

Branches of a twisting tree: Domain-specific threat psychologies derive from shared mechanisms

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Threat intensifies ideological investment (e.g., ethnocentrism, religiosity) as well as a diverse and orthogonally related set of responses, such as aesthetic preferences or tendencies to seek physical proximity with others. An emerging consensus unifies these diverse threat-responses as superficially varied expressions of a single underlying process designed to reduce anxiety. In contrast, evolutionary thinking favors hypothesizing multiple functions designed to strategically manage specific threats (e.g., pathogen threats should motivate responses targeted to deter contagion), and views anxiety as a proximate tool rather than an ultimate problem. As distinct threat adaptations co-opt proximate mechanisms related to anxiety, focusing on anxiety-reduction risks obscuring important functional differences. Here, current accounts of threat-modulated bias are evaluated through an evolutionary functional lens.

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The odds are that, within several decades at best, your heart will stop. Before dying, you will suffer infectious diseases, often acquired through pathogen-transmission events beyond your personal control. At times, you will find yourself isolated and uncertain, perhaps lost in an unfamiliar city or mired in a troubled relationship. You may even be physically assaulted. While one hopes that many years elapse before you actually face such calamities, research indicates that merely having imagined them — just now — may influence you in surprising ways.

Over the past 25 years, social psychologists have compiled extensive evidence that threat cues (e.g., of death, isolation, disease, violence, or confusion) can mobilize investment in ethnocentric, political, and religious values, as well as responses that are unrelated or indirectly related to

ideology [1–3]. For example, briefly contemplating death can lead judges to set higher bonds for alleged prostitutes [4], picturing the unraveling of a valued relationship can heighten religious commitment [5], and reading about disease can increase preferences for physical attractiveness [6]. Some responses appear specific to particular threats, whereas others (e.g., intensified group chauvinism) have been documented to follow numerous manipulations [1,3]. Although debate continues over which threat management account most parsimoniously encompasses all observations, the prevailing approaches in social and personality psychology agree that the function of threat-induced bias is to allay anxiety of one kind or another (see [Table 1](#)) [2,3].

Evolutionary perspectives, by contrast, conceptualize threat-induced biases as functional strategies to neutralize threats. Anxiety, on this view, is a proximate means of regulating cognitive and behavioral responses, not an ultimate problem. As unique problem-features distinguish varieties of threat, an evolutionary approach implies multiple content-dedicated systems rather than any single function [7]. Importantly, specialized threat systems should derive from an efficiently shared neurocognitive substrate, as mental functions arise via modification of existing structures [8,9]. Appreciating that domain-specific threat systems draw on common mechanisms, and therefore share family resemblances, may help to resolve disputes over the general versus specialized function(s) of threat-responses.

Domain-general accounts and fluid compensation

The *meaning maintenance model* (MMM) frames threat-biases as attempts to cope with the anxiety elicited by any inconsistency between experience and expectation [2,10]. Within the MMM, ‘meaning violations’ encompass anxiety-eliciting perceptual anomalies, unexpected outcomes, or overt threats [11]. The *reactive approach motivation* model (RAM) similarly posits that the anxiety evoked when goals are threatened problematically inhibits functioning [12,13]. According to both approaches, anxiety is palliated by activating the behavioral approach system thought to mediate all goal-directed activities — including the affirmation of cherished convictions [3,11]. Illustrative of the generality of the cues that can elicit ideological bias, MMM investigators have shown that exposure to surrealism, subliminal nonsense phrases, or change blindness can intensify the financial punishment of a prostitute [14–16], and RAM researchers have shown

Table 1

Theoretical perspectives relating threat to response biases.

| Theoretical approach | Proposed elicitor | Proposed response | Proposed function | Reference |
|------------------------------|-----------------------|--------------------------|--------------------------------|-----------|
| Meaning maintenance model | Any inconsistency | Fluid compensation | Palliate anxiety | [10] |
| Reactive approach motivation | Threat to valued goal | Fluid compensation | Palliate anxiety | [12] |
| Compensatory control theory | Lack of control/order | Affirm control/order | Palliate control/order anxiety | [39] |
| Group-based control theory | Lack of control | Affirm group identity | Palliate control anxiety | [42] |
| Terror management theory | Death cues | Affirm values | Palliate death anxiety | [43] |
| Unconscious vigilance | Subtle affective cue | Affective sensitization | Attend to hazards/resources | [1] |
| Coalitional psychology | Need for group aid | Signal group affiliation | Bolster social support | [36] |
| Behavioral immune system | Pathogen cues | Pathogen aversion | Avoid contagion | [46] |

Note. This list is intended to be representative but not exhaustive.

that undergraduate students manipulated to feel insecure about their intellect or valued relationships report more fervent religiosity [12], among other examples [3]. The ostensible interchangeability of threats and biases is often termed *fluid compensation*: anxiety-eliciting stimuli prompt anxiety-reducing responses, and content domains are only relevant inasmuch as individual, contextual, and sociocultural factors modulate the degree of anxiety or compensatory well-being that they engender [11,17].

Contrary to the MMM and RAM emphasis on anxiety-reduction via arbitrary approach, some putatively fluid outcomes appear strategic. For instance, threat primes related to death [18] or valued relationships [12] intensify inclinations to consume food and other material resources, consistent with facultative shifting toward future-discounting strategies when future prospects are uncertain. A future-discounting interpretation appears particularly illuminative of responses to cues of physical hazard, as death primes lead individuals to accept smaller short-term rewards over larger future rewards, to pursue riskier financial strategies [19], and to desire earlier procreation [20,21]. These preferences also track the number of close bereavements individuals have actually experienced [22*]. Notably, these findings bear out directional hypotheses concerning adaptive behavioral responses to risky environments that are unrelated to putative benefits of anxiety-reduction.

Fluid compensation or neural co-optation? At the mechanistic level, proponents of fluid compensation often highlight observations of comparable brain reactivity to diverse sorts of threat [2,3,11,17]. The amygdala and the anterior cingulate cortex have received particular attention because they are responsive to a wide array of threatening or anomalous stimuli [23], including reminders of death [24]. The recurrent activation of these regions in diverse contexts is not surprising as they are embedded in circuits subserving widely varying functional behavior (e.g., thirst, child protection) [25,26]. Distinct threat-response systems should be expected to share neurocognitive structures as selection derives new mental functions by co-opting and elaborating existing structures

[7*,8*,9**,27*]. For example, the dorsal anterior cingulate cortex and anterior insula appear important for representing the distress associated with both social isolation and physical pain, but physical pain also activates the posterior insula and somatosensory cortices [28], suggesting that subcomponents of the pain system were re-purposed to represent isolation. Future initiatives to individuate threat systems against their backdrop of shared neurocognitive architecture may examine the differential involvement of areas associated with components unique to particular threats, such as the representation of uncertainty [29], or, in the cases of social threats that strongly involve others' perspectives, the 'Theory of Mind' network [30].

The degree of fluid interchangeability reputed to characterize threats and biases is probably inflated, as qualitatively different judgments (e.g., derogating immigrants versus financially penalizing prostitutes) are frequently treated as equivalent measures of 'worldview defense' or 'value-affirmation'. This conflation obscures whether threats exert greater influence on thematically related versus unrelated judgments. Nevertheless, in addition to strategic functional responses, incidental responses may be expected insofar as activating the neurocognitive architecture related to threats of one type potentiates circuits relevant to others as a side-effect of co-optation. Such collateral activation may generate patterns consistent with fluid compensation in some circumstances, but more aptly characterized as 'glitch' interactions between domain-specific processes than as evidence of a single process. By the same token, dampening mutually co-opted mechanisms should reduce responsiveness in distinct functional systems. For example, down-regulating dorsal anterior cingulate reactivity via acetaminophen administration reduces physical pain, isolation distress [28], and ideological biases following primes of death or randomness [31].

Many fluid effects follow subliminal primes, or subtle manipulations with distraction and delay [1,3]. These methods may evoke a state of 'alarm' which, though relatively undifferentiated, complements domain-specific threat responses. Unconsciously detected threats can

activate subcortical structures (e.g., amygdala, locus coeruleus) which innervate diffuse cortical regions, triggering low-level arousal thought to potentiate both reflexive responses (e.g., recoiling) and further processing to recruit applicable networks [32–34]. Thus, rather than a problem to be solved, low-level anxiety evoked by unconscious threats appears to be a functional precursor to the activation of threat-relevant systems. Relatedly, *unconscious vigilance* (UV) is a hypothesized state of affective sensitivity triggered when threats, rewards, or anomalies are detected outside of focal awareness, thereby enabling functional systems to acquire the eliciting stimulus within conscious awareness and respond appropriately [1]. UV may also accentuate incidental affective reactions via misattribution, potentially explaining some threat-response phenomena. Indeed, subtle reminders of death exaggerate liking/disliking judgments of valenced sounds or images that have no evident adaptive significance, yet parallel the effects of death primes on group bias [1,35]. However, future research may determine that domain-specific architectures customize UV mechanisms, rendering individuals particularly sensitive to affective targets integral to the domain of the eliciting stimulus. Alternatively, due to processing constraints on un- or peripherally conscious representations, UV may equivalently influence affective responses. Regardless, a domain-general UV process cannot theoretically explain observations of content-specific connections between threats and biases.

Domain-specific responses to lack of control, death and disease

Behavioral adaptations configure cognitive, affective, and somatic profiles to address specific challenges, but this does not imply that all responses will differ. For example, given the advantages of social support in addressing diverse threats (e.g., of illness, resource scarcity, or hostile conspecifics), distinct threat systems may comparably up-regulate group investment [36]. Therefore, the question is not whether different threats produce similar responses, but whether they also produce divergent functional responses.

Studies designed to compare the effects of cues of death versus lack of control provide evidence of functional specificity. Death primes can experimentally increase religiosity regardless of framing [37,38*], whereas cues of lack of control only increase religiosity when God is framed as a controller [39]. Correspondingly, threats to control increase support for ideological constructs espousing group order to a greater extent than constructs related to the long-term perpetuation of one's group; the reverse obtains for participants primed with thoughts of death [40]. *Compensatory control theory* [41] posits endorsement of ideologies as providing a reassuring sense of personal agency in a disorderly world (e.g., libertarianism) or portrayal of world events as externally ordered (e.g., belief in divine providence). The *group-based control model* [42]

similarly suggests that threats to personal control over events motivate group identification and bias in order to gain the perceived effectance of collective action. Although these control-based approaches, like the MMM and RAM, construe the alleviation of anxiety as the focal function, their data suggest that cues specific to social disorder or lack of control may prompt strategic shifts toward self-reliance (e.g., in social contexts that appear un conducive to cooperation), attempts to increase order (e.g., via support for norm-enforcing individuals or coalitions), and/or solicitation of group aid.

With regard to the influence of reminders of death, *terror management theory* (TMT) attributes threat-modulated judgment biases to an adaptation to quell death anxiety [43]. Although the evolutionary plausibility of TMT has been widely critiqued [36,44,45], hundreds of studies attest to the effects of death cues on ethnocentrism and other biases [3,43]. This corpus suggests that, for reasons potentially quite distinct from those proposed within TMT, cues of death may modulate judgment in adaptive ways, such as inspiring normative sentiments that attract coalitional aid [36], or shifting toward fast life history strategies [19–21].

Research on responses to the threat of disease provides particularly compelling evidence of functional specificity [46]. For example, viewing images related to infectious disease (e.g., dirty toilets) — but not images related to threats of violence (e.g., guns pointed at the camera) — triggers physiological changes in oral immune function to counter pathogen ingestion [47], and causes trait germ aversion to negatively correlate with short-term mating orientation and anticipated sexual promiscuity [48], shifts that appear targeted to counter disease transmission. Priming threats of pathogen-contact — but not of violent attack — also increases the value ascribed to physical attractiveness, a heuristic cue of health [6]. Disease primes induce withdrawal from physical contact [49], whereas reminders of death increase tendencies to seek physical contact [50], presumably to foster social aid [45]. Individual differences in trait sensitivity to disease similarly predict avoidance of physical contact [49], and trait disgust sensitivity tracks political intolerance of acts that are pertinent to contamination (e.g., violations of sex norms), but not contamination-irrelevant policies (e.g., welfare) [51*]. Out-groups in ancestral environments were likely to harbor unfamiliar pathogens [46], which may explain why hand-washing moderates whether disease primes intensify prejudice against outgroups [52]. Convergent evidence thus indicates that, although threat systems related to disease and death can both increase ethnocentric bias, disease cues activate a suite of responses specifically designed to minimize risk of contagion [53].

Domain-specificity or moderation of a generic anxiety-reduction process? Proponents of generalist interpretations

acknowledge observations of content-specific relationships between threats and biases, but portray these patterns as evidence that threats moderate the expression of a domain-general anxiety-reduction process by rendering related goals or values salient [2,3,54]. However, it appears highly implausible that, for example, the constellation of responses specific to pathogen threats actually reflect affirmations of health values functioning to assuage anxiety about getting sick. Future research designed to identify strategic psychobiological shifts is likely to reveal comparable domain-specificity in ideological and other responses customized to counter non-disease threats. Without question, threats can elicit responses germane to unrelated threat-domains, and thereby allay anxiety due to down-regulation of shared mechanisms — but such patterns should not necessarily be taken as evidence of functional design to compensate for anxiety. To the contrary, such an overarching anxiety-reduction system would be redundant to the domain-specific threat systems, needlessly violating parsimony.

Conclusion

Social and personality psychologists investigating threat-modulated biases are converging on anxiety-reduction as a way of making sense of the sprawling patchwork of results produced in recent years. This approach fundamentally confuses the proximate and ultimate levels of analysis, mistaking the co-optation of neural regions (e.g., anterior cingulate cortex) across contexts with an illuminating functional explanation. Perspectives focusing on parallels between threat-responses usefully draw attention to neurocognitive resources that are efficiently recycled, but risk overlooking domain-specific relationships distinguishing subtypes of threats, output biases, and mediating processing algorithms. Conversely, researchers who conceive threat management architectures as discretely encapsulated risk overlooking the structural resemblances and processing constraints entailed by co-optation. Rather than forcing the varied pattern of threat-response relationships into any single model, or assuming that adaptive systems arise *de novo*, threat psychologies should be individuated as branches within a family tree.

Conflict of interest

None declared.

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