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It's All in the Anticipation: How Perception of Threat Is Enhanced in Anxiety

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The importance of top-down factors such as goals and expectations is well-established in both visual perception and anxiety. However, researchers have attributed the perceptual prioritization of threatening stimuli in anxiety to bottom-up, automatic processing of these stimuli while neglecting the role of prestimulus, top-down factors. Furthermore, different kinds of anxiety (dispositional versus induced) impact cognitive functions differently, suggesting that top-down factors may have distinct effects on threat perception. In the present study, we examined whether prestimulus representations of threatening stimuli facilitate perception differently, depending on induced and trait anxiety. Two groups of participants completed a cued discrimination task using threatening or neutral cues to identify subsequently presented fearful and neutral faces, degraded to each participant's perceptual threshold. In Group 1, threat of shock induced anxiety ($n = 22$; 12 men), whereas in Group 2, no anxiety was induced ($n = 29$; 7 men). The impact of induced anxiety on perception interacted with trait anxiety. Following fear cues, higher trait anxiety was associated with improved perceptual sensitivity and faster reaction time under threat of shock, and worse perceptual sensitivity and slower reaction time in absence of shock. The present findings represent an important advance in the literature because they elucidate the role of previously ignored top-down factors in threat perception for individuals with varying levels of anxiety and highlight the distinct impact that different types of anxiety have on the perception of threatening stimuli. Furthermore, these findings underline the importance of including top-down factors in future conceptualizations of perceptual bias toward threat in anxiety.

Keywords: perception, expectation, shock, threat, trait anxiety

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Anticipation of aversive future events is an important characteristic of anxiety. In fact, researchers have proposed that focusing on anticipation of aversive events, rather than on the actual response to these events, may be more effective in elucidating the psychological and neurobiological bases of extreme anxiety and clinical anxiety (Davis, Walker, Miles, & Grillon, 2010; Grupe & Nitschke, 2013). Despite the importance of anticipatory, top-down factors, most studies have attributed faster and more accurate perception of threatening stimuli in anxiety to automatic processing of these stimuli, and neglected the role of anticipatory prestimulus factors. Since top-down factors such as expectation and context play a critical role in visual perception (Bar, 2004), a comprehensive understanding of threat perception in anxiety can be gained by examining the role of these factors in anxiety. Furthermore, induced anxiety and dispositional anxiety vary in how they impact cognitive functions such as attention and working memory (WM; Ashcraft & Kirk, 2001; Pacheco-Unguetti, Acosta, Callejas, & Lupiáñez, 2010; Shackman et al., 2006), suggesting their differential involvement in top-down effects on threat perception. Hence, in the present study, participants with varying levels of trait anxiety performed a task in which we examined the effect of prestimulus threat information on subsequent perceptual decision making. Participants performed a cued discrimination task in which threatening or neutral cues guided them to identify subsequent fearful and neutral faces degraded to each participant's perceptual threshold. One group of participants performed the task under threat of shock and another performed it in the absence of shock, allowing us to examine the effect of both trait and experimentally induced anxiety on how endogenous or top-down factors impact perceptual decision making.

Past empirical researchers examining threat-related perception in anxiety have mainly utilized unanticipated or task-irrelevant stimuli, the properties of which exogenously drive perception and attention. Common tasks employed to study this phenomenon have presented emotional stimuli that "pop out" among nonemotional stimuli (Öhman, Flykt, & Esteves, 2001), are peripheral to fixation (Mogg & Bradley, 1999), appear rapidly in a stream of images (Arend & Botella, 2002), or are irrelevant to the task at hand (Williams, Mathews, & MacLeod, 1996). Studies using similar paradigms have shown increased amygdala and visual cortical activity for phobic objects in anxiety (Etkin & Wager, 2007;

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Lipka, Miltner, & Straube, 2011; Straube, Mentzel, & Miltner, 2005), and it is hypothesized that perceptual enhancements occur as a result of amygdalar feedback mediating exogenous, stimulus-driven mechanisms into visual sensory regions (Pourtois, Schettino, & Vuilleumier, 2013).

Hence the traditional view that enhanced perception of threatening stimuli in anxiety is due to automatic processing of these stimuli. However, the process of perception often starts before an actual physical encounter with the sensory stimulus. Prior knowledge and experience can create expectations about what is relevant or likely, helping us to rapidly and accurately identify subsequent stimuli. Objects such as a loaf of bread are identified more rapidly when they are encountered in a familiar context that creates an expectation of their appearance, such as in a kitchen (Bar, 2004), and spiders are detected in a visual array more quickly when preceded by a cue predicting these stimuli (Aue, Guex, Chauvigné, & Okon-Singer, 2013). Neurally, a sensory percept is instantiated through interactions between prestimulus templates generated from expectation or anticipatory attention and incoming sensory evidence (Friston, Harrison, & Penny, 2003; Summerfield et al., 2006; Zelano, Mohanty, & Gottfried, 2011). Recently, we showed that predictive representations of threatening stimuli are critical for improving both perceptual sensitivity and the speed with which subsequent stimuli are detected (Sussman, Weinberg, Szekely, Hajcak, & Mohanty, 2015). Overall, the importance of anticipatory top-down factors in threat perception and in anxiety development indicates that these factors could play a critical role in threat-related perceptual biases in anxiety.

Threat of shock is a well-validated, translational, experimental model of clinical anxiety that can be used to examine both adaptive and maladaptive effects of anxiety on perception (Robinson, Vytal, Cornwell, & Grillon, 2013). Although there is evidence indicating that both experimentally induced anxiety and dispositional anxiety promote an attentional or perceptual bias toward threatening stimuli, the findings for attentional control and WM are not as consistent. In general, dispositional or trait anxiety has been found to have more general impairing effects on attention and executive control (Ashcraft & Kirk, 2001; Bishop, 2009; Derakshan & Eysenck, 1998), but the same effects are not seen for anxiety induced by threat of shock (Robinson et al., 2013). These differences suggest that these two types of anxiety might impact top-down processes that aid emotional perception in different ways. Hence, we examined whether predictive representations of threat impact perception differently, depending on whether anxiety was experimentally induced or dispositional in nature.

Two groups of participants varying in levels of trait anxiety were cued to detect perceptually degraded threatening or neutral faces presented at the participants' predetermined perceptual threshold in a two-alternative, forced-choice perceptual task. Using cues, we manipulated predictive representations by asking participants to look for one kind of face versus another, rather than manipulating the probability (or likelihood) of viewing a specific face type. Trials started with a cue indicating the type of face participants were looking for, encouraging the use of a threatening or neutral face-perceptual template to detect threatening or neutral perceptually degraded faces. One group of participants completed the perceptual task in the presence of threat of shock (high induced anxiety); there was no potential shock for the other group (low induced anxiety). Thus, in our task, participants were required to maintain threatening or neutral face "sets" or templates for subsequent perceptual decision making regarding faces. Because anxiety is associated with excessive anticipation of threatening information, it is possible that individuals higher in trait anxiety are more effective in using threat-related predictive information when they make perceptual decisions. On the other hand, deficits in WM in trait anxiety (Bishop, 2009; Eysenck, Derakshan, Santos, & Calvo, 2007) could result in poorer online maintenance of threat-related predictive representations in the service of subsequent perceptual decision making. Compared with neutral faces, representations of threatening faces may be maintained in WM with greater detail (Jackson, Linden, & Raymond, 2014; Stout, Shackman & Larson, 2013; Stout, Shackman, Johnson & Larson, 2015), thereby loading WM capacity, which is impacted by both the number of items, and the perceptual complexity of items in WM (Alvarez & Cavanagh, 2004; Eng, Chen, & Jiang, 2005). Detailed representations of threatening faces generally enhance WM (Jackson et al., 2014), but they may overburden WM capacity when it is already depleted from anxiety.

Furthermore, how effectively predictive representations of threat enhance perception in trait anxiety could depend on whether or not an individual is experiencing situational anxiety as a result of imminent danger. Anxiety induced by imminent danger or threat could worsen WM and result in greater inability to maintain and deploy threat-related predictive information for subsequent face perception. On the other hand, additional arousal associated with imminent danger could prioritize and sharpen threat-related representations (Grillon & Charney, 2011; Mather & Sutherland, 2011), making them easier to employ in subsequent decision making. Hence in the present study, we examined two alternative possibilities: (a) trait anxiety and anxiety induced by threat of shock have an additive enhancing effect on perceptual sensitivity following threatening cues, or (b) trait anxiety and anxiety induced by threat of shock have an interactive effect on perceptual sensitivity following threatening cues, such that higher trait anxiety is associated with decrements in perceptual sensitivity in the absence of shock, but also is associated with gains in threat-related perceptual sensitivity in the presence of shock.

Method

Participants

Fifty-one students (19 men, mean age = 21.63 years ± 1.47) performed a task to determine individual perceptual thresholds for fearful and neutral faces, followed by a perceptual discrimination task using these thresholds; see Table 1 for additional demographic statistics. A group of 29 students (seven men, mean age = 21.63 years ± 1.71) completed the tasks in the control condition, without shock. Another group of 22 college students (12 men, mean age = 19.70 years ± 1.92) completed the same tasks under threat of shock. Outliers on behavioral and questionnaire measures were computed as scores ± 2 *SD* from the mean. Two outliers were excluded due to (a) extreme behavioral performance and (b) extreme trait anxiety scores. All participants were recruited from the Stony Brook Psychology Department subject pool, and gave informed consent to participate in the study, which was approved by Stony Brook's institutional review board.

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Table 1
Demographic Variables for the Shock and No-Shock Groups

Study group	*n* (No outliers)	Age	*SD*	
No-shock group	27	21.6	1.47	
Shock group	20	19.7	1.92	
	STAI-T	*SD*	PANAS Fear	*SD*
No-shock group	41.56	10.86	8.44	.46
Shock group	46.70	7.72	13.20	1.07

Note. STAI-T = Trait version of the State–Trait Anxiety Inventory; PANAS Fear = Fear subscale of the Positive and Negative Affect Schedule.

Stimuli

Sixteen fearful and neutral faces from the Nim Stim set (Tottenham et al., 2009) were modified from color to grayscale (512 × 512 pixels). Images were equalized for luminance and spatial frequency using the SHINE toolbox for Matlab (Willenbockel et al., 2010). Researchers examining the effects of top-down processes on face perception have used this toolbox effectively to minimize confounds due to low-level image properties (Fiset, Blais, Gosselin, Bub, & Tanaka, 2008). Masks were made by dividing an image that combined several fearful and neutral faces into 100 pixel squares that were then randomly reorganized. These masks had the same low-level image properties as the target stimuli, and were shown immediately after each target.

Threshold Task

Each participant's threshold for perception (75% correct) was determined separately for fearful face (FF) and neutral face (NF) images using a two-alternative forced-choice perceptual discrimination task (Summerfield et al., 2006). The task had 16 blocks of 16 trials (8 FF and 8 NF), resulting in 128 FF trials and 128 NF trials. Each trial started with a fixation cross (2–3 s) followed by a degraded FF or NF image (100 ms), which was then followed by a mask (300 ms). After stimulus onset, participants used two adjacent buttons to identify the face as fearful or neutral (see Figure 1). FF and NF images were initially presented at a contrast level that ranged between .1 and 0, a level that is visible, but not easy to see. Subsequent trials involved two adaptive staircases to make the images more or less perceptually challenging, depending on the subject's responses. The range of contrast, and hence the ease of identifying subsequent images, was determined by the current most probable Bayesian estimate of participant performance, using the QUEST algorithm (Watson & Pelli, 1983). The range widened when identification was inaccurate, making images easier to identify, and narrowed when performance was accurate, making images harder to distinguish. The task was presented and the data were collected using Psychopy software (Peirce, 2007).

Cued Discrimination Task

A timeline of the task and cue-target combinations are shown in Figure 1. Stimuli consisted of 16 FF and 16 NF stimuli presented across 128 trials. Trials were divided into eight blocks. Each block consisted of 16 trials (eight images of FF and eight images of NF). The thresholds established in the threshold task were used in the subsequent task, in which subjects viewed the FF and NF images the same way, but with three main differences. First, to prevent improved perceptual performance due to practice effects, FF and NF were perceptually degraded and presented at one of eight contrast levels ranging from −6% to +8% contrast around the previously determined perceptual threshold (Adini, Wilkonsky, Haspel, Tsodyks, & Sagi, 2004). Second, prior to the presentation of each perceptually degraded face, the letter "F" (fear cue; FC) or "N" (neutral cue; NC) appeared for 1 s indicating the upcoming perceptual decision. Third, when the face was presented, participants were asked to make a perceptual decision of "fearful face or not" following FC and "neutral face or not" following NC. Hence,

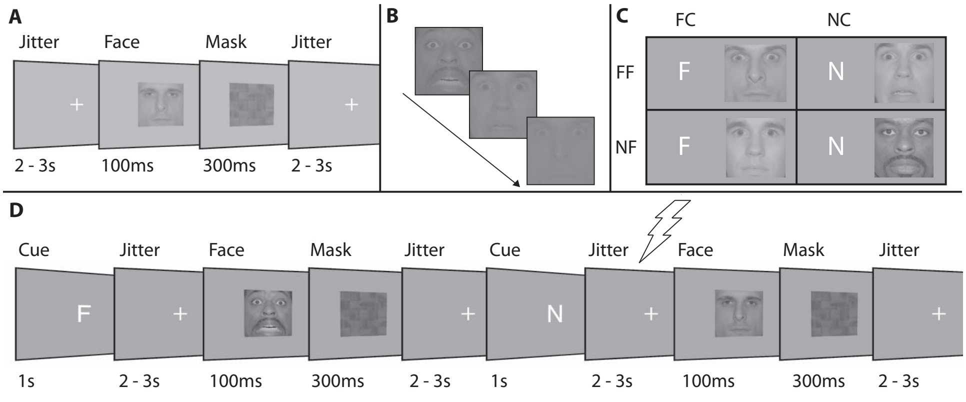

Figure 1. A. Timeline of threshold task. Perceptual thresholds, 75% correct, were found for fearful and neutral faces. B. Adaptive staircases, which made images harder or easier to see based on subject responses, were used in the threshold task to find each participant's perceptual threshold for fearful and neutral faces. C. Cue and stimulus pairs used in the cued task: fear cue/fearful face (FC/FF), neutral cue/fearful face (NC/FF), fear cue/neutral face (FC/NF), and neutral cue/neutral face (NC/NF). D. Timeline of cued task. Participants used cues to respond to a perceptually degraded fearful or neutral face. In the shock condition, participants were shocked once during the second half of each trial block. The shock was given following the cue, before stimulus onset and lasted 500 ms.

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using two fingers and two adjacent keyboard buttons, they were asked to respond by pressing the "yes" button if the face matched the cue (FF following FC or NF following NC), and to respond "no," if the face did not match the cue (NF following FC and FF following NC). It is important to note that the cue determined what the participant was supposed to look for but was not indicative of the probability of an FF or NF target: Each FF and NF was shown four times after each cue type. Low-level physical properties of the images following each cue type were also matched; therefore, differences observed in behavioral data could not be the result of frequency, probability, visibility, or trial-related salience. The measures that were recorded included hit rate, false-alarm rate, reaction time (RT), and accuracy. Perceptual sensitivity, or d' (a signal-detection parameter), was calculated using both hit rate and false-alarm rate.

Anxiety Induction

Anticipation of electric shock was used to induce anxiety. Electrical shocks were delivered using an electrical stimulator (Contact Precision Instruments, Boston, MA) that produced 60-Hz constant alternating-current (AC) stimulation between 0 and 5 mA for 500 ms. Before the threshold task, participants chose their level of shock. They were presented with a mild shock on the left triceps followed by increasingly intense shocks until they reached a level that was uncomfortable but not intolerable, "like a bee sting." The level each participant chose was used throughout the experiment. The shock procedure used during the cued discrimination task was based on preceding paradigms (Robinson, Letkiewicz, Overstreet, Ernst, & Grillon, 2011). Participants were shocked once per block during the second half of each block. The shock always occurred after cue presentation and before stimulus presentation.

Measures of Individual Differences

After the computer tasks, participants completed the Trait version of the State–Trait Anxiety Inventory (STAI-T; Spielberger, Gorsuch, Lushene, Vagg, & Jacobs, 1983) and the Fear subscale of the Positive and Negative Affect Schedule–Expanded Form (PANAS-X; Watson, Clark, & Harkness, 1994). The STAI-T is a 20-item self-report questionnaire that assesses frequency of trait anxiety-related symptoms. It has adequate test–retest reliability and internal consistency in college samples (Spielberger et al., 1983). Trait anxiety was measured by asking participants to report how they felt in general using a Likert-type scale ranging from *not at all* to *very much so*. The Fear scale of the PANAS-X consists of six items assessing fear-related emotions. Participants reported how much they experienced each specific emotion during task completion on a Likert-type scale that ranged from *not at all* to *extremely*.

Results

Because our study focused on whether predictive representations of threatening stimuli would facilitate perception, we first examined whether FC resulted in greater perceptual sensitivity than NC. Across the whole study sample, perceptual sensitivity was greater, $t(46) = 7.75$, $p < .001$ and RT was faster on trials following FC than on those following NC, $t(46) = 10.71$, $p < .001$. The shock manipulation was successful in inducing fear. Participants reported experiencing more fear on the PANAS-X Fear scale (Watson et al., 1994) under the threat of shock, $t(45) = -4.49$, $p < .001$. Finally, there was no significant difference in STAI-T scores (Spielberger et al., 1983) between the shock and no-shock groups, $t(45) = -1.90$. Descriptive statistics of behavioral variables can be found in Table 2.

Next, we examined whether perceptual facilitation due to FC varied based on levels of trait and induced anxiety. Multivariate multiple regression analyses were used to examine the effect of anxiety induced by threat of shock as a dichotomous variable, and mean-centered STAI-T scores (Spielberger et al., 1983) as a continuous variable predicting both d' for FC and NC as dependent variables. Tests of the assumption of collinearity indicated that multicollinearity was not a concern in these data (variance inflation factor; VIF < 2). Regression slopes were reported with a 95% confidence interval (CI). Results show a main effect of anxiety induced through threat of shock, such that participants performed better under threat of shock, regression slope = .48, CI [.002, .962], $F(1, 43) = 4.11$, $p < .05$ and a main effect of trait anxiety, such that participants higher in trait anxiety performed more poorly, regression slope = −.04, CI [−.07, −.01], $F(1, 43) = 7.46$, $p < .01$, as well as an interaction between the two on perceptual sensitivity following FC, regression slope = .06, CI [.01, .12], $F(1, 43) = 5.33$, $p < .05$ (see Figure 2). Probing the structure of the two-way interaction showed that the slope of perceptual sensitivity over trait anxiety in the absence of anxiety induction differed significantly from the same slope in the presence of anxiety induction for trials following FC, $t(43) = 2.55$, $p < .05$ (see Figure 2). Hence, for trials following FC, as trait anxiety increased, d' increased in the presence of shock, but decreased in the absence of shock. Conversely, the slopes of perceptual sensitivity over trait anxiety did not differ based on absence or presence of shock for trials following NC, $t(43) = .23$ (see Figure 2).

Finally, we examined whether RT for FC varied based on levels of trait and induced anxiety. Multivariate multiple regression analyses, with induced anxiety and STAI-T scores (Spielberger et al., 1983) as predictors and RT following FC and NC as dependent variables (VIF < 2), showed a significant interaction between induced anxiety and trait anxiety for FC RT, regression slope = −.01, CI [−.03, .00], $F(1, 43) = 4.15$, $p < .05$ and NC RT, regression slope = −.02, CI [−.03, .00], $F(1, 43) = 5.37$, $p < .05$. Although RT was faster for FC than NC overall, high trait anxiety was associated with faster RT under threat of shock and slower RT in the absence of shock (see Figure 2). Slope analyses

Table 2
Mean and Standard Deviations of d', Reaction Time, and Accuracy in Both the No-Shock Group and the Shock Group

	No-shock group		Shock group	
Variable	Mean	*SD*	Mean	*SD*
d', Fear cue	2.84	.91	3.26	.71
d', Neutral cue	2.06	.88	1.76	.95
RT(s), fear cue	1.07	.18	1.09	.19
RT(s), neutral cue	1.19	.18	1.23	.21
Accuracy, fear cue	.90	.06	.92	.06
Accuracy, neutral cue	.82	.11	.78	.12

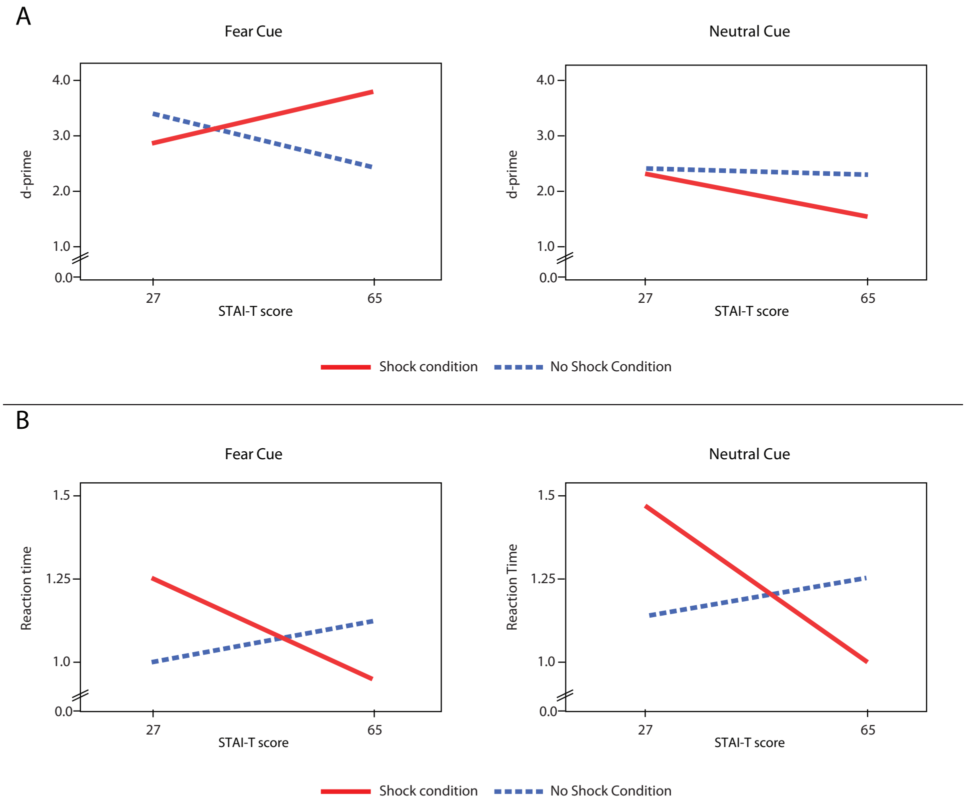

Figure 2. A. The effects of trait anxiety (ranging from a score of 27 to a score of 65 on the STAI-T in our sample) and threat of shock on perceptual sensitivity (d-prime) following fear and NCs. Higher trait anxiety was associated with decrements in perceptual sensitivity in the absence of shock but associated with gains in threat-related perceptual sensitivity in the presence of shock. B. The effects of trait anxiety and the threat of shock on RT following fear and NCs Higher trait anxiety was associated with slower RTs in the absence of shock, and faster RTs under threat of shock. While the FC-related RT changes were accompanied by changes in perceptual sensitivity (A), NC-related RT changes did not show such an association. See the online article for the color version of this figure.

showed that the slope of RT over trait anxiety in the absence of anxiety induction differed significantly from the same slope in the presence of anxiety induction for trials following FC, $t(43) = 1.97$, $p = .05$ and NC, $t(43) = 2.22$, $p < .05$ (see Figure 2). Following both FC and NC, RT slowed as trait anxiety increased under threat of shock, and RT decreased with higher trait anxiety in the absence of shock.

Discussion

Despite considerable research indicating the importance of top-down anticipatory processes in anxiety (Grupe & Nitschke, 2013), the literature has mainly focused on how the salience or physical properties of threatening stimuli drive perception in anxiety (Öhman et al., 2001; Vuilleumier, Armony, Driver, & Dolan, 2001). Our study represents a conceptual advance by establishing the importance of top-down processes in the perceptual prioritization of threat in anxiety. First, in line with an investigation (Sussman, Weinberg, Szekely, Hajcak, & Mohanty, 2015), we have demonstrated in the present study that prestimulus representations of threat play an important role in explaining how emotional information is prioritized in visual perception. Compared with NCs, threat-related cues improved perceptual sensitivity (d') and decreased RT, resulting in more accurate and rapid detection of faces. These results suggest that predictive representations of threatening stimuli are a key factor in their improved detection and further establish the role of top-down, endogenous factors in perceptual prioritization of emotional stimuli. The enhanced perceptual sensitivity following FCs may be attributable to more specific prestimulus perceptual templates that have been shown to enhance perceptual sensitivity (Schmidt & Zelinsky, 2009).

Second, there was a main effect of induced anxiety on perceptual sensitivity such that d' was greater following FCs when anxiety was induced. This is consistent with earlier findings demonstrating that threat of shock changes neural processing to a sensory-vigilance mode that prioritizes threatening stimuli (Arnsten, 2009; Shackman, Maxwell, McMenamin, Greischar, & Davidson, 2011), and with studies showing that fear-states can improve motor performance (Davis & Whalen, 2001). In all of these studies, threat of shock and threat cues improved performance. Finally, we have shown that trait anxiety and anxiety induced by threat of shock have an interactive, rather than additive, effect on perceptual sensitivity following threatening cues. Specifically, fol-

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lowing FCs, higher trait anxiety was associated with both improved perceptual sensitivity and faster RT in the presence of shock. On the other hand, higher trait anxiety was associated with decreased perceptual sensitivity and slower RT in the absence of shock. The interaction between trait and induced anxiety seen for FC RT was also seen for NC RT, with faster RT for those higher in trait anxiety under threat of shock. Hence, lower anxiety was associated with slower RT in the presence of shock, but there was no concurrent change in perceptual sensitivity following NCs (see Figure 2), indicating a more cautious response style.

The decrement in threat-related perceptual sensitivity in high trait anxiety in the absence of shock may be attributed to a combination of poorer WM and attentional control seen in anxiety (Eysenck et al., 2007) and greater WM load for maintaining threat-related representations (Jackson et al., 2014). The attentional control theory proposes that trait anxiety impairs the top-down (i.e., goal-driven) attentional system, as worrisome thoughts consume resources that would otherwise support WM while boosting bottom-up (i.e., stimulus-driven) processing (Eysenck et al., 2007). Making use of predictive cues requires the maintenance of perceptual templates; that is, a visual template must be kept online in WM to match against incoming stimuli (Sreenivasan, Sambhara, & Jha, 2011). Because emotional representations are maintained with greater vividness (Bywaters, Andrade, & Turpin, 2004; Stout et al., 2013; Stout, Shackman, Johnson & Larson, 2015), they may tax WM resources more than neutral templates. Summerfield and colleagues (2006) presented participants with identical stimuli while manipulating perceptual set and recording brain activity. They reported that predictive representations of upcoming target stimuli are maintained in prefrontal regions of the brain, specifically, the dorsal and ventral medial prefrontal cortex. Due to poorer recruitment of the dorsal medial prefrontal cortex (Shin et al., 2005) and the dorsolateral prefrontal cortex (Bishop, 2009), individuals higher in anxiety may have an impaired ability to maintain and deploy threat-related perceptual templates in the service of threat perception. Furthermore, low trait-anxious individuals benefit from cues preceding a visual search task, whereas individuals high in trait anxiety are not able to use these cues as effectively (Berggren & Derakshan, 2013). In our study, decreased perceptual sensitivity in high trait anxiety was observed for FCs but not NCs. Because the adverse impact of anxiety on performance becomes greater with increasing task demands on the central executive (Eysenck et al., 2007), it is possible that maintenance of a perceptual set for threatening faces is more demanding than maintaining a perceptual set for neutral faces.

On the other hand, gains in threat-related perceptual sensitivity in the presence of shock in high trait anxiety maybe may be due to the additive enhancing effects of high trait anxiety and induced anxiety of sensory-perceptual functions (Robinson et al., 2013). These enhancing effects can be explained by any of the following mechanisms supporting threat perception. For example, according to the predictive coding hypothesis, higher order brain regions anticipate likely sensory input based on context and create a template against which incoming sensory evidence is matched (Friston, 2005; Summerfield & de Lange, 2014). Within this framework, enhanced perception for threatening stimuli may result from more robust activation of threat-related than neutral templates in anxiety, leading to faster and more accurate matching, and improved perceptual sensitivity in upcoming trials. Models of anticipatory attention also propose that top-down processing plays an important role in stimulus detection; prior knowledge of a target's features is hypothesized to form a template that is matched against incoming sensory information (Wolfe, Horowitz, Kenner, Hyle, & Vasan, 2004), with more specific and informative templates leading to improved detection of expected stimuli (Schmidt & Zelinsky, 2009). In the present study, high-anxiety subjects in a threat context might have been more attuned to detecting threatening stimuli than low-anxiety subjects, leading to improved performance. This attunement could have involved the production of more specific templates for the FC, as well as better online maintenance of these templates, ultimately resulting in improved target detection. In addition, in high trait anxiety, arousal associated with induced anxiety may further sharpen FC-related predictive representations, as would be predicted by the arousal-based competition theory (Mather & Sutherland, 2011). Conversely, in lower trait anxiety, arousal due to induced anxiety may have had the opposite effect for NCs by making people respond more cautiously (Robinson et al., 2013) and slowing RT, as demonstrated in our study.

Enhanced perception following FCs in high trait anxiety, under threat of shock, could also be understood in terms of a model of decision making that posits that populations of neurons gather sensory information until neuronal activity exceeds a boundary, allowing a perceptual decision to be made (Bowman, Kording, & Gottfried, 2012; Heekeren, Marrett, & Ungerleider, 2008; Ratcliff & McKoon, 2008). In this context, threat-related templates could aid perception by requiring less sensory information to cross the decision boundary, which could be achieved by increased firing rates in sensory cortices at baseline (Kastner, Pinsk, De Weerd, Desimone, & Ungerleider, 1999; Lim, Padmala, & Pessoa, 2009). Anticipating threat stimuli could also boost the signal-to-noise ratio (Arnsten, 2009) by sharpening tuning curves in sensory neurons attending to features that distinguish threat stimuli, resulting in improved accumulation of sensory evidence or greater drift rate (Ratcliff & McKoon, 2008). Finally, induced and trait anxiety could impact any or several of these parameters of perceptual decision, further enhancing the effect of prior threat-related information on perception. Future research targeting specific decision-making components and neural mechanisms in the perceptual prioritization of threat via endogenous processes may greatly elucidate mechanisms of anxiety development and maintenance.

Overall, results from the present study show that predictive representations of threat enhance perceptual sensitivity, confirming the importance of endogenous top-down factors in how emotional information is prioritized in visual perception. Although both induced anxiety and trait anxiety have been associated with faster detection of threatening stimuli, our results indicate that when it comes to endogenously guided threat perception, induced anxiety and trait anxiety show interactive effects. The decrements in perceptual sensitivity for threat cues associated with higher levels of trait anxiety in the absence of induced anxiety may be due to impairment of top-down, goal-driven systems, possibly mediated by poorer recruitment of prefrontal brain regions. On the other hand, under the influence of induced anxiety, high trait anxiety individuals may be able to better marshal their goal-driven resources, and use threat cues more effectively. Low statistical power due to the relatively small size of our sample ($n = 47$, 20 in the induced-anxiety group and 27 in the absence-of-induced-

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anxiety group) may have limited our ability to detect some differences. However, present findings represent a conceptual advance in the literature because they elucidate the role of previously ignored top-down factors in threat perception in anxiety, and highlight the distinct impact that different types of anxiety have on the perception of threatening stimuli. They demonstrate how predictive representations facilitate perception of threatening stimuli in anxiety; however, an inability to maintain these representations online could impede the perception of threatening stimuli. The examination of top-down factors such as predictive representations, context, and expectations in the voluntary guidance of threat-related perception and attention may yield important clues into clinical anxiety. For example, this research could help clarify how worry, rumination, and threat-based schemas contribute to the development of perceptual biases toward threatening information and ultimately to the development and maintenance of anxiety disorders.

References

Adini, Y., Wilkonsky, A., Haspel, R., Tsodyks, M., & Sagi, D. (2004). Perceptual learning in contrast discrimination: The effect of contrast uncertainty. *Journal of Vision, 4*(12), 993–1005.

Alvarez, G. A., & Cavanagh, P. (2004). The capacity of visual short-term memory is set both by visual information load and by number of objects. *Psychological Science, 15,* 106–111. http://dx.doi.org/10.1111/j.0963-7214.2004.01502006.x

Arend, I., & Botella, J. (2002). Emotional stimuli reduce the attentional blink in sub-clinical anxious subjects. *Psicothema, 14,* 209–214.

Arnsten, A. F. (2009). Stress signalling pathways that impair prefrontal cortex structure and function. *Nature Reviews Neuroscience, 10,* 410–422. http://dx.doi.org/10.1038/nrn2648

Ashcraft, M. H., & Kirk, E. P. (2001). The relationships among working memory, math anxiety, and performance. *Journal of Experimental Psychology: General, 130,* 224–237. http://dx.doi.org/10.1037/0096-3445.130.2.224

Aue, T., Guex, R., Chauvigné, L. A., & Okon-Singer, H. (2013). Varying expectancies and attention bias in phobic and non-phobic individuals. *Frontiers in Human Neuroscience, 7*(418), 1–8. http://dx.doi.org/10.3389/fnhum.2013.00418

Bar, M. (2004). Visual objects in context. *Nature Reviews Neuroscience, 5,* 617–629. http://dx.doi.org/10.1038/nrn1476

Berggren, N., & Derakshan, N. (2013). Trait anxiety reduces implicit expectancy during target spatial probability cueing. *Emotion, 13,* 345–349. http://dx.doi.org/10.1037/a0029981

Bishop, S. J. (2009). Trait anxiety and impoverished prefrontal control of attention. *Nature Neuroscience, 12,* 92–98. http://dx.doi.org/10.1038/nn.2242

Bowman, N. E., Kording, K. P., & Gottfried, J. A. (2012). Temporal integration of olfactory perceptual evidence in human orbitofrontal cortex. *Neuron, 75,* 916–927. http://dx.doi.org/10.1016/j.neuron.2012.06.035

Bywaters, M., Andrade, J., & Turpin, G. (2004). Determinants of the vividness of visual imagery: The effects of delayed recall, stimulus affect and individual differences. *Memory, 12,* 479–488. http://dx.doi.org/10.1080/09658210444000160

Davis, M., Walker, D. L., Miles, L., & Grillon, C. (2010). Phasic vs sustained fear in rats and humans: Role of the extended amygdala in fear vs anxiety. *Neuropsychopharmacology, 35,* 105–135. http://dx.doi.org/10.1038/npp.2009.109

Davis, M., & Whalen, P. J. (2001). The amygdala: Vigilance and emotion. *Molecular Psychiatry, 6,* 13–34. http://dx.doi.org/10.1038/sj.mp.4000812

Derakshan, N., & Eysenck, M. W. (1998). Working memory capacity in high trait-anxious and repressor groups. *Cognition and Emotion, 12,* 697–713. http://dx.doi.org/10.1080/026999398379501

Eng, H. Y., Chen, D., & Jiang, Y. (2005). Visual working memory for simple and complex visual stimuli. *Psychonomic Bulletin & Review, 12,* 1127–1133. http://dx.doi.org/10.3758/BF03206454

Etkin, A., & Wager, T. D. (2007). Functional neuroimaging of anxiety: A meta-analysis of emotional processing in PTSD, social anxiety disorder, and specific phobia. *The American Journal of Psychiatry,* 1476–1488. http://dx.doi.org/10.1176/appi.ajp.2007.07030504

Eysenck, M. W., Derakshan, N., Santos, R., & Calvo, M. G. (2007). Anxiety and cognitive performance: Attentional control theory. *Emotion, 7,* 336–353. http://dx.doi.org/10.1037/1528-3542.7.2.336

Fiset, D., Blais, C., Gosselin, F., Bub, D., & Tanaka, J. (2008). Potent features for the categorization of Caucasian, African American and Asian faces in Caucasian observers [Abstract]. *Journal of Vision, 8,* 258. http://dx.doi.org/10.1167/8.6.258

Friston, K. (2005). A theory of cortical responses. *Philosophical Transactions of the Royal Society of London: Series B. Biological Sciences, 360,* 815–836. http://dx.doi.org/10.1098/rstb.2005.1622

Friston, K. J., Harrison, L., & Penny, W. (2003). Dynamic causal modelling. *NeuroImage, 19,* 1273–1302. http://dx.doi.org/10.1016/S1053-8119(03)00202-7

Grillon, C., & Charney, D. R. (2011). In the face of fear: Anxiety sensitizes defensive responses to fearful faces. *Psychophysiology, 48,* 1745–1752. http://dx.doi.org/10.1111/j.1469-8986.2011.01268.x

Grupe, D. W., & Nitschke, J. B. (2013). Uncertainty and anticipation in anxiety: An integrated neurobiological and psychological perspective. *Nature Reviews Neuroscience, 14,* 488–501. http://dx.doi.org/10.1038/nrn3524

Heekeren, H. R., Marrett, S., & Ungerleider, L. G. (2008). The neural systems that mediate human perceptual decision making. *Nature Reviews Neuroscience, 9,* 467–479. http://dx.doi.org/10.1038/nrn2374

Jackson, M. C., Linden, D. E., & Raymond, J. E. (2014). Angry expressions strengthen the encoding and maintenance of face identity representations in visual working memory. *Cognition and Emotion, 28,* 278–297. http://dx.doi.org/10.1080/02699931.2013.816655

Kastner, S., Pinsk, M. A., De Weerd, P., Desimone, R., & Ungerleider, L. G. (1999). Increased activity in human visual cortex during directed attention in the absence of visual stimulation. *Neuron, 22,* 751–761. http://dx.doi.org/10.1016/S0896-6273(00)80734-5

Lim, S. L., Padmala, S., & Pessoa, L. (2009). Segregating the significant from the mundane on a moment-to-moment basis via direct and indirect amygdala contributions. *PNAS: Proceedings of the National Academy of Sciences of the United States of America, 106,* 16841–16846. http://dx.doi.org/10.1073/pnas.0904551106

Lipka, J., Miltner, W. H., & Straube, T. (2011). Vigilance for threat interacts with amygdala responses to subliminal threat cues in specific phobia. *Biological Psychiatry, 70,* 472–478. http://dx.doi.org/10.1016/j.biopsych.2011.04.005

Mather, M., & Sutherland, M. R. (2011). Arousal-biased competition in perception and memory. *Perspectives on Psychological Science, 6,* 114–133. http://dx.doi.org/10.1177/1745691611400234

Mogg, K., & Bradley, B. P. (1999). Orienting of attention to threatening facial expressions presented under conditions of restricted awareness. *Cognition and Emotion, 13,* 713–740. http://dx.doi.org/10.1080/026999399379050

Öhman, A., Flykt, A., & Esteves, F. (2001). Emotion drives attention: Detecting the snake in the grass. *Journal of Experimental Psychology: General, 130,* 466–478. http://dx.doi.org/10.1037/0096-3445.130.3.466

Pacheco-Unguetti, A. P., Acosta, A., Callejas, A., & Lupiáñez, J. (2010). Attention and anxiety: Different attentional functioning under state and trait anxiety. *Psychological Science, 21,* 298–304. http://dx.doi.org/10.1177/0956797609359624

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Peirce, J. W. (2007). PsychoPy: Psychophysics software in Python. *Journal of Neuroscience Methods, 162*(1–2), 8–13. http://dx.doi.org/10.1016/j.jneumeth.2006.11.017

Pourtois, G., Schettino, A., & Vuilleumier, P. (2013). Brain mechanisms for emotional influences on perception and attention: What is magic and what is not. *Biological Psychology, 92,* 492–512. http://dx.doi.org/10.1016/j.biopsycho.2012.02.007

Ratcliff, R., & McKoon, G. (2008). The diffusion decision model: Theory and data for two-choice decision tasks. *Neural Computation, 20,* 873–922. http://dx.doi.org/10.1162/neco.2008.12-06-420

Robinson, O. J., Letkiewicz, A. M., Overstreet, C., Ernst, M., & Grillon, C. (2011). The effect of induced anxiety on cognition: Threat of shock enhances aversive processing in healthy individuals. *Cognitive, Affective & Behavioral Neuroscience, 11,* 217–227. http://dx.doi.org/10.3758/s13415-011-0030-5

Robinson, O. J., Vytal, K., Cornwell, B. R., & Grillon, C. (2013). The impact of anxiety upon cognition: Perspectives from human threat of shock studies. *Frontiers in Human Neuroscience, 7*(203), 1–21. http://dx.doi.org/10.3389/fnhum.2013.00203

Schmidt, J., & Zelinsky, G. J. (2009). Search guidance is proportional to the categorical specificity of a target cue. *The Quarterly Journal of Experimental Psychology, 62,* 1904–1914. http://dx.doi.org/10.1080/17470210902853530

Shackman, A. J., Maxwell, J. S., McMenamin, B. W., Greischar, L. L., & Davidson, R. J. (2011). Stress potentiates early and attenuates late stages of visual processing. *The Journal of Neuroscience, 31,* 1156–1161. http://dx.doi.org/10.1523/JNEUROSCI.3384-10.2011

Shackman, A. J., Sarinopoulos, I., Maxwell, J. S., Pizzagalli, D. A., Lavric, A., & Davidson, R. J. (2006). Anxiety selectively disrupts visuospatial working memory. *Emotion, 6,* 40–61. http://dx.doi.org/10.1037/1528-3542.6.1.40

Shin, L. M., Wright, C. I., Cannistraro, P. A., Wedig, M. M., McMullin, K., Martis, B., . . . Rauch, S. L. (2005). A functional magnetic resonance imaging study of amygdala and medial prefrontal cortex responses to overtly presented fearful faces in posttraumatic stress disorder. *Archives of General Psychiatry, 62,* 273–281. http://dx.doi.org/10.1001/archpsyc.62.3.273

Spielberger, C. D., Gorsuch, R. L., Lushene, R., Vagg, P. R., & Jacobs, G. A. (Eds.). (1983). *Manual for the State–Trait Anxiety Inventory*. Palo Alto, CA: Consulting Psychologists Press.

Sreenivasan, K. K., Sambhara, D., & Jha, A. P. (2011). Working memory templates are maintained as feature-specific perceptual codes. *Journal of Neurophysiology, 106,* 115–121. http://dx.doi.org/10.1152/jn.00776.2010

Stout, D. M., Shackman, A. J., Johnson, J. S., & Larson, C. L. (2015). Worry is associated with impaired gating of threat from working memory. *Emotion, 15*(1), 6–11. http://dx.doi.org/10.1037/emo0000015

Stout, D. M., Shackman, A. J., & Larson, C. L. (2013). Failure to filter: Anxious individuals show inefficient gating of threat from working memory. *Frontiers in Human Neuroscience, 7*(58), 1–10. http://dx.doi.org/10.3389/fnhum.2013.00058

Straube, T., Mentzel, H. J., & Miltner, W. H. (2005). Common and distinct brain activation to threat and safety signals in social phobia. *Neuropsychobiology, 52,* 163–168. http://dx.doi.org/10.1159/000087987

Summerfield, C., & de Lange, F. P. (2014). Expectation in perceptual decision making: Neural and computational mechanisms. *Nature Reviews Neuroscience, 15,* 745–756. http://dx.doi.org/10.1038/nrn3838

Summerfield, C., Egner, T., Greene, M., Koechlin, E., Mangels, J., & Hirsch, J. (2006). Predictive codes for forthcoming perception in the frontal cortex. *Science, 314,* 1311–1314. http://dx.doi.org/10.1126/science.1132028

Sussman, T. J., Weinberg, A., Szekely, A., Hajcak, G., & Mohanty, A. (2015). *Here comes trouble: Prestimulus brain activity predicts enhanced perception of threat*. Manuscript submitted for publication.

Tottenham, N., Tanaka, J. W., Leon, A. C., McCarry, T., Nurse, M., Hare, T. A., . . . Nelson, C. (2009). The NimStim set of facial expressions: Judgments from untrained research participants. *Psychiatry Research, 168,* 242–249. http://dx.doi.org/10.1016/j.psychres.2008.05.006

Vuilleumier, P., Armony, J. L., Driver, J., & Dolan, R. J. (2001). Effects of attention and emotion on face processing in the human brain: An event-related fMRI study. *Neuron, 30,* 829–841. http://dx.doi.org/10.1016/S0896-6273(01)00328-2

Watson, A. B., & Pelli, D. G. (1983). QUEST: A Bayesian adaptive psychometric method. *Perception & Psychophysics, 33,* 113–120. http://dx.doi.org/10.3758/BF03202828

Watson, D., Clark, L. A., & Harkness, A. R. (1994). Structures of personality and their relevance to psychopathology. *Journal of Abnormal Psychology, 103,* 18–31. http://dx.doi.org/10.1037/0021-843X.103.1.18

Willenbockel, V., Sadr, J., Fiset, D., Horne, G. O., Gosselin, F., & Tanaka, J. W. (2010). Controlling low-level image properties: The SHINE toolbox. *Behavior Research Methods, 42,* 671–684. http://dx.doi.org/10.3758/BRM.42.3.671

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

Wolfe, J. M., Horowitz, T. S., Kenner, N., Hyle, M., & Vasan, N. (2004). How fast can you change your mind? The speed of top-down guidance in visual search. *Vision Research, 44,* 1411–1426. http://dx.doi.org/10.1016/j.visres.2003.11.024

Zelano, C., Mohanty, A., & Gottfried, J. A. (2011). Olfactory predictive codes and stimulus templates in piriform cortex. *Neuron, 72,* 178–187. http://dx.doi.org/10.1016/j.neuron.2011.08.010

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