

What Do We Know About Threat-Related Perceptual Decision Making?

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Abstract

The ability to make rapid and precise decisions regarding the presence or absence of threats in the environment is critical for survival. Although threatening stimuli may be detected more accurately and faster because of the bottom-up salience of their features, in the real world, these stimuli are often encountered in familiar environments in which top-down cues signal their arrival. There has been significant progress in understanding of the mechanisms by which people make perceptual decisions regarding relatively routine stimuli; however, the mechanisms of threat-related perceptual decision making remain unclear. In this review, we discuss the psychological, computational, and neural mechanisms by which information from threatening stimuli is integrated with prior knowledge from cues and surrounding contexts to guide perceptual decision making.

Keywords

perceptual, decision making, threat, top-down, bottom-up

Imagine that you are walking rapidly on a path on a bitterly cold, snowy day. You see a shiny patch on the road ahead and you must quickly decide if it is black ice or water. Because it is snowing, it is hard to clearly see the patch, and the sensory information your eyes receive is shrouded by uncertainty. This example illustrates how the brain is regularly challenged to make fast and accurate decisions about stimuli relevant to survival using unreliable information. Understanding the psychological and neural mechanisms by which people overcome this challenge is critical because such *perceptual decision making* serves as the gateway to higher-order cognition. Any errors at this stage (e.g., inaccurately identifying black ice as water and/or being overconfident in this decision) are likely to propagate downstream, with consequences such as biased attention or behavior resulting in maladaptive interactions with the environment. This has relevance not only in day-to-day life, such as when someone is deciding whether a friend's expression looks angry or whether there is a snake ahead on a trail path, but also for understanding clinical conditions such as anxiety (Glasgow et al., 2022). Understanding the mechanisms

of threat-related perceptual decision making will also help advance understanding of how threat influences other cognitive functions because principles of perceptual decision making may apply to other types of decisions and cognitive functions (Shadlen & Kiani, 2013).

Cognitive neuroscience research has made significant progress in unraveling the mechanisms of perceptual decision making regarding relatively routine stimuli (Heekeren et al., 2008; Shadlen & Kiani, 2013); however, this knowledge has yet to be applied to perceptual decisions regarding threatening stimuli. There is also considerable research showing that threat influences decision making (Lerner et al., 2015); however, very little of this research has focused on decisions regarding incoming sensory information (i.e., perceptual decision making). Finally, although research has shown why the human visual system prioritizes perception of threatening stimuli (Brosch et al., 2010), it is unclear how perceptual decisions differ between threatening and neutral

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stimuli. In this review, we first discuss some of the psychological, computational, and neural mechanisms of basic visual perceptual decision making and then apply this knowledge to understanding threat-related perceptual decision making.

What Is Perceptual Decision Making?

Perceptual decision making is the process by which sensory information from the environment is gathered and integrated by the sensory systems to influence behavior (Heekeren et al., 2008; Shadlen & Kiani, 2013). This process is shaped not only by bottom-up, stimulus-related information, such as the physical features of the stimulus, but also by top-down context-related factors, including the observer's attention, expectation, prior knowledge, and learning (Summerfield & de Lange, 2014). In real life, people often encounter perceptual stimuli in noisy environments, requiring them to gather sensory evidence to make a perceptual decision with varying degrees of uncertainty. In the lab, such decision making is typically mimicked by asking participants to discriminate between two possible stimuli (one deemed the *signal*, and the other *noise*), such as left- versus right-moving dots or houses versus faces, that are made more or less clear by reducing or adding noise to them (Gold & Shadlen, 2007). In such tasks, top-down factors can be manipulated via prestimulus cues that tell participants which target stimulus is relevant or likely. Participants are then asked to decide whether the stimulus (i.e., signal) is present or not. This allows researchers to classify stimuli as true positives, or *hits* (i.e., the signal is present and judged as being present), or as false positives, or *false alarms* (i.e., the signal is absent but judged as present). The process by which a decision maker samples the sensory evidence and arrives at a decision can be formalized using signal detection theory (Green & Swets, 1966). In this framework, the subject's performance can be characterized by *sensitivity* to signal presence versus absence and by the *decision criterion* (i.e., the threshold for deciding the signal is present), which can be biased (i.e., liberal or conservative). Research shows that cues (e.g., location or features) indicating the relevance of upcoming targets increase sensitivity to the signal (thereby increasing true positives), whereas cues indicating a high probability of target occurrence bias observers to adopt a more liberal decision criterion, yielding more true and false positives (Lu & Doshier, 2008; Wyart et al., 2012).

Although signal detection theory describes a snapshot of decision making regarding sensory stimuli, in real life it takes time to accumulate sensory evidence to reach a perceptual decision. Computational models incorporating sequential sampling allow for the integration of sensory

evidence for competing decisions as it accumulates over time. A type of sequential sampling model referred to as the drift diffusion model (DDM) has been used to successfully model perceptual decision making (Gold & Shadlen, 2007; Ratcliff & McKoon, 2008). In the DDM framework, sensory evidence is accumulated in a single decision variable, from a starting-point value between the two decision boundaries. Evidence accumulation begins shortly after stimulus presentation, and the rate at which evidence is accumulated toward a decision is referred to as the drift rate. The drift rate reflects the effectiveness with which the signal is extracted from the surrounding noise. When evidence accumulation reaches a decision boundary, the corresponding decision is made. Although cues indicating relevant or highly probable targets can bias decision making by shifting the starting point toward the corresponding boundary (Mulder et al., 2012), they also improve the drift rate (Dunovan & Wheeler, 2018). Thus, top-down factors can enhance the extraction of bottom-up signals.

Visual sensory stimuli are represented in the parts of brain responsible for visual processing, such as the fusiform face area, which is specialized for facial recognition (Heekeren et al., 2008). Evidence represented in relevant sensory areas is integrated by more downstream parietal and frontal brain regions to form a perceptual decision (Gold & Shadlen, 2007; Shadlen & Kiani, 2013). Computational biases in starting point correspond to the fact that prestimulus cues indicating the occurrence of a stimulus (e.g., a face) can increase baseline neural activity in relevant sensory areas or evoke context-dependent predictive representations in the frontal and parietal brain areas that subsequently modulate processing in sensory areas (Mulder et al., 2012; Summerfield & de Lange, 2014). Additionally, prestimulus cues can yield increased activity in response to the cued stimulus in the relevant sensory regions (e.g., for a review, see Gilbert & Li, 2013). Thus, bottom-up stimulus-related neural processing can be enhanced by top-down cues during the perceptual decision-making process, an effect that is consistent with changes in drift rate.

Although the computational and neural mechanisms by which bottom-up and top-down factors interact in the service of basic perceptual decision making are well established, these mechanisms remain unclear in the case of threat-related perceptual decision making.

What Is Threat-Related Perceptual Decision Making?

A key question is why perceptual decision making would differ between threatening and neutral stimuli. Emotional stimuli are salient for survival and elicit a

wide array of changes in feelings, physiology, and behavior (Lang, 1968), all of which could influence decisions regarding these stimuli. Several explanations for why emotional stimuli are prioritized by the human perceptual system have been proposed (Brosch et al., 2010), and these theories differ in their focus on bottom-up factors, such as the physical features of the stimulus, and top-down factors, such as the observer's prior knowledge, attention, and expectation (Fig. 1). Although it is clear that these factors interact with each other to influence perception, most empirical research on threat perception has focused on the role of bottom-up factors. There has been a tendency to utilize tasks in which unanticipated or task-irrelevant threatening stimuli drive perception in a bottom-up manner and, correspondingly, a tendency to examine the neural pathways that promote "automatic" perception of emotional stimuli (Mohanty & Sussman, 2013; Sussman, Jin, & Mohanty, 2016). Even in studies in which top-down factors were examined, these factors tended to be orthogonal or irrelevant to threat perception and were studied by directing attention away from threatening targets (e.g., Bar-Haim et al., 2007; Cisler & Koster, 2010), rather than voluntarily directing attention toward them.

More recently, top-down influences in threat perception have been examined with tasks in which participants used anticipatory threat-related and neutral cues to discriminate between subsequently presented threatening and neutral faces (Imbriano et al., 2020; Sussman, Szekely, et al., 2016; Sussman et al., 2017). In these tasks, the cues themselves were not acute threats (e.g., a picture of a snake or angry face) and were relatively benign (e.g., the letter "F"), but they indicated whether future threats were relevant or not (Fig. 2a). Other studies have used tasks in which the cues provided information about the probability with which upcoming threatening targets would appear (Aue & Okon-Singer, 2015). These cued threat-related tasks are akin not only to commonly used cued perceptual tasks in which cues indicate the location or features of upcoming targets but also to how humans, in their day-to-day life, use environmental cues or contextual knowledge in a top-down manner to detect existing threats (e.g., Fig. 1).

Below, we discuss the computational and neural mechanisms by which top-down factors such as attention, expectation, and imagery may enhance threat-related perceptual decision making but individual differences in anxiety may impair it. These factors have been well examined in research using nonthreatening stimuli, which has shown that they are closely intertwined, influencing each other as well as having additive or interactive effects on visual perception (Mather & Sutherland, 2011; Summerfield & Egner, 2009). Their

neural mechanisms may sometimes be similar (e.g., cue-related anticipatory attention and expectation both activate prefrontal regions) but at times may differ (e.g., attended stimuli increase activity in the sensory cortex, but expected stimuli decrease such activity; Summerfield & de Lange, 2014).

What Are the Mechanisms Involved in Threat-Related Perceptual Decision Making?

Attention

Because of their salience, threatening stimuli and cues can enhance perceptual decision making, by capturing involuntary attention and driving voluntary attention, respectively. For example, cues that indicate the possible presence of salient targets along with their location result in faster target detection than do cues indicating the possible presence of neutral targets (Mohanty et al., 2008, 2009). In addition, cues indicating the possible presence of a threatening target are more effective if they also provide information about its location, which indicates that attention toward threatening targets is enhanced not just by bottom-up target features but also by top-down guidance toward them. How exactly do threat-related cues enhance perceptual decision making? Is it by increasing sensitivity to the occurrence of threat (i.e. by making it easier to tell threatening stimuli apart from neutral stimuli) or by causing a shift to a more liberal criterion for deciding that threat is present? Using signal detection theory, which is amenable to examining mechanisms of threat-related decision making (Lynn & Barrett, 2014), studies have shown that cues indicating the threat relevance of upcoming targets improve the hit rate and the sensitivity of decision making without changing the decision criterion (e.g., Imbriano et al., 2020; Sussman, Szekely, et al., 2016; Sussman et al., 2017; Fig. 2b). It remains to be examined if, in line with evidence we reviewed earlier regarding decision making more generally, threat-related (compared with neutral) cues enhance the sensitivity of decision making both by shifting the starting point toward the decision boundary for threat and by enhancing the rate of evidence accumulation for both threatening and neutral targets, making them easier to tell apart (Fig. 2c).

Neurally, the enhancement in perceptual decision making due to threat cues has been shown to be mediated via interactions among sensory, frontal, parietal, and limbic regions. Even before a stimulus arrives, threat cues, compared with neutral cues, increase activity in sensory regions relevant to processing the stimulus, as well as frontal and parietal brain regions involved in attention generally (Mohanty et al., 2009; Sussman et al.,

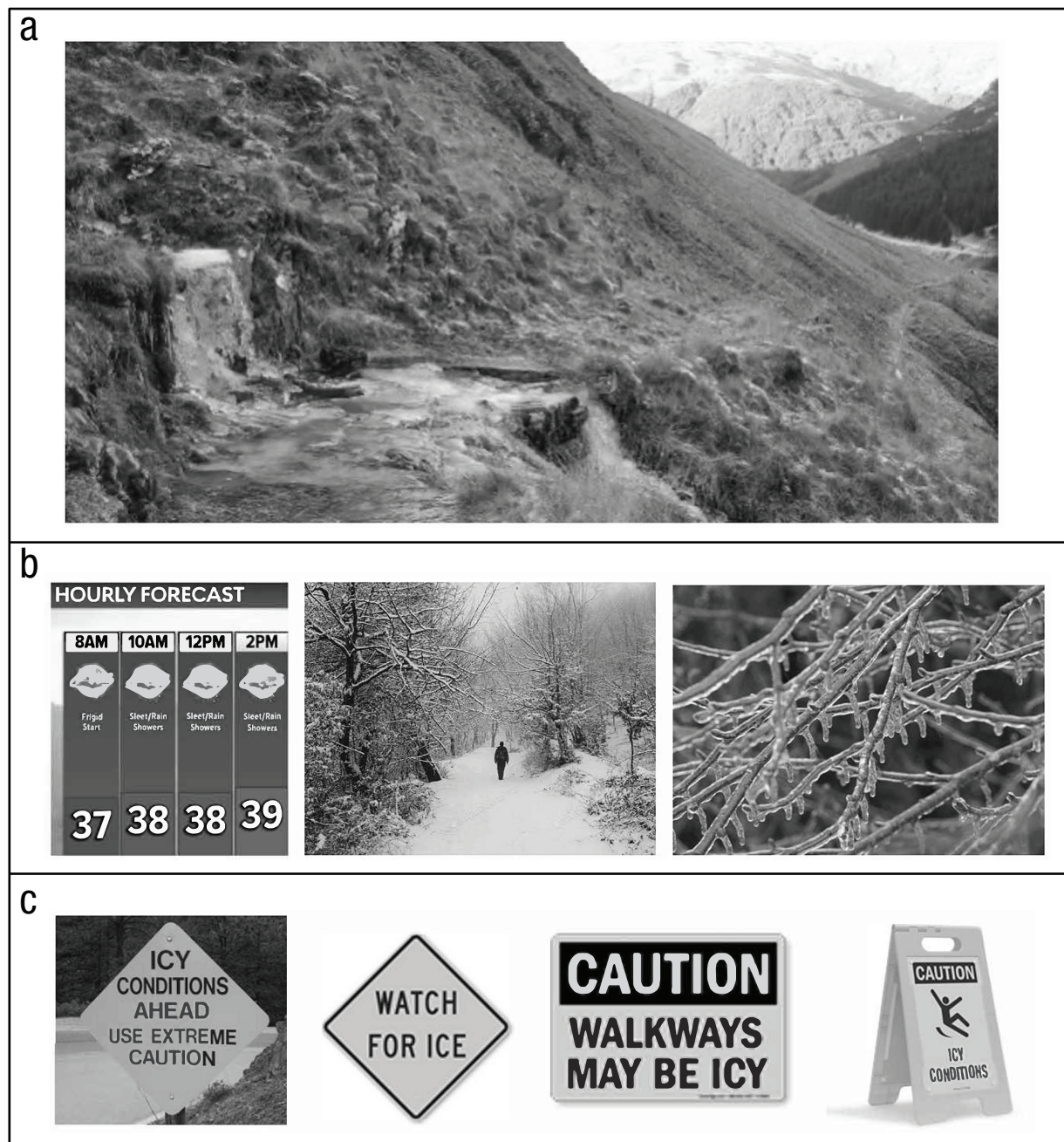


Fig. 1. Influence of bottom-up and top-down factors on threat-related perceptual decision making. An example of a real-life perceptual decision-making task, illustrated in (a), is deciding whether there is a threatening stimulus, such as a patch of black ice (in this context, the *signal*), on the path ahead, which is filled with water, grass, black rocks, and snow (*noise*). According to evolutionary accounts, the patch of black ice would be automatically detected in a bottom-up, stimulus-related manner because of the salience of its physical features (e.g., black color and sheen) for survival. However, according to appraisal theories, perception of a threat would be driven by an interaction of bottom-up and top-down, context-related factors. Decision makers typically encounter black ice in contexts in which they have access to implicit knowledge or explicit cues regarding what stimuli are relevant and likely. Such implicit and explicit knowledge can influence their expectations, attention, arousal levels, and anxiety, guiding perception of the stimulus features in a top-down manner. For example, because of implicit expectations, on a snowy day with weather reports of subzero temperature (b) and/or after encountering explicit cues indicating the possible presence of ice (c), a decision maker may view the probability of black ice as higher than that of a puddle of water. Because the cost of missing black ice may be higher than the cost of misidentifying a puddle of water as black ice, the decision maker may adopt a liberal criterion when deciding whether black ice is present. On the other hand, implicit and explicit cues indicating simply that black ice is possible (without indicating how likely it is) can make a person more vigilant or sensitive and thus better at extracting black-ice-related signals. Finally, constructivist theories emphasize even more the influence of top-down mental representations and linguistic categories. According to these theories, perception will depend on the decision maker's evaluation of the internal and external context, and this perception will lead to linguistic label of "threat" when the decision maker encounters a patch of black ice.

2017). This increase in threat-cue-related neural activity is associated with better behavioral discrimination of subsequently presented threatening and neutral stimuli. Frontal and parietal regions show increased connectivity with the amygdala after threat-related cues, which suggests that such cues enhance input of these attentional regions into the amygdala (Mobanty et al., 2009). Finally, threat-related cues lead to increased amygdala activity specifically in response to threatening (and not neutral) stimuli (Sussman et al., 2017). These results suggest that the amygdala plays a role in integrating top-down (threat-cue-related) and bottom-up (threat-stimulus-related) influences during perceptual decision making.

Although these studies shed light on how explicit threat-related cues enhance perceptual decision making, in real life people do not always have access to explicit cues indicating what threats to look out for. Rather, they use knowledge of the context to guide perception (Barrett et al., 2011). Indeed, individuals can learn which contexts threatening stimuli are likely to appear in much faster than they can learn which contexts neutral stimuli are likely to appear in (Szekely et al., 2017). Furthermore, learning that a given context is threatening is persistent and benefits detection of subsequent nonthreatening stimuli presented in the same context (Szekely et al., 2019).

Expectation

Whereas attention prioritizes perception of stimuli that are salient or relevant to goals, expectations influence perception on the basis of the probability of encountering these stimuli. Expectation and attention involve different psychological and neural mechanisms (Summerfield & de Lange, 2014). For example, attentional cues that indicate threatening stimuli are relevant but do not provide information about their probability enhance perceptual sensitivity more than corresponding neutral cues do; however, cues indicating high probability of upcoming threatening stimuli do not show the same benefits (Glasgow et al., 2022), perhaps because adding probabilistic information to cues indicating neutral targets brings them on a par with cues indicating threat-related targets. Furthermore, once the probability of an aversive outcome crosses the zero threshold, subsequent increases in probability appear to have little additional impact on emotions and, consequently, little incremental impact on decision making (Loewenstein et al., 2001). This suggests an insensitivity to probability variations in the case of cues indicating threatening compared with neutral targets. It is possible that, as suggested by earlier studies (Gold & Shadlen, 2007; Summerfield & de Lange, 2014), cues indicating high probability of upcoming threatening

a

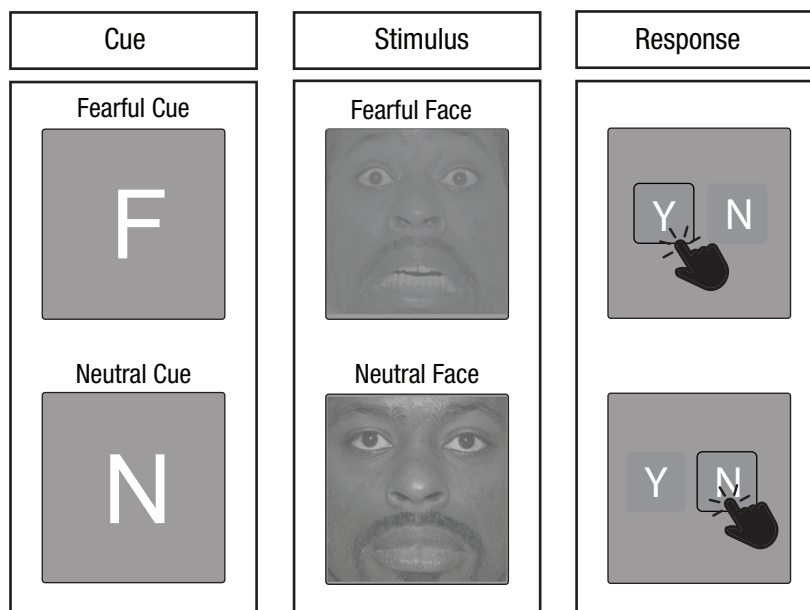


Fig. 2. (continued on next page)

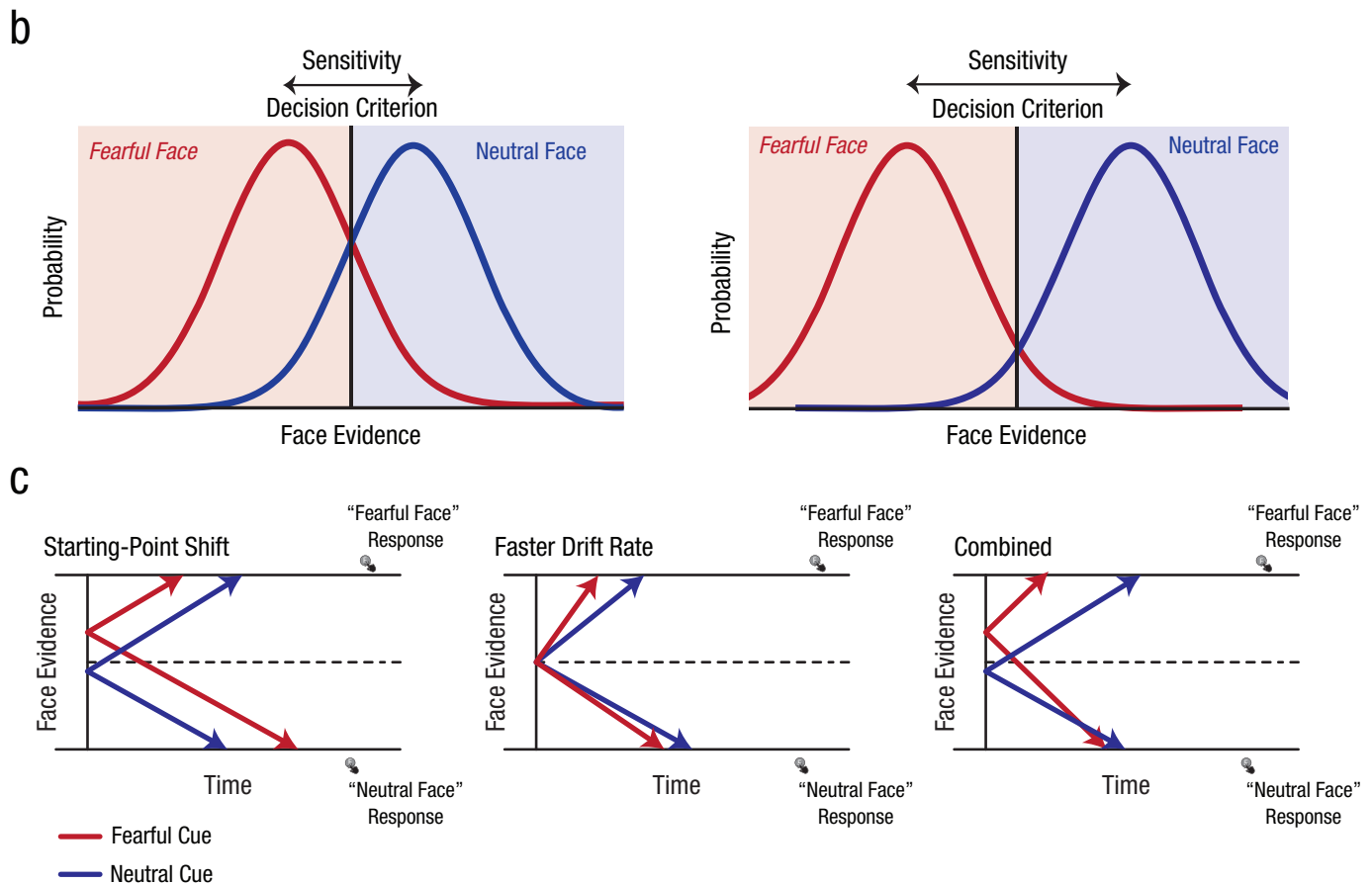


Fig. 2. Measurement of top-down threat-related influence on perceptual decision making. In one task used for this purpose (a), on each trial participants view a cue indicating that they will be making a decision as to whether the subsequent stimulus is fearful (“F”; referred to as a fearful cue) or a cue indicating that they will be making a decision as to whether the subsequent stimulus is neutral (“N”; referred to as a neutral cue). This cue is followed by a fearful or a neutral face presented at participants’ own threshold of perception. Participants then decide if the face is fearful or if it is neutral and make a corresponding response (“Y” for “yes” or “N” for “no”). Note that in this version of the task, the cues do not provide information regarding the probability of upcoming faces (i.e., there is an equal probability of encountering fearful or neutral faces). However, by indicating the type of upcoming decision, the cues encourage participants to use the corresponding top-down perceptual or attentional set when making their decision. Following a fearful cue, for example, a response can be classified as a hit (“yes” response when a fearful face is present), false alarm (“yes” response when a neutral face is present), miss (“no” response when a fearful face is present), or correct rejection (“no” response when a neutral face is present). Performance across trials can be characterized by two measures: sensitivity and the decision criterion. Signal detection models of a decision maker’s distributions for the probabilities of fearful faces (red curves) and neutral faces (blue curves) are shown in (b). Perceptual sensitivity is the separation between the distributions, and the vertical black lines indicate the decision criterion. The model on the left shows distributions in the absence of a cue. The model on the right shows that fearful cues reduce the overlap between the two distributions (i.e., increase perceptual sensitivity) without influencing the decision criterion (Glasgow et al., 2022; Sussman et al., 2017). Hypothetically, this fearful-cue-related improvement in perceptual sensitivity can be modeled in the drift diffusion model (c) not simply as a shift in the starting point of evidence accumulation closer to the threshold for deciding that the stimulus is a fearful face, reducing the amount of evidence needed to make this decision (left), or as more efficient evidence accumulation (steeper slope for the drift rate) toward the decision thresholds (middle) but rather as a combination of the two (right).

stimuli, compared with corresponding cues regarding neutral stimuli, bias observers to adopt a more liberal decision criterion, but this hypothesis remains to be examined.

Imagery

Prior knowledge can benefit perceptual decision making by leading to the formulation of perceptual templates or a mental representation of a stimulus that is relevant or

likely (Lu & Doshier, 2008; Summerfield & de Lange, 2014). Visual imagery is associated with increased activity in the visual cortex and aids the formation of better perceptual templates (Albright, 2012). Hence, threat cues may benefit perceptual decision making because they increase the vividness of imagery and thereby the precision of perceptual templates, ultimately improving target detection. In line with this hypothesis, a recent study showed that more precise and rapid perceptual decision making following threatening cues is associated with

greater vividness of visual imagery (Imbriano et al., 2020).

Arousal

There is evidence showing that emotions triggered in anticipation of upcoming threats influence decision making (Loewenstein et al., 2001); however, the effect of emotional arousal on perceptual decision making has not been examined. Threatening contexts, cues, and stimuli can increase autonomic arousal, causing changes in heart rate, galvanic skin response, and pupil dilation, as well as levels of stress hormones, such as epinephrine and cortisol (Lang, 1968; Mather & Sutherland, 2011). According to arousal-biased competition theory, this arousal amplifies the bottom-up salience of stimuli and the top-down competitive advantage of high-priority information (Mather & Sutherland, 2011). Hence, threat-related cues' ability to enhance detection of threatening stimuli (Sussman, Szekely, et al., 2016; Sussman et al., 2017) could be attributed to arousal elicited by these stimuli, a hypothesis that remains to be examined with behavioral and psychophysiological data.

Anxiety

Anxiety is defined as an anticipatory response to uncertain, future threats. Exaggerated attention toward future threats, especially under conditions of uncertainty, can bias perceptual decision making when people are anxious. Studies show that in individuals with anxiety disorders, higher anxiety is associated with lower perceptual sensitivity following threat-related versus neutral cues, mainly because of false alarms (i.e., inaccurate identification of subsequent neutral stimuli as threatening). This relationship is seen only when cues indicate threat is relevant (without providing information about probability), not when cues indicate high probability of threat (Glasgow et al., 2022). The relationship between individual differences in anxiety and threat-cue-related perceptual sensitivity has been replicated in nonclinical participants (Karvay et al., 2022; Sussman, Szekely, et al., 2016).

Conclusion

The ability to discriminate threatening stimuli from benign ones is critical for adaptive interactions with the environment, yet threat-related perceptual decision making has been relatively understudied. We have highlighted some of the top-down and bottom-up mechanisms by which threat enhances perceptual decision making generally but impairs it at high levels of anxiety. Important directions for future research are to apply neurocomputational approaches from the field of perceptual decision

making to advance understanding of how threat-related perceptual decisions are made and how they are impaired in individuals with clinical disorders, such as anxiety disorders. Furthermore, other aspects of perceptual decision making, such as confidence in decisions and the impact of threat-related perceptual decisions on downstream cognitive functions, should be examined. Although the field's focus has largely been on bottom-up mechanisms of threat perception, research highlighted here shows the importance of top-down threat-related factors in influencing perceptual decision making.

Recommended Reading

- Glasgow, S., Imbriano, G., Jin, J., Zhang, X., & Mohanty, A. (2022). (See References). A report on a study of how anxiety can impair threat-related perceptual decision making.
- Heekeren, H. R., Marrett, S., & Ungerleider, L. G. (2008). (See References). A comprehensive review of the literature on humans' perceptual decision making, including a guide to principles that can be applied to threat-related perceptual decision making.
- Lynn, S. K., & Barrett, L. F. (2014). (See References). A tutorial on how signal detection theory can be applied to the study of threat-related decision making.
- Summerfield, C., & de Lange, F. P. (2014). (See References). A comprehensive review of top-down mechanisms in perceptual decision making.
- Sussman, T. J., Weinberg, A., Szekely, A., Hajcak, G., & Mohanty, A. (2017). (See References). A report providing a good example of how threat-related perceptual decision making can be examined in humans.

Transparency

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