

Physiological signatures of threat: A systematic review of threat-related stimuli processing

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Abstract

Threatening stimuli engage cascades of autonomic (e.g., cardiovascular, respiratory, and electrodermal) and skeletomotor (e.g., postural freezing, startle, facial expressions, and goal-directed actions) responses, yet empirical findings across experimental paradigms remain heterogeneous and difficult to reconcile. This systematic review aimed to synthesise physiological findings published between 2000 and 2025 and indexed in PubMed and Web of Science, relating to the processing of threat-related stimuli across different stimulus categories. We synthesised the results by stimulus and measurement type. Twenty-six experiments (across 20 studies) met the inclusion criteria and comprised samples of healthy participants. Eighteen experiments used inherently emotional stimuli (e.g., pictures) and eight used conditioned threat cues. In terms of measurement type, we identified studies that measured skin conductance responses (SCR), heart rate (HR), respiration, pupil diameter, electromyography (EMG), and vocal intensity. Across studies examining emotional stimuli, SCR increased in response to threat, whereas HR and respiration exhibited mixed patterns reflecting orienting-related deceleration and arousal-related acceleration. Pupil diameter and startle responses were sensitive to threat but were also influenced by factors such as awareness and task demands. Facial EMG and vocal intensity increased in response to threatening images. Conditioning studies revealed robust SCR effects, reliable pupil generalisation gradients, and startle potentiation under learned threat. HR responses predominantly showed deceleration, modulated by anxiety levels and contextual factors. Together, these findings demonstrate that certain physiological markers reliably indicate threat perception, whereas the reliability of others depends on contextual factors. This body of evidence emphasises the value of physiological measures as indicators of attention to threats and suggests their potential as biomarkers in clinical research.

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Abstract

Threatening stimuli engage cascades of autonomic (e.g., cardiovascular, respiratory, and electrodermal) and skeletomotor (e.g., postural freezing, startle, facial expressions, and goal-directed actions) responses, yet empirical findings across experimental paradigms remain heterogeneous and difficult to reconcile. This systematic review aimed to synthesise physiological findings published between 2000 and 2025 and indexed in PubMed and Web of Science, relating to the processing of threat-related stimuli across different stimulus categories. We synthesised the results by stimulus and measurement type. Twenty-six experiments (across 20 studies) met the inclusion criteria and comprised samples of healthy participants. Eighteen experiments used inherently emotional stimuli (e.g., pictures) and eight used conditioned threat cues. In terms of measurement type, we identified studies that measured skin conductance responses (SCR), heart rate (HR), respiration, pupil diameter, electromyography (EMG), and vocal intensity. Across studies examining emotional stimuli, SCR increased in response to threat, whereas HR and respiration exhibited mixed patterns reflecting orienting-related deceleration and arousal-related acceleration. Pupil diameter and startle responses were sensitive to threat but were also influenced by factors such as awareness and task demands. Facial EMG and vocal intensity increased in response to threatening images. Conditioning studies revealed robust SCR effects, reliable pupil generalisation gradients, and startle potentiation under learned threat. HR responses predominantly showed deceleration, modulated by anxiety levels and contextual factors. Together, these findings demonstrate that certain physiological markers reliably indicate threat perception, whereas the reliability of others depends on contextual factors. This body of evidence emphasises the value of physiological measures as indicators of attention to threats and suggests their potential as biomarkers in clinical research.

Keywords : Threat processing; Autonomic nervous system; Psychophysiology; Skin conductance response; Heart rate variability; Conditioning; Pupil dilation; Startle reflex

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Introduction

Encountering a potentially dangerous stimulus, such as an approaching predator, a sudden loud noise, or a socially threatening cue, triggers a cascade of physiological changes that prepare the organism for action. These acute stress responses are classically framed within the 'fight-or-flight' (Cannon, 1929) or later the fight-flight-freeze (Bracha, 2004) model. The polyvagal theory (Porges, 2007, 2025) states that the autonomic nervous system influences emotional states, behaviour, and the sense of safety. It proposes a hierarchy of three defensive states: the ventral vagal state (social engagement), the sympathetic state (fight or flight), and the dorsal vagal state (shutdown or freeze). Porges also emphasises the importance of a ventral vagal 'social engagement' system for feeling safe and connecting with others, and explains how trauma can lead to a hypervigilant or shut-down nervous system. From an evolutionary perspective, this proved adaptive as it provided animals (including humans) with the mechanisms to rapidly respond to threats against survival (Adolphs, 2013; Mobbs et al., 2015). When a threat is perceived, sensory information is rapidly relayed to subcortical structures, particularly the amygdala. The amygdala then acts as a central hub for detecting danger signals that are biologically or personally relevant (Jacobs et al., 2012; Öhman, 2005; Pessoa & Adolphs, 2010; Sander et al., 2003; Vuilleumier, 2005). Through its connections with the hypothalamus and brainstem, the amygdala triggers autonomic and endocrine responses that underlie the physiological signatures of threat.

Physiological states shape cognition, which then shape feelings, and feelings guide behaviour and feed back onto physiology in a recursive loop (Critchley & Harrison, 2013). For example, anxiety can lead people to think: "*If I feel anxious, this must be unsafe*" even when there is no clear external threat, because the bodily or emotional alarm is often taken as proof of danger (Arntz et al., 1995). The adaptive value of anticipating future outcomes helps explain why natural selection favoured both classical and operant conditioning (Nesse, 2005). However, defensive responses to threat are rapid, reflex-like actions, and consciously felt fear is not their initiating cause (LeDoux, 2014). For example, the anxious alert state, when anxiety places the body on high alert, heart rate and blood pressure rise and threats dominate attention, while other inputs, even pain, get less processing (Garfinkel & Critchley, 2016). The simpler notion that '*high places evoke freezing, social threats arouse submission, and predators provoke flight*' (Marks & Nesse, 1994) is likely modulated by additional factors, such as a predator's size, distance, and speed of approach, which can also elicit freezing in animals (e.g., Yang et al., 2020) and may have analogous effects in humans (Coelho et al., 2023).

Physiological responses do not occur in isolation, but rather as coordinated patterns that reflect the interplay of sympathetic and parasympathetic influences. The autonomic nervous system plays a central role in translating the perception of threat into coordinated bodily responses (Garfinkel & Critchley, 2016). When danger is perceived, the sympathetic branch of the autonomic nervous system is rapidly activated, preparing the body for defensive action by increasing the heart rate, raising blood pressure, accelerating respiration, dilating the pupils and increasing electrodermal activity (Cacioppo et al., 2017; Critchley & Garfinkel, 2018). These changes heighten vigilance, redirect energy to large muscle groups and prepare the body for the fight-or-flight response. In parallel, parasympathetic vagal mechanisms modulate these responses, as part of the parasympathetic branch, contributing to more nuanced dynamics, such as initial orienting or freezing responses (Bradley et al., 2001; Porges, 2007). These are reflected in transient heart rate deceleration and reduced respiration, which enhance sensory intake while conserving energy and minimizing detection. Thus, the interplay between sympathetic activation and parasympathetic modulation shapes the sequence of defensive states, ensuring that physiological resources are flexibly allocated depending on whether vigilance, immobility or overt action is most adaptive in the face of threat (Lang et al., 1997; Lang & Bradley, 2013). Although these reactions seem to be automatic, they are actually shaped by complex neural circuits that link perception, emotion, and thought, highlighting that physiological reactivity is also shaped by appraisal, context and learning.

Despite decades of theorizing about the psychophysiology of fear and defence, empirical findings remain highly fragmented, and there has yet to be a systematic review synthesizing the physiological signatures of threat. This gap is significant because integrating across paradigms and measures could clarify the shared and

divergent components of defensive responses. For instance, electrodermal activity has long been considered a reliable indicator of sympathetic activation (Dawson et al., 2017), whereas heart rate exhibits a more intricate pattern: an initial deceleration indicating orienting or freezing, followed by acceleration as danger approaches (Bradley et al., 2001). Likewise, pupil dilation is not only an index of autonomic arousal but is also sensitive to attentional demands and cognitive appraisal (Bradley et al., 2008). Experimental paradigms vary widely. They range from unconditioned threats, such as phobia-relevant stimuli (Öhman, 1986; Öhman & Mineka, 2001), to conditioned threats involving neutral cues paired with aversive outcomes (Lonsdorf et al., 2014). They also include more socially mediated threats, such as evaluative feedback (Somerville et al., 2010). Across these paradigms, researchers employ various measures, including cardiovascular (e.g. heart rate, blood pressure, electrocardiogram), respiratory, pupillometric, electromyographic, electrodermal and thermoregulatory measures, each of which captures different aspects of autonomic or somatic activation. Frameworks, such as the defence cascade (Lang et al., 1997; Mobbs et al., 2009) conceptualize these changes as sequential states of vigilance, freezing and fight-or-flight, each with a distinct physiological profile. Therefore, mapping empirical evidence onto such models is essential in order to determine which physiological markers reliably index threat reactivity, and under what conditions variability emerges.

The aim of this systematic review was to identify and synthesize experimental studies that investigated physiological responses to threatening stimuli. We considered both unconditioned and conditioned threats in the visual, auditory and multimodal domains, covering a broad range of measures including heart rate, blood pressure, electrocardiogram, respiration, pupil dilation, muscle tension, electrodermal activity and body temperature. Our threefold aim was to: (1) provide an integrated overview of the empirical evidence for physiological changes elicited by threats; (2) evaluate how these changes align with prominent theoretical accounts of fear and defensive responses; and (3) identify consistencies, discrepancies and gaps in the literature to inform future research. Understanding the physiological basis of threat responses has far-reaching implications, ranging from advancing basic theories of emotion and cognition to informing clinical interventions for anxiety disorders, phobias, and post-traumatic stress disorder. This systematic review clarifies how the human body registers and prepares for danger and how these processes intersect with the subjective experience of fear by mapping the landscape of physiological reactivity across paradigms.

Methods

The systematic review was prepared in accordance with the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) 2020 checklist (Page et al., 2021). The completed checklist can be found as Supplementary Material. The literature search was conducted on July 1, 2025, using the PubMed and Web of Science databases. The following combinations of keywords and filters were included in the search strategy: ((fear) OR (threat) OR (threatening)) AND ((visual attention) OR (visual search) OR (visual detection)) AND ((physiology) OR (heart rate) OR (HRV) OR (heart rate variability) OR (electrocardiography) OR (ECG) OR (EKG) OR (blood pressure) OR (BPM) OR (respiratory rate) OR (pupil dilation) OR (pupillometry) OR (muscle tension) OR (electromyography) OR (EMG) OR (electrodermal activity) OR (EDA) OR (skin conductance) OR (body temperature)). Filters: English, Humans, Adult: 18+ years, from 01/01/2000 - 30/06/2025. To focus on the last two decades, during which physiological research on emotional responses to environmental threats began to appear in sufficient numbers, we restricted the time frame to studies published from 2000 onward. Eligibility criteria (see Table 1) were predetermined to ensure the relevance of the primary studies. There were no restrictions for experimental methodology or study design. This inclusive approach is intended to capture a comprehensive range of studies investigating the emotional responses to environmental threats using physiological measurements.

Regarding the screening process, we focused on the relevance of each study to the core domains of emotional responses, threat or fear processing, and physiological measurements. This was done in two stages; first, we shortlisted records that met the inclusion criteria based on the title and abstract, and then reviewed the full-text. After data collection, to ensure the eligibility of the chosen papers, three reviewers worked independently to screen all studies. The screening process focused on the relevance of each study to the core domains of threatening or fear-inducing stimuli and physiological measurements. This was conducted in two

stages; first records were examined at the title and abstract, then those that were shortlisted were reviewed at full-text. Any disagreements regarding selected papers were resolved during a meeting of all three reviewers to reach a final consensus on study inclusion. We also applied the Newcastle–Ottawa Scale (Wells et al., 2013) to evaluate the methodological quality and potential risk of bias of the included studies.

Results

The search yielded a total of 644 records published between 2000 and 2025. After careful consideration, we identified 26 experiments in 20 studies that met the inclusion requirements (see Figure 1 for a detailed overview of the selection process). A summary of each article can be found in Table 2.

The eligible studies varied greatly in size (12 to 160 participants), with a mean sample of 59 participants. Most participants were female, and young adults aged 19 to 35 years (one study also included adults aged 50 years and older). However, five studies did not report age data. We only included studies conducted on a healthy sample, defined as having no history of neurological or psychiatric diagnosis. This did not preclude the inclusion of studies reporting individual differences (e.g., high/low anxiety or depression, fearful participants) alongside the main results. All studies included healthy participants. Four experiments (Aue et al., 2016; Mckinnon et al., 2020; Reutter et al., 2025; Yilmaz Balban et al., 2021) included patient groups, but these results were not included in the review.

A substantial proportion of the included experiments (18 out of 26) used stimuli that are inherently emotional or relevant to fear, such as spiders, snakes, aversive images, masked animal pictures, emotional films, or virtual reality (VR) threats, to examine how the autonomic and somatic systems respond to natural threat cues. The remaining experiments (8 out of 26) employed classical conditioning paradigms relying on neutral cues (CS+) paired with an aversive unconditioned stimulus (US), which was electric shock in all cases. These studies examined whether there were differences in physiological responses between CS+ and CS- (the stimulus after which no US follows) during acquisition, generalisation and extinction. In the results section, we present the results of the papers in two main sections: (1) Studies Using Emotional Stimuli and (2) Studies Using Conditioned Emotional Stimuli. A variety of physiological indices were assessed across these studies, including heart rate (HR), skin conductance responses (SCR), pupil diameter, respiratory parameters, facial electromyography (EMG) and vocal features. Together, these findings emphasise the complexity of emotional threat processing, demonstrating that physiological responses vary depending on the modality, measurement window and stimulus characteristics. Therefore, in each of the two main sections, we further introduce separate subsections for each physiological measurement.

Overall, most studies were deemed to be at risk of bias, primarily due to small sample sizes and limited reporting of participant selection procedures and demographic information. Four studies lacked detailed descriptions of randomisation; most lacked details of stimulus presentation blinding. Only half of the studies reported a power analysis; four made their data or analysis scripts available online; and none reported preregistration. The studies showed a wide range of analytical methods, including baseline corrections, probe timings and measurement windows. However, the methods used to acquire and analyse physiological data were generally well documented, and the outcome measures were clearly reported across studies. Selective reporting of physiological data components cannot be ruled out across studies. Several studies reported only significant physiological findings, while null results were often omitted or described inadequately. None of the included studies were preregistered, and few provided open data or analysis scripts. This pattern suggests that reporting bias may have influenced the evidence base.

Studies Using Emotional Stimuli

Studies investigating emotional stimuli show that HR and respiratory sinus arrhythmia are sensitive to threat; however, the direction of change (deceleration vs acceleration) depends heavily on stimulus type, phobic status, context, and measurement window. In emotional-threat studies, heart rate patterns showed the expected mixture of initial deceleration (orienting/freezing) and subsequent acceleration (arousal). However, these patterns were inconsistent across all tasks. Several studies have demonstrated clear HR differentiation for fear-relevant stimuli. For instance, Aue and colleagues found that participants with a fear of spiders

showed greater HR acceleration in response to spider targets than bird targets, whereas controls displayed no such difference (Aue et al., 2016). This suggests that stimuli related to phobias elicit heightened autonomic arousal, which overrides the initial deceleration often associated with orienting. Cue expectancy also modulated HR responses, particularly during the initial processing stages. In Flykt (2005), search arrays containing fear-relevant animals (snakes or spiders) produced reduced HR deceleration compared to neutral arrays, particularly during the first interbeat interval (IBI). The absence of deceleration was interpreted as a fear response. The second IBI showed a marginal continuation of this pattern, indicating sustained modulation of cardiac activity by threat.

Other studies (Flykt et al., 2012; Flykt & Caldara, 2006) have reported HR changes across successive IBIs, but often without robust stimulus-specific effects. In several cases, HR decelerated and then accelerated across the measurement window, regardless of fear relevance, with only subtle modulations by target type or distractor context. These findings suggest that HR patterns in response to emotional stimuli can be sensitive to task demands, array composition, and whether the stimuli are feared or merely fear-relevant. Jensen and Caine (2021) provided further evidence of reliable heart rate deceleration in response to inherently threatening stimuli: snakes elicited a significantly greater heart rate deceleration response than rabbits or bottles, irrespective of whether the stimulus was consciously detected (Jensen & Caine, 2021). It shall be noted that usually people who are strongly afraid of a given stimulus typically show an increase in heart rate, whereas people with little or no fear tend to show a heart-rate decrease, consistent with an orienting response. In Jensen and Caine (2021), the sample excluded individuals with extreme snake fear, which allowed the authors to predict and observe a clear directional heart-rate change toward deceleration. Nevertheless, these results indicate that cardiac responses can be triggered even without explicit awareness.

A more complex pattern emerged in another study (Jonsson & Hansson-Sandsten, 2008), which examined respiratory sinus arrhythmia during the viewing of emotional films. Fear-relevant films elicited the highest respiratory sinus arrhythmia (HF power), while positive films elicited the lowest. HR was similarly reduced during fear-relevant films compared to neutral or positive films. In this case, fear-relevant stimuli were associated with parasympathetic activation, suggesting a freezing-like response rather than an arousal-dominant pattern. The absence of strong interactions with time further suggests stable autonomic engagement throughout the viewing period. Finally, in the VR-based study (Yilmaz Balban et al., 2021), the majority of participants exhibited increased HR when presented with a height threat, although this effect was less consistent than the SCR response. The variability in HR responses across VR conditions suggests that cardiac changes may reflect novelty or postural factors, as well as threat.

Across almost all studies investigating emotional stimuli, SCR has proven to be one of the most reliable indicators of threat. For example, Hedger and colleagues found that threatening images reliably elicited larger SCRs than neutral images, but only when the images were consciously perceived (Hedger et al., 2015). In contrast, under continuous flash suppression, threat-related SCR enhancement disappeared completely, implying that electrodermal threat responses may require a minimal level of conscious awareness. Jensen and Caine (2021) reported substantial increases in SCRs to snake stimuli compared with rabbits and bottles, independent of conscious detection. This suggests that certain threatening stimuli (particularly those with an evolutionary relevance) reliably produce sympathetic activation, regardless of awareness. A more recent study by Flykt and colleagues also reported clear SCR differentiation in unmasked trials: feared animals elicited larger SCRs than non-feared, fear-relevant animals and rabbits (Flykt et al., 2017). Under masked conditions, however, SCRs did not differentiate between animals, indicating that stimulus visibility strongly influences the sympathetic response. Wiemer and colleagues found that spider images in an inattention blindness paradigm elicited higher SCRs than flower images, both when detected and when unnoticed (Wiemer et al., 2013). This again emphasises that electrodermal responses can occur even in the absence of reported awareness. In the breathing-load study by Pappens et al. (2010), aversive pictures elicited an increased SCR compared to no-stimulus conditions. However, SCR responses did not differ significantly from those to respiratory loads. This suggests that SCR may reflect general aversiveness or workload rather than threat per se. Finally, the VR heights study showed that almost all participants exhibited significant increases in SCR when viewing the height environment, and SCR clearly differentiated between the heights and no-heights

conditions, unlike HR or respiration. A similar skin conductance increase was found in another VR study (Hagni et al., 2008) when the right virtual arm of the participants was unexpectedly “stabbed” by a knife and began “bleeding”. These studies overall show SCR as a robust marker of sympathetic arousal to threat, typically strengthened by conscious awareness but still evident for evolutionarily salient threats even when participants do not report seeing them.

Aue et al. (2016) and McKinnon et al. (2020) examined pupil-based threat responses. In the former study, emotional images produced complex and partly counterintuitive patterns: baseline-corrected pupil diameter was larger for bird images than for spider images, contradicting typical arousal predictions. Pupil responses were also modulated by expectancy cues, with spider phobics generally showing smaller pupil dilations than controls. McKinnon et al. (2020) reported a more systematic pattern: pupil constriction was reduced (i.e. larger pupil size) in individuals with PTSD, particularly in response to fear-related and happy stimuli. The emotional modulation of pupil size was greater in individuals with PTSD than in trauma-exposed or control groups, suggesting either exaggerated autonomic arousal or impaired regulatory mechanisms. These studies demonstrate that, while pupil responses can indicate threat processing, they are significantly impacted by clinical status and task design.

March and colleagues found that threatening visual stimuli elicited larger SCR and startle-eyeblick responses than negative, neutral or positive stimuli in multiple experiments (March et al., 2022). Facial EMG responses were sensitive to threat under both visible and ‘unseen’ stimulus conditions, supporting their role as rapid threat indicators. Similarly, another study (Flykt et al., 2017) also found that voice intensity increased when participants were presented with images of feared animals in unmasked trials. This highlights the fact that vocal output can reflect the rapid emotional arousal triggered by threat.

Although respiratory responses were measured less frequently, Pappens and colleagues demonstrated that viewing aversive pictures modestly altered respiration compared to baseline, albeit not as significantly as respiratory loads (Pappens et al., 2010). In a VR study (Yilmaz Balban et al., 2021), tidal volume increased for most participants when viewing heights; however, differences from the no-heights condition were not always consistent. These findings suggest that respiration is sensitive to threat, but that it may also be influenced by contextual factors and task constraints.

Studies Using Conditioned Emotional Stimuli

During conditioning, HR responses typically showed deceleration for CS+ relative to CS-. Reutter et al. (2025) found that heart rate deceleration was greater for all threat-level stimuli than for CS- during generalisation. Notably, individuals with higher social anxiety exhibited reduced HR deceleration, suggesting reduced parasympathetic engagement. This suggests that the HR response is sensitive to both learned threats and individual differences. Stegmann and colleagues also observed an HR reduction in response to threatening contexts and CS+ cues, although context effects appeared to dominate baseline levels (Stegmann et al., 2023). Analyses without baseline correction revealed that threatening contexts induced an initial HR deceleration that persisted during cue processing. In contrast, Andreatta and colleagues reported weaker HR findings, with no significant cue-related HR effects in most analyses. This may be due to task demands, the VR environment, or measurement intervals (Andreatta et al., 2020).

SCR was one of the most consistently sensitive indices of conditioned threat. Dowd and colleagues demonstrated the successful acquisition of differential SCR: participants exhibited significantly higher SCRs in response to the CS+ than to the CS- during conditioning, but not during the baseline period (Dowd et al., 2016). This clearly indicates a conditioned autonomic response. Two studies by Flykt and colleagues reported robust conditioning effects across experiments (Flykt et al., 2007; Flykt & Caldara, 2006). In both the evolutionary relevant (snake) and modern (gun) threat groups, SCR was higher for the CS+ than the CS- during acquisition. The extinction patterns depended on whether extinction was masked or unmasked; unmasked extinction produced larger differential responses than masked extinction, indicating that awareness facilitates extinction learning. In the second experiment, evolutionary relevant threat CSs elicited larger SCRs overall than modern threat CSs. Pupil-based and SCR generalisation effects were evident in Reutter

and colleagues' study (Reutter et al., 2025). Pupil dilation increased systematically along a generalisation gradient (GS3, GS4, CS+) compared to the CS-. This demonstrated graded sympathetic activation based on learned threat similarity. Although skin conductance was not measured in this study, HR and pupil data clearly showed conditioning effects. Stegmann et al. (2022) found that SCR responses were higher in threatening contexts than in neutral contexts, and also higher for the CS+ than for the CS-. Bayesian analyses supported a model in which cue-related sympathetic responses were independent of context, suggesting that cue and context effects combine additively rather than interactively. Consistently, across studies, SCR reliably distinguished CS+ from CS-, confirming its utility as a conditioned threat marker.

Reutter et al. (2025) provided strong evidence that pupil dilation is proportional to learned threat. Pupil size increased progressively across the generalisation gradient, being largest for stimuli most similar to the CS+. The magnitude of dilation was also influenced by diagnostic facial features. This aligns with evidence from emotional-stimulus studies, but also clearly demonstrates that threat can be acquired, rather than being triggered naturally.

Startle measures showed potent conditioned differentiation. In Andreatta and colleagues, startle responses (but not SCR) differentiated between the conditioned stimulus (CS+) and the unconditioned stimulus (CS-) during acquisition in the threat context, but not in the safety context (Andreatta et al., 2020). Startle potentiation occurred specifically for the CS+ stimulus in the fear context during the second acquisition phase, which suggests that conditioning is modulated by context. Generalisation phases showed CS+ potentiation independent of context. Bublatzky and colleagues found strong startle potentiation during instructed threat-of-shock conditions across sessions and days (Bublatzky et al., 2014). Startle amplitude decreased across blocks and sessions (habituation); however, threat-related startle potentiation persisted, particularly at the beginning of sessions. These effects occurred even when no shock was delivered, demonstrating stable instructed-threat conditioning. Pappens et al. (2010) demonstrated that EMG startle enhancement occurred during the viewing of aversive pictures and under light-load conditions at specific probe times (1500 ms), although moderate load did not increase startle compared to no stimulus. This suggests that conditioned and aversive stimuli have a similar impact on startle reactivity.

Discussion

The overarching aim of this review was to identify and synthesize experimental studies that investigated physiological responses to either inherently threatening stimuli or stimuli that were conditioned as threatening. We aimed to determine how well various physiological responses in experimental settings align with previous theories on the nervous system underlying threat processing, and to connect the literature on physiological threat responses with foundational theories of fear and defensive behaviour (Lang & Bradley, 2013; LeDoux & Pine, 2016; Porges, 2025). Our aim in integrating findings from emotional stimulus and conditioning paradigms was to clarify which physiological indices consistently signal threat reactivity, and how these responses vary depending on stimulus type and awareness. This would reveal more about the underlying mechanisms of defensive responses. Our findings strongly support the idea that threat processing is not a single process, but rather involves the rapid coordination of multiple stages across the sympathetic and parasympathetic systems. This coordination is shaped by subcortical survival circuits and cortical appraisal mechanisms.

We found that findings vary based on the type of stimuli used in the studies: emotional stimuli trigger responses that are influenced by perceptual and evaluative processes, whereas conditioned stimuli cause more specific physiological reactions driven by learned threat associations. Studies using emotional stimuli revealed a high degree of variability in physiological patterns, which aligns with theories emphasising the combined influence of automatic survival circuit activation (LeDoux, 2022) and higher-order cognitive appraisal (Hermann et al., 2013; Moors et al., 2013). These defensive mechanisms seem to be biologically prepared but not fully automatic (Coelho & Purkis, 2009). Defensive reaction and action circuits likely operate in interaction (Cardinal et al., 2002), and fear can modulate these defensive mechanisms via medial prefrontal control of fear-related processing (Adolphs, 2013; Zsido et al., 2020). Emotional stimuli, such as spiders, snakes and threatening scenes, often elicited flexible patterns of heart rate responses varying from

deceleration (e.g. freezing or orienting) to acceleration (e.g. arousal or mobilisation), depending on the content of the stimulus, its relevance to phobias, or the demands of the task (Aue et al., 2016; Flykt, 2005; Jensen & Caine, 2021). Similarly, pupil dilation reflected both autonomic arousal and attentional processing, which is consistent with the two-system framework’s distinction between subcortical survival responses and conscious perceptual representations (LeDoux & Pine, 2016). This variability also reflects the defence cascade model’s assertion that organisms shift between orienting, freezing and mobilisation depending on the context (Bracha, 2004; Bradley et al., 2001). The presence of both deceleration (parasympathetic engagement) and acceleration (sympathetic activation) is also consistent with the polyvagal theory (Porges, 2007, 2025), which proposes that threat responses dynamically alternate between vagal-mediated immobilisation and sympathetic mobilisation. The fact that emotional stimuli produce context- and awareness-dependent effects is consistent with theoretical accounts that threats engage both bottom-up and top-down components of the threat-detection system (Coelho et al., 2023). By contrast, conditioned stimuli elicited more consistent, cue-specific physiological responses, in line with predictions from survival-circuit theory. This theory proposes that learned associations between a neutral cue and an aversive event result in the rapid and robust activation of subcortical defensive circuitry (LeDoux & Pine, 2016). Our review strongly supports this prediction. Almost all conditioning studies have reported significant differences between CS+ and CS- in terms of SCRs and startle reflex potentiation. Furthermore, threat responses also consistently conformed to the expected defensive patterns even when conscious threat awareness was absent (e.g., when the CS was presented in a masked manner), demonstrating the robustness of the associative learning mechanisms that activate defensive physiology. These findings confirm the expectation that conditioning activates the conserved amygdala–brainstem pathways that are responsible for rapid defensive mobilisation (LeDoux, 1998, 2000). Overall, conditioned stimuli produced clearer and more reliable physiological differentiation than emotional stimuli. This difference highlights the importance of conditioning paradigms for identifying specific components of defensive responses, and indicates that, although emotional-stimulus paradigms are more ecologically valid, they reflect a broader and more heterogeneous set of psychophysiological processes. The distinction between emotional and conditioned stimuli is crucial for comprehending the mechanisms of fear learning and the circumstances in which physiological reactivity reflects or does not reflect subjective fear.

These findings have several implications for future studies investigating the physiological responses underlying threat processing and behavioural outcomes. Firstly, the reliability of SCRs and startle responses in conditioning paradigms highlights their value as primary indices of threat learning. Future research aiming to study associative processes or extinction mechanisms would therefore benefit from prioritising these measures. Secondly, the variability in heart rate and pupil responses to emotional stimuli suggests that these measures may be more appropriate for examining perceptual, attentional or appraisal processes than for serving as stand-alone threat indicators. Thirdly, we want to emphasize the importance of considering stimulus awareness, phobic status and contextual cues when interpreting physiological results. Although they are more variable, emotional-stimulus paradigms capture real-world complexity, including perceptual richness, appraisal, awareness and individual differences such as phobias and PTSD (Aue et al., 2016; Mckinnon et al., 2020). Finally, the differential reliability of different measures and stimulus types provides a useful framework for multimodal psychophysiological research. Given that no single measure fully captures the threat response, studies should employ multimodal physiology. SCR and startle are reliable indices of sympathetic and defensive arousal, while HR and pupil dilation capture complementary processes. This highlights the importance of integrating complementary autonomic and somatic indices, rather than relying on any single measure.

As with any study, there are limitations to this review that warrant consideration. Firstly, we classified the studies as either emotional or conditioned based on the type of stimuli used, resulting in some conservative categorisations. Secondly, the heterogeneity of analytical practices, such as baseline corrections, probe timings and measurement windows, made comparisons between studies difficult. Thirdly, indices measured less frequently (e.g., respiration, temperature, RSA) lacked sufficient data to draw strong conclusions. Fourthly, many studies relied on healthy young adults, limiting the generalisability to clinical populations where threat

processing is altered. Finally, publication bias may have favoured the reporting of significant physiological effects.

In sum, our review provides a comprehensive synthesis of the physiological responses to emotional and conditioned threats found in the experimental psychology literature. By integrating these findings with theories of fear and defensive behaviour, we demonstrated that conditioned stimuli elicit strong and reliable physiological differentiation, whereas emotional stimuli evoke more variable, yet ecologically meaningful, responses that reflect perceptual and cognitive influences. These insights are essential for directing future research into fear learning, threat appraisal and clinical disorders involving dysregulated defensive responses. Knowing which physiological systems reliably indicate threat and under what conditions does so offers a basis for designing more precise experimental paradigms, developing biomarkers for anxiety-related disorders and advancing theoretical models of emotion and survival behaviour.

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Table1_Inclusion and exclusion criteria.docx available at <https://authorea.com/users/1006596/articles/1366921-physiological-signatures-of-threat-a-systematic-review-of-threat-related-stimuli-processing>

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Table2_Study overview.docx available at <https://authorea.com/users/1006596/articles/1366921-physiological-signatures-of-threat-a-systematic-review-of-threat-related-stimuli-processing>