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Knowledge of Threat Biases Perceptual Decision Making in Anxiety: Evidence From Signal Detection Theory and Drift Diffusion Modeling

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ABSTRACT

BACKGROUND: Threat biases are considered key factors in the development and maintenance of anxiety. However, these biases are poorly operationalized and remain unquantified. Furthermore, it is unclear whether and how prior knowledge of threat and its uncertainty induce these biases and how they manifest in anxiety.

METHOD: Participants (n = 55) used prestimulus cues to decide whether the subsequently presented stimuli were threatening or neutral. The cues either provided no information about the probability (high uncertainty) or indicated high probability (low uncertainty) of encountering threatening or neutral targets. We used signal detection theory and hierarchical drift diffusion modeling to quantify bias.

RESULTS: High-uncertainty threat cues improved discrimination of subsequent threatening and neutral stimuli more than neutral cues. However, anxiety was associated with worse discrimination of threatening versus neutral stimuli following high-uncertainty threat cues. Using hierarchical drift diffusion modeling, we found that threat cues biased decision making not only by shifting the starting point of evidence accumulation toward the threat decision but also by increasing the efficiency with which sensory evidence was accumulated for both threat-related and neutral decisions. However, higher anxiety was associated with a greater shift of starting point toward the threat decision but not with the efficiency of evidence accumulation.

CONCLUSIONS: Using computational modeling, these results highlight the biases by which knowledge regarding uncertain threat improves perceptual decision making but impairs it in case of anxiety.

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A vast and influential cognitive literature has focused on the importance of perceptual and attentional biases toward threatening stimuli that are heightened in anxiety. The view that our sensory systems are biased to detect threatening stimuli is based on evidence showing faster detection of threatening compared with neutral stimuli in the general population, an effect that is even more pronounced in anxiety (1,2). Additional evidence of this bias is reflected by a tendency to interpret neutral stimuli as being negative (3,4). Treatment strategies such as attentional bias modification are believed to work by ameliorating these attentional or perceptual biases in anxiety (5). Despite the hypothesized importance of these threat biases in anxiety, several questions remain unanswered. Below, we highlight four key issues regarding threat biases in anxiety. Then, we address these issues by quantifying bias through computational modeling and examining how it is influenced by prior knowledge regarding the relevance and uncertainty of threatening stimuli. An understanding of these computational mechanisms will help elucidate the downstream cognitive, emotional, and social consequences of threat biases in anxiety and guide points of intervention to refine anxiety treatments.

First, according to several influential frameworks, anxiety is clinically conceptualized as a response to potential future threat emphasizing the importance of top-down factors such as schemas, anticipation, and expectation of threat [see (6) for review]. However, threat-related biases have typically been examined using experimental paradigms in which threatening stimuli capture attention in a relatively automatic and bottom-up manner because they are presented peripherally or as distractors and are irrelevant to task goals (1,2). This selective focus in the literature has led to the view that threat biases in anxiety are associated with greater capture of attention which is automatic or involuntary in nature, and the role of top-down voluntary guidance by threat-related information remains unexamined. The mismatch between the clinical nature of anxiety as an anticipatory top-down process and cognitive bias toward threat as an involuntary bottom-up process may have contributed to the limited success of therapies based on such paradigms (7–9). Furthermore, anxiety is not a monolithic construct and consists of 2 primary dimensions, namely anxious arousal and anxious apprehension (i.e., worry) (10). Anxious apprehension is defined as persistent and repetitive negative thought patterns about uncertain future negative outcomes (11), and it indexes inflated expectations regarding costs and undesirable outcomes (12). It is likely to involve alterations in anticipatory top-down processes. Therefore, high expectations associated with elevated levels of anxious apprehension may be associated with top-down anticipatory threat bias in perceptual decision making.

Second, in real life, we do not encounter threatening or neutral stimuli in a vacuum. Rather, top-down contextual cues often provide us with information that conveys varying degrees of certainty about what threatening or neutral stimuli are relevant or likely in our environment. Perceptual decision making, the basic process by which sensory inputs are collected and integrated to identify a stimulus (13–15), involves a complex process of integrating bottom-up sensory evidence arising from the stimulus with top-down information such as the observer's perceptual set, attention, and expectations (16). However, the mechanisms by which prior knowledge of threat biases perceptual decisions compared with knowledge of relatively safe or benign targets generally and in anxiety specifically remain unknown. For example, threat-related knowledge could bias one's tendency to endorse the presence of threat irrespective of the stimulus or it could bias the way that one acquires and interprets sensory information from the stimulus (17).

Third, it is well established that prior knowledge regarding which stimuli are relevant (involving attention) influences decision making differently than prior information regarding the probability (involving expectation) of such stimuli (18,19). Because uncertainty in the environment is aversive and linked with exaggerated threat expectations (6,20,21), it is likely that cues that indicate uncertain threat will influence decision making differently than cues that indicate more probable threat. Additionally, given that anxiety is characterized by misestimation of uncertainty, exaggerated expectations (4,6), and higher arousal for uncertain future threats (6,22,23), it is critical to examine how prior knowledge regarding the uncertainty of future threats influences perceptual decision making differently than knowledge of more certain threats in anxiety.

Finally, threat biases in anxiety are largely inferred from reaction time (RT) differences for threatening and neutral stimuli and are not well operationalized or quantified. Here, we operationalize threat-related biases within the context of signal detection theory (SDT) and drift diffusion modeling (DDM) (Figure 1B, C). SDT provides one common framework for operationalizing how a decision maker samples the sensory evidence arising from stimuli and/or how top-down information biases their decision (24). When deciding whether a stimulus is threatening or neutral, SDT can be used to examine how top-down threat-related information biases perceptual sensitivity or d' (i.e., the degree to which threatening and neutral stimuli can be discriminated) and criterion shift or c (i.e., the tendency to report whether a threatening or neutral signal is present or absent). Although SDT is suitable for quantifying decision bias,

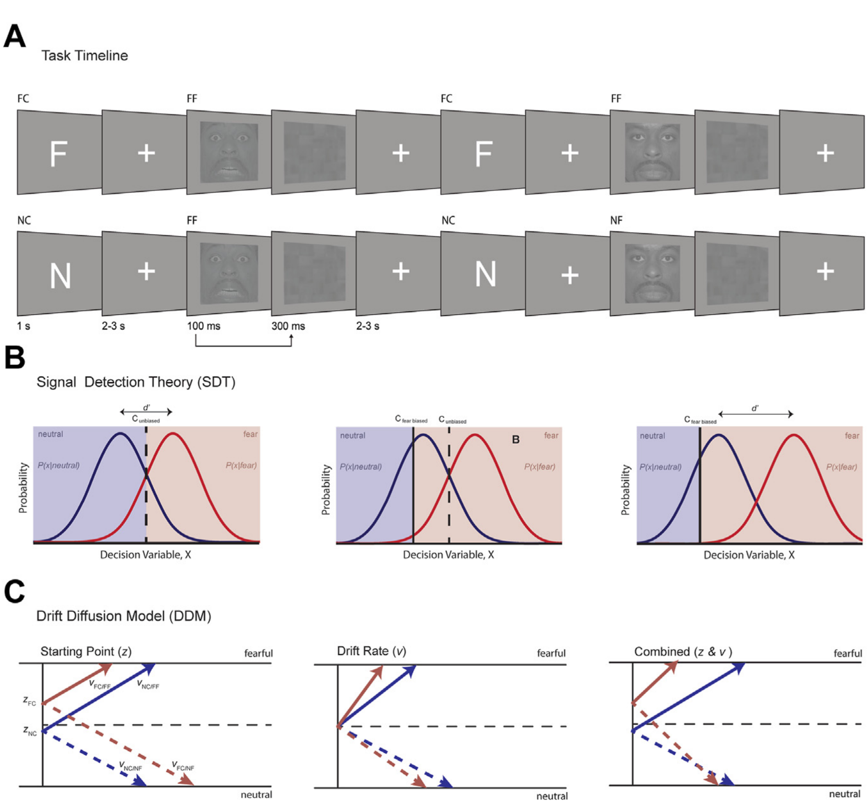

Figure 1. **(A)** In the perceptual decision-making tasks, participants viewed a fearful cue (FC) (top) which was the letter "F" and indicated that they would decide whether the subsequent face was fearful or not. FC was followed by a fixation cross followed by a perceptually degraded fearful face (FF) or neutral face (NF). The face was followed by a perceptual mask after which the participant responded about whether the face was fearful or not. In a similar timeline, participants viewed a neutral cue (NC) which was the letter "N" (bottom) which indicated that they would be deciding whether the subsequent face was neutral or not. **(B)** Signal detection theory (SDT) provides a means for measuring the observer's ability to differentiate FF (red) from NF (blue) signal distributions via d' and c. Compared with an unbiased observer (left panel), an FC can bias decision making by shifting the decision criterion to the left ($c_{fear\text{-}biased}$ line), manifesting as a bias favoring the fearful decision (middle panel). Additionally, an FC can reduce the overlapping area between the FF and NF signal distributions, resulting in an increased d' (right panel). **(C)** FC-related bias can be modeled via drift diffusion model as 1) a shift in the starting point (z_{FC} red line, left panel) of FF-related evidence accumulation closer to the fearful decision boundary reducing the amount of evidence needed to decide that the face is fearful, more than z_{NC} shifts toward corresponding boundary, 2) more efficient evidence accumulation (steeper slope for drift rate v, middle panel) for subsequently presented FFs ($v_{FC/FF}$) and NFs ($v_{FC/NF}$) than in the case of NC ($v_{NC/FF}$ and $v_{NC/NF}$), or 3) a combination of the two (right panel). **(B)** Depicts an illustration of the FC condition. In **(B)**, the red and blue curves indicate distributions for FF and NF, whereas in **(C)** red and blue lines indicate evidence accumulation following FC and NC.

it does not make claims about any underlying psychological processes and provides static rather than dynamic descriptions of the decision maker's performance. Alternatively, sequential sampling models, such as the DDM, are a family of race models which assume that sensory evidence for competing decisions is accumulated over time until a decision boundary is reached (25,26). Within the DDM framework, anticipatory threat-related bias can be conceptualized either as a 1) shift in the starting point or z of the evidence accumulation process toward a threat decision, irrespective of stimulus, and/or 2) enhancing the rate of evidence accumulation (drift rate or v) once the stimulus is encountered (26–29). Overall, SDT and DDM provide ways of quantifying bias (27,30,31) (Figure 1B, C) that can be used to determine how prior knowledge of threat can guide perceptual decision making or misguide it in anxiety.

Here, we draw from research in basic visual-perceptual decision making to examine how prior knowledge regarding future threatening targets and their uncertainty can (mis)guide perceptual decision making in individuals with anxiety. This research shows that cues indicating the relevance of targets improve d', while cues indicating the probability of targets influence c measured via SDT (19). Furthermore, probabilistic cues can bias decision making by influencing either the z, v, or both in DDM (27,28). Based on this literature, we hypothesized that cues indicating uncertain threatening stimuli would bias decision making by improving d' and increasing v for following stimuli while cues indicating highly probable threatening stimuli would shift c and z toward the threat decision boundary. Because anxiety is associated with exaggerated expectations regarding uncertain threat and misinterpretation of neutral stimuli as threatening (4,6), we hypothesized that anxious apprehension would be associated with worse d', greater false alarms for neutral stimuli, greater shift in z toward threat decisions, and lower v for neutral stimuli following uncertain threat cues. Overall, by quantifying different kinds of biases and examining how they are impacted by threat relevance and probability, these hypotheses will help elucidate the computational mechanisms of threat-related perceptual decision making in anxiety.

METHODS AND MATERIALS

Participants

Fifty-nine participants were recruited through the undergraduate participant pool at Stony Brook University. After completing an online screening, participants were invited to complete the in-person portion of the experiment, which consisted of 3 behavioral tasks and a battery of individual difference measures, all of which were conducted on a computer. Four participants in total were excluded due to outlier behavioral performance (defined as larger than ± 2 standard deviations of the mean d' for threat and neutral cues [NCs]) in either one of the tasks. Of the 55 participants (36 female, 19 male) included in the final sample, 67.3% identified as Asian, followed by Caucasian (18.2%), Hispanic/Latinx (9.1%), and African American (5.5%). The age range was between 18 and 21 years. Six of these participants did not complete either one of the experimental tasks. The study was approved by Stony Brook University's Institutional Review Board. All participants provided written informed consent.

Anxiety Measure

The Penn State Worry Questionnaire (PSWQ) (24) was used to measure an individual's degree of anxious apprehension, which is considered a trait-like transdiagnostic dimension of anxiety (10). The PSWQ is a widely used and extensively validated 16-item self-report questionnaire that assesses subjective feelings of worry. Compared with other trait measures of anxiety (like the State-Trait Anxiety Inventory-Trait version) that are more generic measures of negative affect, general distress, or general vulnerability to psychopathology (32–35), the PSWQ specifically measures anxious apprehension (10). It has excellent test-retest reliability (36) and good convergent validity (37). It is rated on a 5-point Likert scale ranging from "not at all typical of me" to "very typical of me," with a focus on overall (lifetime) levels of worry.

Stimuli

Following a previously established paradigm (38), 32 female (16 fearful faces [FFs] and 16 neutral faces [NFs]) and 32 male (16 FFs and 16 NFs) face stimuli were obtained from the NimStim set (39). Perceptual masks were created by averaging 4 randomly selected face images (2 FFs and 2 NFs). See Supplemental Methods for details regarding creation of stimuli and perceptual masks.

Behavioral Tasks

Perceptual Thresholding Task. Prior to the 2 experimental conditions, all participants first completed a thresholding task, with the aim of determining each participant's individual perceptual thresholds (75% accuracy) for FFs and NFs independently (40). The task involved 16 blocks of 16 trials (8 FFs and 8 NFs), totaling 128 FF trials and 128 NF trials. At the trial onset, a fixation cross was presented for 3 to 5 seconds. Subsequently, a degraded FF or NF was displayed (100 ms), followed by a mask (300 ms). At the end of each trial, participants were asked to identify the facial stimulus as fearful or neutral using 2 adjacent keys (left and down arrows) on a keyboard. An adaptive staircasing procedure was used to estimate the perceptual threshold of FFs and NFs for each participant (41). See Supplemental Methods for details regarding adaptive staircasing. PsychoPy 2 was used for data collection and task presentation (42).

Cued Perceptual Discrimination Tasks. Upon determining individual perceptual thresholds, participants completed 2 tasks: low-uncertainty task (LUT) and high-uncertainty task (HUT) (Figure 1A). Both tasks were identical to the thresholding task above, except for 2 important differences. First, face stimuli were presented with the contrast level ranging from -6% to $+8\%$ of each participant's predetermined perceptual threshold (38,43). For example, if a participant's threshold for FFs was 0.1 using the thresholding task above, then FFs in the discrimination task were subsequently shown with a contrast level ranging from 0.094 to 0.108. The stimuli were presented at a range of contrast levels to prevent practice effects. Second, a fear cue (FC) or NC was presented prior to each facial stimulus (FF or NF). An FC indicated that the participant would be making a "fearful face or not decision" on encountering the

Table 1. Hierarchical Drift Diffusion Modeling Models and Model Fit

HDDM Models	Cue	Stimulus	DIC for HUT	DIC for LUT
Model 1	–	*v*	15,518.91	11,027.23
Model 2	*z*	*v*	13,126.38	8755.37
Model 3	*z* and *v*	*v*	12,094.32[a]	8573.97[a]

Three models (Model 1–3) were tested. Drift rate, *v*, represents the speed or efficiency of evidence accumulation in reaching either of the 2 decision boundaries. Starting point bias, *z*, represents the initial amount of bias in favor of each of the 2 decision choices. Across 3 models, cue and/or stimulus were allowed to vary by either starting point (*z*) or drift rate (*v*). The 2 columns on the right display DIC for both tasks as a measure of model fit.

DIC, deviance information criterion; HDDM, Hierarchical Drift Diffusion Modeling; HUT, high-uncertainty task; LUT, low-uncertainty task.

[a]Values indicate better model fit.

FF or NF while NC indicated that they would make a “neutral face or not” decision on encountering the subsequent FF or NF.

Thus, in both the LUT and HUT, the cues indicated the nature of the subsequent decision (Figure 1A for task details and timeline). In the HUT, by indicating that a fearful or neutral face was relevant to the upcoming decision, the cues encouraged participants to use a FF- or NF-related perceptual set but provided no information regarding the probability of encountering these faces. Unbeknownst to the participants, there was a 50% probability of an FF or NF following FC and NC. In contrast, in the LUT, participants were explicitly informed that cues also indicated that the target stimulus (FFs for FC and NFs for NC) was “highly likely.” There was a 75% probability that FC was followed by a FF and NC was followed by a NF. To ensure that the participants did not confuse the 2 types of cues across the 2 tasks, the cues were blue in HUT but light gray in the LUT. Both tasks included a total of 160 trials (80 FCs and 80 NCs), wherein 128 trials (64 FFs and 64 NFs) were followed by presentation of degraded face stimuli. The remaining 32 trials were catch trials, where cues were not followed by targets. The trials were divided into 4 blocks of 40 trials (20 FC and 20 NC). Participants first completed the thresholding task, followed by HUT and then LUT. This order remained fixed across participants. The reason we did not counterbalance HUT and LUT was that administering HUT after LUT would require participants to unlearn the contingencies between cues and stimuli in the LUT, which would involve a fundamentally different process than the one under examination in the current study.

Data Analyses

SDT Measures. For each participant, 2 SDT measures (Figure 1B), d' and c, were computed using hit rate and false alarm rate (FAR) under the equal-variance Gaussian assumptions (24) for each of the cues (FC and NC) and each of the tasks (LUT and HUT) (41). d' measured the ability to discriminate between 2 different stimulus distributions, FFs and NFs. c quantified the position of the decision criterion, which can indicate a more liberal or conservative decision bias. A liberal bias (a more negative value) would indicate a higher likelihood of making a threat decision following FC or a higher likelihood of making a neutral decision following NC, whereas a conservative bias (a more positive value) would be the opposite. See Figure 1B for details about how d' and c index bias in decision making in tasks used in the current study.

Hierarchical DDM. DDM (44–46) was applied to the behavioral data choice and RT to examine the decision-making components that are influenced by FC and NC in each task (Figure 1C). In DDM, stochastically sampled perceptual evidence accumulating over (a short period of) time is represented by a single decision variable. The accumulation begins from a starting point (denoted as z) between the 2 decision boundaries (with the distance between these boundaries denoted as a), each of which represents a choice alternative (i.e., fearful and neutral decisions in our task). The speed at which evidence is accumulated is reflected by the drift rate (denoted as v). There is also a nondecision (sensory encoding and motor execution) component (denoted as t). The parameters (z, a, v, and t) can be estimated based on the shape of the RT distributions for fearful and neutral decisions. Based on an earlier literature showing that cues can bias decision making by influencing the z and v (27,28), we examined whether FC and NC impact these decision-making components toward a fearful or neutral decision boundary (Figure 1C). DDM modeling was conducted using an open-source Python package that estimates the parameters of the DDM using a hierarchical Bayesian approach (hierarchical DDM) (47). For details regarding DDM, see Table 1 and Supplemental Methods.

Table 2. Descriptive Statistics for Signal Detection Theory Parameters Calculated Separately for Fear Cues and Neutral Cues in the High- and Low-Uncertainty Tasks

SDT Parameters	Fear Cue	Neutral Cue	*t* Test	*p* Value	Cohen’s *d*
High-Uncertainty Task					
False alarms	0.148 (0.144) [7]	0.235 (0.157) [12]	$t_{54} = -3.9$	<.001	−0.53
Hit rate	0.86 (0.088) [56]	0.733 (0.23) [52]	$t_{54} = 4.46$	<.001	0.6
Perceptual sensitivity (d')	2.126 (0.903)	1.761 (0.936)	$t_{54} = 6.26$	<.001	0.84
Criterion shift (c)	0.06 (0.396)	0.034 (0.394)	$t_{54} = 0.37$	.716	0.05
Low-Uncertainty Task					
False alarms	0.233 (0.214) [8]	0.253 (0.161) [14]	$t_{52} = -0.84$	.406	0.12
Hit rate	0.86 (0.118) [54]	0.798 (0.171) [53]	$t_{52} = 3.18$	<.001	0.44
Perceptual sensitivity (d')	2.093 (0.879)	1.739 (0.936)	$t_{52} = 17.76$	<.001	0.88
Criterion shift (c)	−0.111 (0.502)	−0.107 (0.417)	$t_{52} = -1.51$	.138	0.51

Values under Fear Cue and Neutral Cue columns are presented as mean (SD) [median # of trials] or mean (SD).

SDT, signal detection theory.

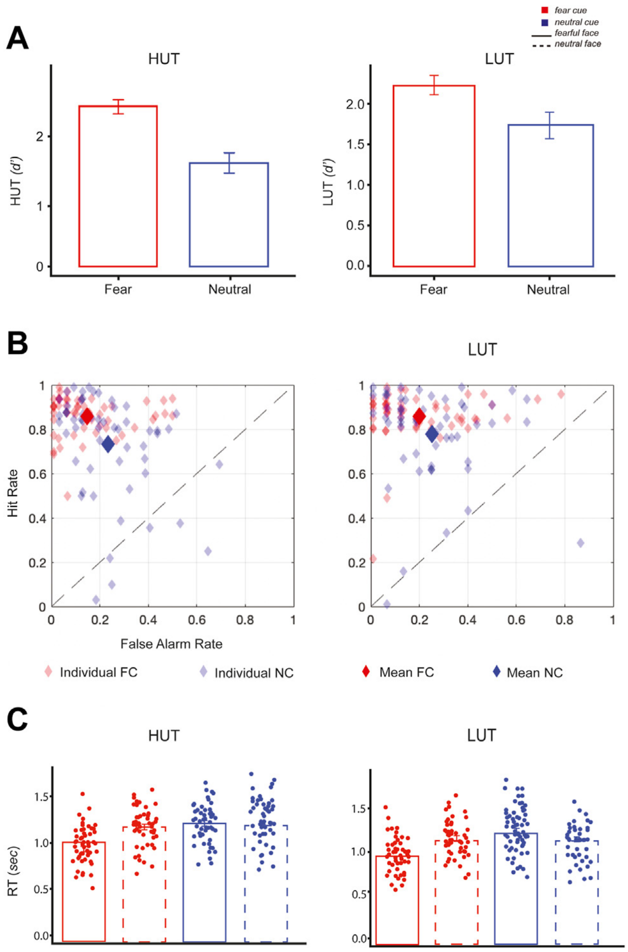

Figure 2. Signal detection theory results. **(A)** Higher perceptual sensitivity or d' for fear cue (FC) vs. neutral cue (NC) for both the high-uncertainty task (HUT) (left panel) and the low-uncertainty task (LUT) (right panel) **(B)**. Greater hit rate and smaller false alarm rate for FC (red) vs. NC (blue) in both the HUT (left panel) and the LUT (right panel). **(C)**. Detection of fearful faces was faster than neutral faces following FC compared with NC in both the HUT (left panel) and LUT (right panel).

Analyses Strategy. In our analytic strategy, we first demonstrated task effects and then examined their relationships with individual differences in anxiety. See Supplemental Methods for details regarding the strategy we used for analyses.

RESULTS

Anxiety Measures

The variance of PSWQ scores in the current sample was similar to that of other samples of individuals with and without anxiety disorders (see Supplemental Results).

Threat Cues Enhance the Sensitivity of Perceptual Decision Making

Our SDT results, depicted in Table 2, show that FC led to better d' (Figure 2A), higher hit rate, and lower FAR (Figure 2B) than NC in HUT, but there was no difference in c. In the case of LUT, d' (Figure 2A) and hit rate (Figure 2B) were higher for FC than NC, but there was no difference in FAR or c. Comparison of the 2 tasks showed that FC improved d' more than NC, more so in HUT and LUT, whereas c was higher for LUT than HUT, irrespective of cue (see Supplemental Results).

Table 3. Speed of Perceptual Decision Making

Effects	Mean Square	F Test	p Value	η_p^2
HUT				
RT cue	0.554	$F_{1,50}$ = 80.99	<.001	≤0.618
Error	0.007			
RT stimulus	0.264	$F_{1,50}$ = 19.04	<.001	≤0.276
Error	0.014			
Cue × stimulus interaction	0.358	$F_{1,50}$ = 53.14	<.001	≤0.515
Error	0.007			
LUT				
RT cue	0.642	$F_{1,48}$ = 77.431	<.001	≤0.617
Error	0.008			
RT stimulus	0.203	$F_{1,48}$ = 9.598	.003	≤0.167
Error	0.021			
Cue × stimulus interaction	0.675	$F_{1,48}$ = 77.44	<.001	≤0.601
Error	0.009			

Mean RT for fearful (HUT = 1.079 ± 0.200; LUT = 1.014 ± 0.212) and neutral (HUT = 1.240 ± 0.202; LUT = 1.188 ± 0.222) faces following fearful cue as well as fearful (HUT = 1.274 ± 0.204; LUT = 1.256 ± 0.278) and neutral (HUT = 1.237 ± 0.228; LUT = 1.186 ± 0.224) faces following neutral cue was compared via a 2 × 2 repeated measures analysis of variance with cue (fearful and neutral) and stimulus (fearful and neutral) as factors.

HUT, high-uncertainty task; LUT, low-uncertainty task; RT, reaction time.

Threat Cues Improve Speed of Decision Making

In HUT, results demonstrated that FC led to significantly faster detection of FFs than of NFs while no difference in speed was noted following NC. In the LUT, FC led to significantly faster detection of FFs versus NFs while NC led to faster detection of NFs versus FFs (Table 3). Comparison of the tasks showed that FC led to significantly faster RTs than NC in HUT compared with LUT (see Supplemental Results).

Threat Cues Bias the Starting Point and Efficiency of Sensory Evidence Accumulation

Examination of DDM parameters with model comparison showed that, based on deviance information criteria, the best-fitting model was model 3 for both HUT and LUT (Table 1), meaning that cues impacted both starting point and drift rate. Model 3 also performed better than a control model with the same number of parameters (see Supplemental Results). For model 3, visual inspection of parameter convergence and Gelman-Rubin convergence statistic both suggested adequate model convergence. The posterior predictive check reproduced key aspects of the behavioral findings (see Supplemental Results).

Next, for model 3, we examined how cues impacted z and v for HUT and LUT. In the case of HUT, inspection of the posterior distribution of the group level means of the parameter estimates showed that FC shifted z closer to the fearful decision boundary (posterior probability of $z > 0.50$ was $q > .99$).

Interestingly, NC also shifted z slightly toward the fearful decision boundary (posterior probability of $z > 0.50$ was $q = .98$) (Figure 3A). However, FC shifted z closer to the fearful decision boundary than NC did to the corresponding boundary ($q > .99$). An examination of v showed that, compared with NC, FC led to a higher v for FFs (posterior probability of $v_{FC/FF} > v_{NC/FF}$ was $q > .99$) and NFs (posterior probabilities of $v_{FC/NF} > v_{NC/NF}$ were $q = .99$), but the increase for FFs was greater than the increase for NFs (posterior probabilities of $v_{FC/FF} > v_{FC/NF}$ were $q = .93$) (Figure 3B).

In the case of LUT, the posterior probability distribution showed that FC shifted z closer to the fearful decision boundary (posterior probability of $z > 0.50$ was $q > .99$); however, NC did not shift z too far from the midline (posterior probability of $z > 0.50$ was $q = .83$). Furthermore, FC shifted z closer to the fearful decision boundary than NC did toward the corresponding boundary ($q > .99$) (Figure 3A). Compared with NC, FC led to a higher v for FFs (posterior probability of $v_{FC/FF} > v_{NC/FF}$ was $q = .99$) and NFs (posterior probabilities of $v_{FC/NF} > v_{NC/NF}$ were $q = .99$ and $q = .97$, respectively) with no difference between FFs and NFs (posterior probabilities of $v_{FC/FF} > v_{FC/NF}$ was $q = .12$) (Figure 3B).

In summary, FC shifted z more toward the fearful decision boundary than NC did to the corresponding boundary in both HUT and LUT. Furthermore, FC increased v for both FFs and NFs but more so for FFs in HUT.

Anxiety Worsens Threat Cue–Related Perceptual Sensitivity

Linear regression analysis showed that only in HUT, lower FC d' (i.e., worse discrimination of FFs and NFs) was associated with higher PSWQ scores, while such a relationship was not seen for NC (Table 4; Figure 4A). Follow-up regression analyses showed that higher FAR following FC, but not NC (Figure 4B), was associated with higher PSWQ scores. In contrast, c in HUT and both c and d' in LUT were not associated with PSWQ scores (all $ps > .05$). For comparisons of the strengths of these relationships across different tasks, see Supplemental Results.

Anxiety Biases Threat Cue–Related Starting Point of Evidence Accumulation

Linear regression analyses showed that in HUT, a greater shift in z toward the fearful decision boundary following FC (Table 4; Figure 4C) and a lower shift in z toward the neutral decision boundary following NC were associated with higher PSWQ scores. In contrast, we did not observe a significant relationship of v following FC or NC for any of the stimulus types with PSWQ scores. In LUT, individual differences in anxiety were not associated with either z or v (all $ps > .05$).

DISCUSSION

Prioritized perception of threat is often attributed to threat-related biases in the general population, which are accentuated in anxiety. Our study breaks new ground with regard to the examination of these biases in several ways. First, our investigation demonstrated the role of top-down biases in perceptual decision making in anxiety. These biases have been overlooked in favor of experimental designs that highlight bottom-up processing (1,2) despite the hallmark of anxiety being negative anticipatory cognitions. Even in experiments in which threat anticipation has been examined, its effect on perception has not been explored (43,48,49). Second, this project utilized novel paradigms from cognitive neuroscience

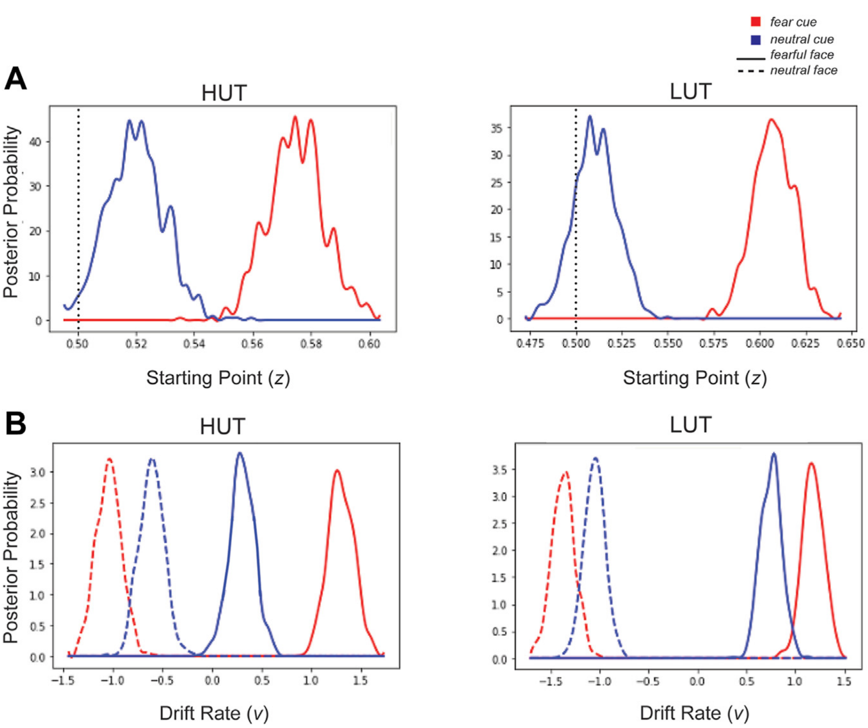

Figure 3. Group-level means of the drift diffusion model parameter estimates from model 3. **(A)** For both the high-uncertainty task (HUT) (left panel) and low-uncertainty task (LUT) (right panel), fear cues (red line) shifted the starting point (z) of evidence accumulation away from the midpoint (denoted by black dashed line) and closer to the fearful decision boundary, whereas neutral cues (blue line) did not shift the starting point away from the midpoint and closer to neutral decision boundary. **(B)** In both the high (left panel) and low (right panel) uncertainty tasks, fear cues (in red) facilitated the rate of evidence accumulation (v) for subsequently presented fearful faces (solid line) and neutral faces (dashed line) compared with neutral cues (in blue). More extreme values indicate faster drift rate, with a positive sign denoting drifting toward the fearful decision boundary and a negative sign denoting drifting toward the neutral decision boundary.

Table 4. Multiple Regression Results For Signal Detection Theory And Drift Diffusion Model Parameters as Independent Variables Predicting Anxious Apprehension (Penn State Worry Questionnaire Scores) as Dependent Variable in the High- and Low-Uncertainty Tasks

Regression Results	p Value	β	R^2
High-Uncertainty Task			
Perceptual Sensitivity (d')			
FC	.0018[a,b]	−0.369	0.104
NC	.156	0.305	
False Alarms (FAR)			
FC	.033	0.317	0.094
NC	.113	−0.233	
Starting Point (z)			
FC	.026[b,c]	0.283	0.199
NC	.02[b,c]	−0.298	
Drift Rate (v)			
FC/FF	.635	−0.067	0.085
FC/NF	.064	0.389	
NC/FF	.112	0.351	
NC/NF	.216	0.194	
Low-Uncertainty Task			
Perceptual Sensitivity (d')			
FC	.196	0.255	0.034
NC	.287	−0.21	
False Alarms (FAR)			
FC	.524	−0.114	0.01
NC	.868	0.03	
Starting Point (z)			
FC	.424	0.14	0.019
NC	.465	−0.128	
Drift Rate (v)			
FC/FF	.939	0.016	0.024
FC/NF	.684	0.091	
NC/FF	.589	0.116	
NC/NF	.574	0.119	

FAR, false alarm rate; FC, fear cue; FF, fearful face; NC, neutral cue; NF, neutral face.

[a] $p < .01$.

[b] Indicates the statistic is significant following correction for multiple comparisons at a false discovery rate of 0.1 using Benjamini-Hochberg procedure.

[c] $p < .05$.

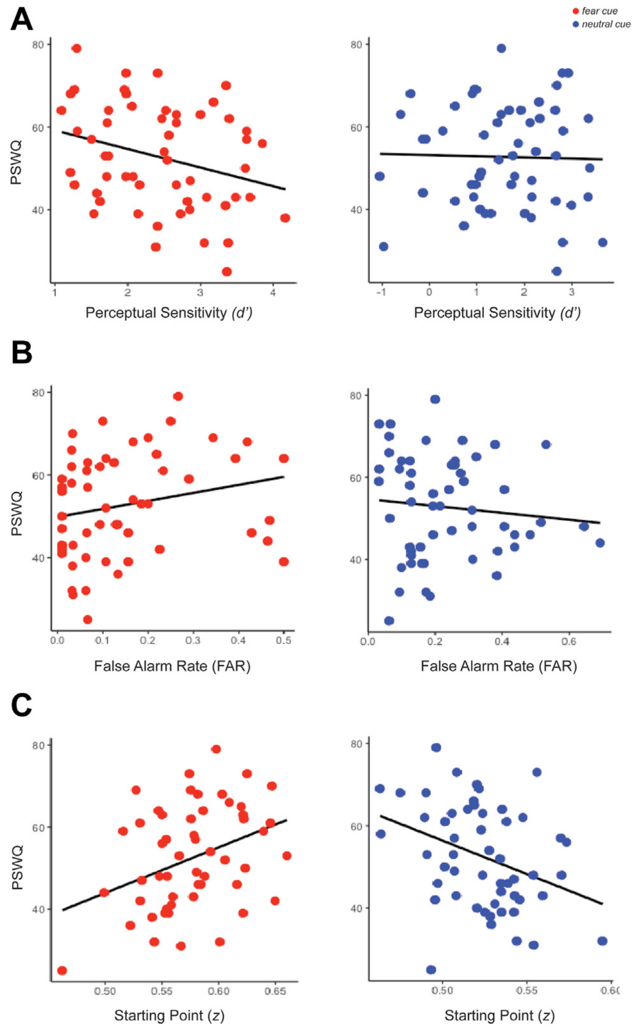

Figure 4. Relationship between anxious apprehension measured via Penn State Worry Questionnaire (PSWQ) and biases in decision making in the high-uncertainty task. Higher PSWQ scores were associated with **(A)** worse perceptual sensitivity, i.e., lower perceptual sensitivity (d') following fear cues (left panel) but not neutral cues (right panel); **(B)** more false alarms following fear cues (left panel) but not neutral cues (right panel); and **(C)** greater fear cue–induced shift in the starting point (z) of evidence accumulation toward the fearful decision boundary (left panel) and lesser neutral cue–induced shift in the starting point (z) of evidence accumulation toward the neutral decision boundary (right panel).

in which anticipatory cues provide information about the relevance and probability of upcoming threatening stimuli, allowing us to examine threat biases in ways that align with anticipatory conceptualizations of anxiety. These paradigms also align with perceptual decision making in real life where cues and contexts often provide us information with varying degrees of certainty about threats that are relevant or likely. Finally, our study used SDT and DDM to quantify threat cue–related biases that have so far only been inferred from faster detection of threats (1,2).

We showed that cues indicating that threat is relevant (on the HUT) or highly probable (on the LUT) both facilitated perceptual sensitivity, yielding more hits and fewer false alarms than NCs. While this facilitating effect of threat cues was seen for both tasks, it was greater in the HUT than in the LUT. This may be because adding probabilistic information to NCs in the LUT makes them as effective as threat cues, thereby reducing any differences in subsequent decision making. Consistent with earlier studies (18,19), high-probability cues in the LUT biased participants to adopt a more liberal decision criterion (i.e., to make decisions congruent with prestimulus cues); however, this criterion did not differ for threatening cues versus NCs. This insensitivity to probability variations in threatening cues versus NCs may occur because once the probability of an aversive outcome crosses the 0 threshold, subsequent increases in probability appear to have little additional impact on emotions and thereby decision making (50).

Using hierarchical DDM, we next examined the computational mechanisms contributing to the facilitative effect of threat cues on the sensitivity of decision making. Threat cues shifted the starting point of evidence accumulation closer to the decision boundary for endorsing the presence of a threatening target, allowing participants to reach this decision efficiently with less evidence. These findings are consistent with earlier studies that used model-based approaches to investigate how prior knowledge biases choice behavior (30,51–53), but they extend the literature by showing the unique effect of threat cues. Furthermore, the greater shift in starting point toward a threat response boundary following threat cues may be the computational mechanism by which factors such as alertness or hypervigilance (54–56) aid faster detection of threats. However, the starting point bias toward endorsing threat irrespective of stimulus characteristics may actually compromise discrimination between subsequent threatening versus neutral stimuli. Indeed, our results showed that threat cues also influenced the drift rate or accumulation process itself such that evidence was accumulated more efficiently not only for threatening but for also neutral stimuli. This indicates that attention to threat may involve facilitated encoding of the attended stimulus such that threatening signals are better differentiated from nonthreat signals, thus resulting in enhanced decision making (57). Computationally, these findings can also be understood as the threat cues yielding more precise estimates of the incoming sensory signals and their causes (58).

Overall, our findings suggest that cues and contexts that signal threat may bias decision making in an adaptive manner, more so when threat is relevant but uncertain than when it is highly probable. While the starting point of evidence accumulation shifts toward threat to allow for a faster decision, this is balanced with more efficient extraction of evidence from threatening as well as neutral stimuli, allowing for better discrimination of these stimuli. However, the same pattern of results was not seen in individuals with higher levels of anxiety. Rather, following threatening cues on the HUT, higher anxious apprehension was associated with worse discrimination between threat and neutral stimuli and more false alarms. DDM showed that for these cues, higher anxious apprehension was associated with a greater shift in the starting point of evidence accumulation toward the threat decision boundary but no change in efficiency of evidence accumulation for subsequent stimuli. This relationship was not seen when the cues indicated more certain threats. Interestingly, higher anxious apprehension was also associated with a greater shift in the starting point of decision making toward the threat decision boundary following NCs. These effects in anxiety may be due to hypervigilance regarding the probability of encountering threatening stimuli irrespective of what the cues indicate, especially under uncertain conditions (6,59).

Theoretical frameworks regarding threat biases in anxiety have differentiated between selective attention to threat and hypervigilance for threat (60). Hypervigilance involves monitoring for potential threats by broadening attention to scan the environment for whether an actual threatening stimulus is present or not. Not only does hypervigilance for threat lead to faster detection of threats but it also leads to increased arousal and misinterpretation of neutral stimuli (61). On the other hand, selective attention involves narrowing of attention onto the threatening stimulus, thereby allowing for increased processing of these stimuli. Our modeling results showing a greater threat cue–related shift of the starting point of evidence accumulation toward a threat response (before arrival of the stimulus) with increasing anxiety provide evidence for the role of hypervigilance in anxiety.

Despite limitations (see Supplemental Discussion), our findings conceptually advance the field by highlighting top-down biases to threat in anxiety, the importance of uncertainty in inducing these biases, and the computational mechanisms underlying them. At the neural level, our findings indicate the need to examine threat cue–related anticipatory or prestimulus neural activity in visual sensory and prefrontal regions (25,29,40,62,63) in threat-related perceptual biases in anxiety. Our research also points to the importance of examining how anxiety-related threat biases that impact perception can have downstream consequences on attention and behavior. Clinically, the findings highlight the importance of transdiagnostic symptoms of anxious apprehension and their relationships with top-down threat biases in perceptual decision making. Our findings are relevant for the area of psychosis because dimensions such as paranoia and hallucinations are associated with overreliance on Bayesian priors on perception (64,65); however, the influence of threat-related priors remains relatively understudied. Additionally, novel cognitive paradigms that are ecologically valid and modeling approaches like ours can help identify quantifiable targets for intervention research and implementation. For example, in the case of anxious apprehension, training strategies could be used that are more proactive and are implemented prior to the arrival of threatening stimuli. These strategies could focus on reducing the response bias toward threat as well as more accurate prediction of threat as amendments to attentional bias modification, which relies largely on altering bottom-up capture by threat (66). Overall, comprehensive approaches such as those used in the current study can help advance the field toward more ecologically valid cognitive models of anxiety that align with the experiential aspects of anxiety.

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