participants were faster to visually fixate and manually detect the target lion when the lion

Overall model	Composite factor
Posture	123.94 (< 0.0001)*
Animal type	27.6 (< 0.0001)*
Image type	223.2 (< 0.0001)*
Posture × animal type	1.11 (0.30)
Posture × image type	0.63 (0.43)
Animal type × image type	12.47 (0.00080)*
Posture × animal type × image type	1.42 (0.24)
Gender	0.33 (0.57)
Trial order	36.64 (< 0.0001)*
Comparisons	
Target Lion Standing vs. Target Lion Reclining	6.18 (< 0.0001)* [0.64]
Target Impala Standing vs. Target Impala Reclining	4.12 (0.0001)* [0.49]
Target Lion Standing Control vs. Target Lion Reclining Control	5.44 (< 0.0001)* [0.47]
Target Lion Standing Control vs. Target Lion Reclining Control	6.28 (< 0.0001)* [0.65]
Target Lion Standing vs. Target Impala Standing	2.78 (0.0073)* [0.42]
Target Lion Standing Control vs. Target Impala Standing Control	0.69 (0.49) [0.16]
Target Lion Reclining vs. Target Impala Reclining	5.88 (< 0.0001)* [0.61]
Target Lion Reclining Control vs. Target Impala Reclining Control	0.86 (0.39) [0.16]

was standing rather than reclining; they also looked at more distractors and spent more time viewing those distractors

when the distractors were standing lions versus reclining lions ($t(1,58) = 6.18, p < 0.0001$). In the natural images, participants were 1.15 times faster at detecting (via visual fixation) the standing versus reclining lions. Similarly, participants visually fixated standing impala faster than reclining impala and were faster to manually detect standing impala versus reclining impala; they looked at more distractors and spent more time viewing those distractors when the distractors were standing impala versus reclining impala ($t(1,58) = 4.12, p = 0.0001$). In the natural images, participants were 1.07 times faster at detecting (via visual fixation) the standing versus reclining impalas.

Surprisingly, participants were generally faster at visually fixating and manually responding to targets with standing impalas compared with standing lions or reclining impalas compared with reclining lions; they also looked at fewer distractors and spent less time doing so for the impala versus lion distractors (Lion Standing vs. Impala Standing $t(1,58) = 2.78, p = 0.0073$; lion reclining vs. impala reclining $t(1,58) = 5.88, p < 0.0001$). However, after controlling for low-level features, participants' latency to visually fixate and manually respond to targets with standing lions and standing impalas was similar; they also looked at a similar number of distractors and spent a similar amount of time doing so regardless of whether the distractors were standing lions or standing impalas (Lion Standing Control vs. Impala Standing Control $t(1,58) = 0.69, p = 0.49$). Similarly, after controlling for low-

level features, participants' latency to visually fixate and manually respond to targets with reclining lions and reclining impalas was similar; they also looked at a similar number of distractors and spent a similar amount of time doing so regardless of whether the distractors were reclining lions or reclining impalas (Lion Reclining Control vs. Impala Reclining Control $t(1,58) = 0.86, p = 0.39$).

Overall, participants were faster to detect the natural compared with control images ($F(1,58) = 223.2, p < 0.0001$). Gender of the participants did not impact detection ($F(1,92) = 0.33, p = 0.57$). Analyses of the individual variables showed similar effects (Table S1; Figure S2). Overall, the lion images (mean $\pm$ SE 0.29 ± 0.03) exhibited greater Weber contrast than the impala images (mean $\pm$ SE 0.29 ± 0.03 (lions), 0.19 ± 0.02 (impalas); $F(1,92) = 10.00, p = 0.0021$) but Weber contrast did differ between neither the standing and reclining lions ($t(1,92) = 0.34, p = 0.74$) nor the standing and reclining impalas ($t(1,92) = 1.36, p = 0.18$).

Discussion

Participants were faster to detect upright animals (lions and impala) compared with reclining animals. These results support the hypothesis that animals, both predators and prey, exhibiting upright postures attract more attention than reclining animals. These results were upheld when controlling for some low-level confounds. Furthermore, contrast between the animals and their backgrounds was not driving the results: the contrast in the standing and reclining lion images was similar and the contrast in the standing and reclining impala images was similar.

We found that humans' attention to predators depends on the predators' posture. Human participants were faster to detect standing lions compared with reclining lions. Upright lions likely represent a greater level of risk because they could be hunting (searching, stalking or attacking their prey), whereas reclining lions are resting and not hunting (Elliot et al. 1977). Even if a reclining lion shifted into a hunting motivational state, it would likely take longer to initiate an attack from a reclining versus upright position because of the time required to transition between postures (Kralj et al. 1990; Turesson et al. 2009; Carr and Lima 2012). Given that human subjects detected standing lions approximately 131 ms faster than reclining lions, standing lions would be detected when they were 1.8 m farther from the subjects compared with reclining lions (assuming that lions sprint at approximately 13.9 m/s; Elliot et al. 1977; Schaller 1972). Because lions are less successful in capturing prey that are farther from them (Elliot et al. 1977), this extra distance between the lions and humans could lower predation rates. Similarly, individuals in other species vary in their latency to detect predators and this likely impacts their predation rates (Hilton et al. 1999).

Human participants were also quicker to detect standing impala compared with reclining impala. This behavior may be evolutionary adaptive because humans, like lions, incur costs when hunting prey (Mukherjee and Heithaus 2013). Predators can minimize their costs by avoiding prey that are difficult to capture (FitzGibbon 1989, 1990; Schaller 1972). Standing prey are likely harder to hunt because they can likely detect approaching predators at a greater distance and initiate flight much faster than reclining prey that must first stand up before fleeing (Kralj et al. 1990). Humans could therefore terminate their hunting effort when prey indicate (via alertness and standing posture) that they have detected the hunters (Coss 2017). Similarly, our previous work found that humans are faster at detecting forward-facing impala compared with impala facing away (Yorzinski et al. 2018). Alternatively, it is possible that humans' rapid detection of standing prey is a non-adaptive carryover effect from their ability to rapidly detect standing predators. They may actually be less efficient at hunting prey if their attention is drawn toward standing prey that are more difficult to capture rather than focusing on reclining prey that are easier to capture. By tracking the gaze of hunters in naturalistic settings, a future study could test how attention toward prey exhibiting different postures impacts hunting efficiency. Another possibility is that familiarity influences detection; if humans more often see images of animals in certain postures rather than others, their search performance could be affected (Shen and Reingold 2001).

Unexpectedly, humans detected standing lions among reclining lions at similar latencies as standing impala among reclining impalas. This finding was unexpected because previous work has found that humans are faster at detecting standing lion targets within arrays of impala distractors compared with standing impala targets within arrays of standing lion distractors (Penkunas and Coss 2013a, b; Yorzinski et al. 2014); however, these previous studies (Penkunas and Coss 2013a, b; Yorzinski et al. 2014) compared target lions within arrays of impala distractors (and vice versa) while this study compared target lions within arrays of lion distractors (and target impalas within arrays of impala distractors). Though, a previous study found that humans are faster at finding lions with direct gaze among lions with averted gaze compared to impalas with direct gaze among impalas with averted gaze (Yorzinski et al. 2018). Contrary to previous studies demonstrating increased attentional capture for threat-related stimuli (reviewed in Öhman and Mineka 2001), our results indicated that humans are adept at rapidly detecting standing animals that are facing them attentively, regardless of whether those animals are predators or not. It is possible that detection was fast for all standing animals because standing animals have a defined feature (i.e., four legs) that may be more salient than the animal type (i.e., dangerous vs. non-dangerous). Previous work has demonstrated that targets defined by the presence of a specific feature are easier to find than targets lacking that

feature (Treisman and Souther 1985; Wolfe 2001). In a classic example of search asymmetries, humans are faster at finding a circle with a vertical line through it among regular circles compared with a regular circle among circles with vertical lines (Treisman and Souther 1985). Given that standing animals roughly resemble elliptical shapes with attached vertical lines (straight legs) while reclining animals roughly resemble unadorned ellipses, the above classic search asymmetry is consistent with our findings. The facilitative role of subjects' expectations of target shapes in selectively guiding visual attention requires further study (cf. Theeuwes 1992; Benoni 2018).

Human participants were slower to detect reclining lions and impala because they spent more time looking at the standing distractor animals. These results support the enhanced dwell-time hypothesis, which posits that relevant animals are effective at maintaining attention or delaying disengagement (Fox et al. 2002; Yorzinski et al. 2014), as participants were slow to disengage their attention from the standing predators and prey. Moreover, the reliably faster attentional disengagement from standing impalas while searching for reclining impala targets, compared with the slower disengagement from standing lions while searching for reclining lion targets, could reflect a more prolonged assessment of standing lion dangerousness. Furthermore, these results also support the pop-out hypothesis, which states that relevant animals exogenously attract attention through low-level features (such as edges and shapes; Treisman 1988; Simons 2000), as participants looked at a larger number of standing distractor predators and prey. These results indicated that the standing predators and prey drew attention despite the participants being instructed to search for reclining predators and prey. We also found that other low-level features (luminance and spatial frequency) did not impact the quicker detection of standing predators or prey.

Rather than simply responding to the presence or absence of predators and prey, individuals can employ sophisticated strategies to evaluate them (Carlson et al. 2017). Previous studies have found that attention in humans is rapidly drawn toward people with threatening postures (Bannerman et al. 2009; Bannerman et al. 2010; Gilbert et al. 2011). Our results extend these findings by demonstrating that attention in humans is also rapidly drawn toward non-human animals with specific postures. Additional research investigating how predator and prey behavior guide attention will provide further insight into predator-prey dynamics (Lima 2002).

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Compliance with Ethical Standards The current research was approved by the Institutional Review Board of Texas A&M University (protocol #2016-0575D).

Conflict of Interest The authors declare that they have no conflict of interest.

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