The Same, Only Different:

Threat Management Systems as Homologues in the Tree of Life

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Social and personality psychologists have accumulated an enormous corpus of data documenting interrelationships between threat processes and ideological modes of cognition. Unfortunately, these important findings are embedded in a formidably dense and contested patchwork of theories. Indeed, the four chapters making up this section highlight only a subset of the diverse, productive, yet largely disconnected theoretical approaches that have grown around *worldview defense* (i.e., the intensification of ideological adherence upon detection of a threat). Consider the following selection of perspectives posited to account for the relationship between threat detection and worldview defense (Table 1):

Insert Table 1 about here

That's a lot of parallel theories.

Perhaps surprisingly, we will argue that it is not the proliferation of proposed threat management systems that poses the greatest concern. Rather, the deeper problem is the murkiness surrounding how any of these theories might be meta-theoretically integrated, and what sort of evidence is necessary to compel retaining a theory rather than abandoning it as redundant. Can multiple accounts be usefully complementary, or is there one underlying threat management process that parsimoniously explains all observations? Here, we draw on basic evolutionary concepts to propose a meta-theoretical framework within which to systematically integrate seemingly disparate threat management accounts. We introduce the concept of psychological homology, then consider the implications of this approach for the threat management literature, with special attention to the ideas discussed in the present chapters.

Homology

The core idea organizing our proposal is that of *homology*, or the parallels between traits possessed by different species by virtue of their descent from a common ancestral trait (Griffiths, 2007). Homology is ubiquitous in nature, and often intuitively apparent. For example, the subtypes of teeth evident in different species of mammals possess overlapping, shared structural elements derived from a common ancestor (van Valen, 1994), as do variations among the leaves of various types of trees, or, at ultimate remove, the DNA of all members of the phylogenetic tree of life on Earth (Wagner, 2014). Importantly, homologous traits (homologues) can appear quite distinct from the shared ancestral trait from which they derive. Consider, for example, the divergences in shape and size distinguishing the tusks of elephants (useful for functions such as digging and fighting) from the front teeth of beavers (useful for chewing through tree trunks). Despite evincing strikingly distinct physical qualities and functional ends, both the tusks of elephants and the front teeth of beavers derive, via modification, from the basic incisor tooth structure of a shared ancestor (Springer & Holley, 2012). Likewise, the limbs of primates, lizards, birds, and whales, despite their dramatic physical and functional differences, are all homologues tracing back to a common ancestral trait (Wagner, 2014).

Crucially, the concept of homology—originally developed to account for bodily similarities across species tracing back to the traits of a common ancestor—is applicable to psychological systems (Lorenz, 1958; Moore, 2013; Parkinson & Wheatley, 2013). This powerful approach reconciles appreciation of the unifying superordinate traits shared across homologous mental systems with the specializations that differentiate them. We feel that this approach holds promise for unifying the archipelago of threat and defense theories—a need that has been widely recognized within the field (e.g., Hart, this volume; Holbrook, Sousa, & Hahn-Holbrook, 2011; Jonas et al., 2014; Proulx, Inzlicht, & Harmon-Jones, 2012), but one that standard social psychological approaches are ill-equipped to address due to the lack of any foundational meta-theory comparable to that of evolution by descent with modification. Here, we propose that many of the parallel theories of threat management describe homologous psychological systems which are both genuinely distinct and structurally related via shared origins.

Serial homology

How might different systems linking threat and ideological adherence that occur within a single organism constitute homologues? When employed to explain similarities across species, the concept of homology addresses traits that are understood as the products of processes of modification operating independently in the lineages of the two species at issue—the elephant's tusks and the beaver's front teeth are each specialized adaptations produced through the extensive remodeling of the teeth possessed by the common ancestor of all mammals. Crucially, in this form of homology, descent with modification replaces the ancestral trait with newer versions thereof. How then can the mind contain multiple, co-extant homologous systems related to threat and ideological adherence? The process of transformation from an ancestral trait into a derived trait would seem to eliminate the original trait—whether we are talking about elephants or beavers, the remarkable front tooth design evident in the extant species replaced the original front tooth design found in the extinct ancestor. Do such examples imply that there is only one contemporary threat management system related to worldview defense, although this single system may derive from older ancestral stages that have been transformed? Not necessarily. In cases of *serial homology,* an ancestral trait can be duplicated with modification while the original trait persists within the same organism.[1] For example, successive vertebrae are duplicates, with modification, of antecedent vertebrae, and all vertebrae simultaneously function within the same organism (Cartmill, 1987). Indeed, both the elephant and the beaver possess many teeth in addition to those at the front of the mouth, each of which can be understood as a modified duplicate of the basic tooth design—the elephant's massive molars, for example, are serially homologous with its tusks. Similarly, multiple serially homologous threat management systems may co-exist within the same mind (Clark, 2010; Holbrook, Piazza, & Fessler, 2014; Moore, 2013).

In our own research on threat representation, for example, we have posited that the threat that individuals are perceived to pose is conceptualized using a serial homologue of the psychological system that represents bodily size and strength. Size and strength have predicted the outcomes of violent conflict throughout both phylogenetic history and ontogenetic experience (Archer, 1988; Sell et al., 2009; Unnever & Cornell, 2003), suggesting that the mind should contain an elementary system which regulates decisions to fight, flee, negotiate, or attempt to appease based on the (literal) size and strength of oneself relative to prospective foes. By contrast, in the modern world, success in combat derives from numerous attributes of oneself and one's potential foes that are incidental to differences in bodily size, such as relative armaments, access to allies, and so forth (e.g., Parker, 1974). Reflectively weighing such factors would be problematically cumbersome and time-consuming, whereas deciding what to do in situations of potential conflict often demands speed. Noting that complex computations over many parameters can be streamlined via heuristic summary representations (e.g., Albrecht & Scholl, 2010; Murphy, 2002)—and that the mind characteristically repurposes older structures to perform newly arising tasks—we have proposed the *formidability representation hypothesis*, which holds that mental representations of prospective foes become larger or smaller, and more or less muscular, contingent on cues of the potential to inflict harm (Fessler, Holbrook, & Snyder, 2012). Importantly, these cues can have no literal relationship to physical size and strength. In support of the existence of a threat-assessment homologue that represents threats unrelated to literal size/strength in terms of physical brawn, the estimated size and strength of adversaries have been documented to be influenced by an array of threat moderators, including the possession of weapons (Fessler et al., 2012), the presence of allies (Fessler & Holbrook, 2013a), cues of the propensity to take physical risks (Fessler, Tiokhin, Holbrook, Gervais, & Snyder, 2014), displays of visible markers of membership in rival coalitions (Fessler, Holbrook, & Dashoff, under review), cues of membership in groups stereotyped as dangerous (Holbrook, Fessler, & Navarrete, under review), temporary physical incapacitation (Fessler & Holbrook, 2013b), parenthood of vulnerable children (Fessler, Holbrook, Pollack, & Hahn-Holbrook, 2014), and the quality of coalitional leadership (Holbrook & Fessler, 2013). Thus, converging lines of evidence militate for the existence of a threat-representation system derived, via serial homology, from an antecedent system that represents bodily size and strength.

Serial homology and neural recycling

We are not proposing that, akin to adjacent spinal vertebrae, the brain and body *physically* duplicate the biological bases of psychological homologues. Rather, following Clark and Fessler (submitted) and Barrett (2012), in moving from somatic to psychological forms of serial homology, we have shifted from physically plural structures (e.g., spinal vertebrae) to plural structures that are instantiated in overlapping, co-opted somatic circuits.

Neuroscientists are increasingly interested in the capacity for mechanisms designed for one function to be re-purposed for later functions (e.g., Anderson, 2010; Anderson & Penner-Wilger, 2013; Dehaene & Cohen, 2007; Gallese & Lakoff, 2005; Parkinson & Wheatley, 2013). The unique human capacity to read illustrates the application of older neural structures to the performance of novel functions. According to the "neuronal recycling hypothesis," visual word recognition results from the recycling of neural structures used in object recognition (Dehaene & Cohen, 2007). Clearly, no neurobiological adaptation evolved to enable reading, as the advent of reading occurred far too recently for natural selection to have operated. Nevertheless, the mind can acquire a reading system, in part, by repurposing object categorization mechanisms to process orthographic categories (Dehaene & Cohen, 2007). The world's writing systems show tremendous variation in the shape and complexity of their constituent characters, yet, underlying these variations, writing symbols (letters, ideograms) are made up of lines that intersect at vertices (Changizi & Shimojo, 2005). Thus, the building blocks of writing systems correspond to fundamental features used in object recognition (Szwed et al., 2011), as the same vertex configurations found in written language are ubiquitous in the natural visual environment, and are known to be exploited by object recognition mechanisms in the brain (Changizi, Zhang, Ye, & Shimojo, 2006; Dehaene & Cohen, 2007). Consonant with serial homology, we retain the ability to recognize objects while gaining the derived capacity to recognize words. Similarly, social neuroscientists have argued that neural mechanisms that originally evolved for spatial reasoning were later co-opted to represent social relations (e.g., "social distance"; Gallese & Lakoff, 2005; Parkinson & Wheatley, 2013). Applying these examples to the threat management literature, one may expect significant cultural variation in the expression of threat management homologues (akin to the cultural variation in the presence or format of reading systems), but this variation will be constrained by the underlying structures inherited from antecedent systems (for more detailed discussion of processing constraints and other issues involved in applying the concept of serial homology to the mind, see Clark, 2010; Clark & Fessler, submitted; Moore, 2013).

Serial psychological homology at phylogenetic and ontogenetic scales

Because the mind is capable of acquiring new functions in a single lifetime through learning, we have also shifted from modification at the phylogenetic scale (e.g., the creation of homologous subtypes of vertebrae) to include relatively abrupt, ontogenetic developments (e.g., the creation of homologous subtypes of complex motor skills, such as typing or playing a musical instrument). Ancient traits can rapidly homologize into novel traits (e.g., reading and writing) within a single lifetime via cultural learning (Barrett, 2012; Moore, 2013; Parkinson & Wheatley, 2013). Importantly, however, although homologous psychological systems can manifest through cultural learning within a single lifetime, homologous derivations can also be produced over deep evolutionary time via natural selection. Thus, a complete natural taxonomy of the homologues catalogued in the worldview defense literature would identify (i) the single, most ancient shared mechanism, (ii) serially homologous derivations of the common mechanism manifesting over evolutionary time, and (iii) serially homologous derivations that require learning over a single lifetime.

For the sake of illustration, assume that early animals evolved a psychological adaptation designed to monitor instances of physical harm. Now assume that, over the course of human evolution, this mechanism was duplicated and modified by natural selection to produce a homologous social harm-monitor which repurposes much of its predecessor’s computational and biological architecture to detect harm to one’s reputation, and thus facilitate maneuvering within human social hierarchies. This hypothetical, homologically derived social harm-monitor represents and processes social insults by recruiting mechanisms used in representing and thinking about injurious physical blows (for a related proposal, see Eisenberger, 2012), by integrating mechanisms for language and for representing the perspectives of other people. Next, and in a similar vein as the proposals of Hart (this volume), van den Bos and colleagues (this volume), and McGregor (2006; McGregor et al., 2010), imagine that, as human capacities to conceptualize and emotionally invest in abstract ideologies evolved, the social harm-monitor was duplicated and modified by natural selection once more to detect slights aimed toward cherished norms and moral values. Fast-forwarding to the present day, how might this most recently derived, "values harm-monitor" operate in modern societies characterized by computer-mediated social networking? In such literate, computer-savvy cultural environments, the values harm-monitor would likely activate in response to insults presented in evolutionarily novel formats. In short, via serial homology, the values harm-monitor would process snide blog posts directed toward favored sports teams, political organizations, or opinions about socialized medicine using mechanisms shared with those used in representing interpersonal social harm qua physical harm. Thus, in this hypothetical example, indirect, computer-mediated affronts against abstract groups or attitudes would be processed using similar—but not identical—neural circuitry to that utilized in representing literal punches.

This simple example demonstrates several key points. To begin, both the personal social harm-monitor and the derived values harm-monitor sensitive to affronts against in-groups or in-group values evolved over evolutionary time and are species-typical, whereas the homologue imagined to operate in a computer-mediated context emerges over ontogeny, and only in technologically advanced societies. Note here that, as in the case of reading, it would be impossible to satisfyingly understand this system without considering its evolutionary context, yet it is neither universal nor an evolved adaptation. Indeed, this new homologue may or may not adaptively enhance reproductive fitness, although the arising of a computer-mediated social harm-monitor may be inevitable given the conjunction within the modern mind of an evolved social harm-monitor, the capacities for abstract representation that enable usage of information technologies, and exposure to social media such as Facebook. Just as psychological systems that were adaptive in the ancestral past may become non-fitness-enhancing or even maladaptive in modern contexts (e.g., dietary preferences for sugar and fat), so may homologous derivations from ancient systems be grounded in adaptations, yet non-adaptive.[2] Consequently, evidence for the mere existence of any given threat-management system in people living in technologically advanced, highly integrated societies should never be taken as sufficient evidence for the adaptiveness of that system. Finally, and perhaps most importantly, all of the hypothetical harm-monitoring systems in this example share substantial—yet distinguishable—psychological and neurobiological structure (more on this below).

The core idea of serial homology is that the same (i.e., not convergently analogous, but historically continuous) structures are duplicated and modified to produce new structures that effect new functions. With respect to neural recycling of psychological systems, serial mental homologues can be adaptations that arise over eons of natural selection, or, as in the derivation of the word-recognition system from the object-recognition system, exaptations (i.e., characteristics that serendipitously perform useful functions that they were not evolved for) that arise through learning within a single lifetime (Gould & Vrba, 1982). These phylogenetic and ontogenetic pathways differ not only in time-scale, but also, and relatedly, in the extent of their functional specialization.

The mechanisms of serially *adapted* homologues may be expected to fit relatively well to their ultimate functions, because adaptations are produced by an extended process of selective refinement that maximizes functionality within the constraints of the antecedent trait. For example, the emotion disgust, originally evolved within the domain of eating to deter ingestion of pathogens, is theorized to have homologized into an adaptation for regulating sexual behavior (Clark & Fessler, submitted). This serially adapted homologue, sexual disgust, is designed to facilitate avoidance of poor mating partners (e.g., close kin, etc.), and has a psychobiological profile indicative of functional modification over evolutionary time (e.g., female fertility modulates sensitivity to sexual disgust; Fessler & Navarrete, 2003). In contrast, serially *exapted* homologues arise due to fortuitous matches between the affordances of the antecedent system and the structure of the environment. Because such exapted homologues are not honed over eons by natural selection, they may therefore be expected to evince a less specialized fit between their structures and their functions. Specifically, because they lack a history of selective refinement to produce functional modifications, serially exapted homologues should be more constrained than serially adapted homologues by the structure of the antecedent systems from which they derive. For example, the serially exapted homologue that enables word-recognition appears to be constrained by the structure of the object-recognition system, such that the mind is not equivalently capable of learning any writing system capable of visually encoding information (e.g., a visual form of Braille, in which letters are represented by the relative orientations of dots), despite the advantages that such flexibility would offer. Rather, as an exaptation drawing on the object-recognition system, the word-recognition system strongly favors writing systems that match the patterns of contours found in natural scenes (Changizi et al., 2006), and that are—

like the brain's object-recognition system—not reliant on detecting differences in size or orientation (see Szwed, Cohen, Qiao, & Dehaene, 2009).

With respect to threat management systems, the distinction between serially adapted and serially exapted mental homologues may similarly illuminate the degree of structural fit between mediating mechanisms and threat reactions. Serially homologous threat management adaptations will show relatively greater structural dedication to managing threats within that domain (e.g., disgust primes and fine-grained taste judgments), relative to exapted domains in which effects are detectable, but comparatively coarse (e.g., disgust primes and political judgments), to the extent that the structure of the new functional domain is only superficially shared with the structure of the domain for which the antecedent adaptation was designed.[3]

Culture and parochial threat management homologues

The example of the mind's ability to build a reading system capable of abstract symbol processing from pre-existing systems (e.g., for object recognition) illustrates that threat management systems may develop in distinct ways contingent on cultural experiences. Much as experience in literate cultures allows the mind to extrapolate a reading system, so may culturally variant transmission of values lead to the development of parochial threat management homologues in some societies, but not in others. For instance, the compensatory control (Kay, Gaucher, McGregor, & Nash, 2010) and group-based control (Fritsche et al., 2013) theories of worldview defense are predicated on the assumption that the ability to personally predict and direct present and future events is a basic human motivation (also see Schoel, Stahlberg, & Sedikides, this volume); correspondingly, threats to one's sense of control are posited to inflate support for religion or in-group ideology in a compensatory attempt to gain a sense of control via divine or collective action (Kay et al., 2010; Fritsche et al., 2013). Although Western psychologists often construe the “need for control” as a universal human motivation, the related imperative to have personal choice over events varies substantially across populations, and appears to be unusually intense in individualistic Western cultures, particularly the United States (Inglehart, Basanez, & Moreno, 1998; for a review, see Henrich, Heine, & Norenzayan, 2010). Speculatively, therefore, Westerners may possess a derived threat management system, sensitive to loss of personal control, which members of societies that place less value on personal control do not share, or do not share to the same extent. Culture may likewise moderate the threat-value attached to other concepts that have been found to trigger worldview defense. For example, collectivist cultures may regard the prospect of social isolation as more threatening than individualist cultures, which may explain why thoughts of social isolation have been found to arouse worldview defense in rural Costa Rica, but not Los Angeles (Navarrete et al., 2004; Navarrete & Fessler, 2005).

Van den Bos, McGregor and Martin (this volume) similarly argue that culture determines the extent to which individuals are prone to invest in ideological values as a means of managing extended periods of threatening uncertainty. They draw on the distinction between “immediate-return” societies, in which resources are often shared, status is relatively non-hierarchical, and the benefits or losses of endeavors are reaped immediately (e.g., hunting), and “delayed-return” societies, which are socially stratified, and in which the benefits or losses of personal endeavors are often experienced in the future (e.g., working for a monthly paycheck), and require long-term interpersonal social commitments. Van den Bos et al. suggest that people living in delayed-return societies, who often experience prolonged periods of uncertainty between investing in endeavors and learning the outcomes (e.g., applying for jobs), may compensate for these prolonged bouts of anxious uncertainty by investing more heavily in ideologies that bolster perceived meaning and certainty. We are skeptical whether deficits in such unfocused categories as “certainty” or “meaning” can constitute the domains of specific threat management systems, and suggest that future work in this area would benefit from theoretically parceling out more specific challenges (e.g., economic uncertainty) endemic to delayed-return cultures. In addition, it seems likely that immediate-return cultures also experience extended periods of anxious uncertainty, such as when recovering from illnesses with prolonged time-courses, or as appears to be routinely the case in cultures characterized by beliefs in witchcraft or malevolent spirits that might strike at any time (Schwartz, 1973). Notwithstanding these relatively minor points of contention, Van den Bos and colleagues importantly demonstrate one way that standard samples may diverge from populations immersed in lifestyles more typical of the ancestral past, such that the atypicality of modern living may significantly alter the manifestations of evolved systems for managing threat.

To date, surprisingly little evidence from societies more closely resembling those in which humans have lived for most of our species’ history has been accrued in the otherwise fecund threat-compensation literature. The bulk of research on the psychology of threat and ideological investment postulates claims about the “human” mind, or “people”, on the basis of research conducted in highly non-representative Western samples, typically from Europe or the United States, or living in urban areas in modern industrial societies outside the West. As Arnett (2008) quipped, the top journal within social psychology might be more aptly titled *Journal of Personality and Social Psychology of American Undergraduate Psychology Students*. This prevailing sample bias should be of profound concern to any investigator interested in the species-typical psychology of threat management. Comparative research indicates that U.S. undergraduate samples are among the most extraordinarily unrepresentative when compared with cross-cultural samples, in domains ranging from low-level spatial reasoning tasks to high-level tasks involving moral reasoning, social cooperation, and causal attribution (for a review, see Henrich et al., 2010). Therefore, to the extent that pan-human conclusions are often generalized from research on such narrow samples, our understanding of the human mind is likely to be significantly distorted. Identifying species-typical threat management homologues will require representative samples.

Neural architecture(s) of threat management

Synthetic perspectives on threat and defense highlight the shared neurobiological mechanisms that have been related to diverse sorts of threat reactions (e.g., Jonas et al., 2014; McGregor, 2006; Proulx et al., 2012). In particular, the amygdala and the anterior cingulate have been implicated in threat-detection of various types (Eisenberger & Lieberman, 2004; Nitschke et al., 2009; Pessoa & Adolphs, 2010), whereas prefrontal areas (e.g., dorsolateral prefrontal and medial orbitofrontal cortices) are implicated in down-regulating anxious responses to a wide array of problems (Harmon-Jones & Harmon-Jones, 2008; Lieberman, 2007; Pizzagalli et al., 2005; Sutton & Davidson, 1997). These findings have been glossed as proof of a single, content-general system that produces analogous threat detection and compensation effects in a diverse array of contexts (e.g., McGregor, 2006; Proulx et al., 2012). Our objective here is not to assess this complex literature in detail (for a review, see Jonas et al., 2014), nor to dispute the value of noting unifying similarities, which we take as illuminating the shared structure uniting diverse homologues. Instead, our intent is to highlight that the recurrent involvement of specific neural regions across various functions does not imply an equivalency between the extended networks supporting each function.

Any emotional reaction is likely to involve motivational structures such as the amygdala, anterior cingulate, nucleus accumbens, and thalamus (Morgane, Galler, & Mokler, 2005; Pessoa, 2008). Therefore, to the extent that these areas are involved in motivated behaviors related to topics as varied as thirst, sexuality, fear, anger, child-provisioning, etc. (Hahn-Holbrook et al., 2011), noting their ubiquitous contribution across functions is not informative about the extended brain circuits or psychological systems particular to a given function. Indeed, threat management (or other motivation-relevant) homologues should be expected to share coarse patterns of activation—how could it be otherwise? We therefore encourage researchers to attend to the specific differences, as well as the bridging similarities, attendant to the psychobiological dimensions of threat management processes.

Consider, for example, the role of the anterior cingulate in resolving threats of differing types. The anterior cingulate cortex is conceptualized as an interface between executive and subcortical regions, and is hypothesized to contribute to dynamic, threat-relevant problem-solving by recruiting responses that are appropriate to the particular conflict at hand (Botvinick, Cohen, & Carter, 2004; Holbrook et al., under review; Kerns et al., 2004; Pessoa, 2008; Sheth et al., 2012). For example, social neuroscience studies have observed anterior cingulate reactivity to various threats or discrepancies within the social domain (Izuma, 2013) as well in physical motor tasks (Shima & Tanji, 1998); anterior cingulate activity correlates positively with strategic behavioral shifts appropriate to reduce the given problem (Amodio & Frith, 2006; Botvinick et al., 2004; Bush et al., 2002; Ridderinkhof, Ullsperger, Crone, & Nieuwenhuis, 2004). Similar observations could be made with regard to the involvement of frontal areas in problem-solving tasks ranging from arithmetic to moral reflection. The take-home conclusion here is that, although valuable insight into the superordinate functions of brain regions may be obtained by observing the range of tasks in which the regions of interest are involved, it is important not to conflate distinct problem-solving architectures merely because they draw on shared mechanisms.

The distinction between parental attachment and romantic attachment provides a clear example of how functional homologues might be mistaken for a unitary process were one to overly weight the importance of shared neural activation. Bartels and Zeki (2004) used functional neuroimaging to compare the brain profiles of both parental and romantic attachment, and found considerable overlapping activity in reward regions rich in oxytocin and vasopressin receptors (e.g., striatum, ventral tegmental area). Taken out of context, one might conclude from these similarities that the two systems are actually equivalent in some sense, and should therefore be collapsed in the interest of parsimony. However, notwithstanding the important similarities between the two, parental attachment is not the same as romantic attachment! Moreover, it bears mentioning that, in this study, the anterior cingulate cortex was also significantly activated by images of either participants' infants or romantic partners relative to control images. In the context of this design, and of the extended simultaneous activation of reward centers, anterior cingulate activation presumably reflected an approach / interest response rather than a threat-reaction, demonstrating how crucial it is to interpret the activity of a given region (e.g., the anterior cingulate) *in situ*.

Differences are as illuminating as similarities. Returning to the Bartels and Zeki (2004) study, as one would expect, parental love stimuli versus romantic love stimuli elicited distinct as well as shared activation patterns. For example, periaqueductal grey reactivity was detected for maternal—but not romantic or paternal—love, echoing findings in animal studies showing that periaqueductal grey activity is highly involved in maternal behavior (Lonstein & Stern, 1998). Likewise, the hypothalamus was only activated in response to images of romantic partners, which appears to owe to the erotic component of romantic—but not parental—attachment (Karama et al., 2002). Similarly distinct activation patterns may be expected to hold between homologous threat systems. For example, prior research suggests that threats that are strongly related to aversive uncertainty may differentially involve the posterior parietal cortex (Bach, Seymour, & Dolan, 2009; Bach, Hulme, Penny, & Dolan, 2011); social threats that strongly involve others' perspectives regarding oneself may differentially involve the temporoparietal junction and the medial parietal cortex "Theory of Mind" network (Mar, 2011; Van Overwalle, 2009). We point to the comparative approach taken by Bartels and Zeki (2004) as paradigmatic for future neuroscientific investigations in this area.

Neural kluges and "fluid compensation"

The mind appears to be, to a great extent, a jury-rigged collection of inter-connected kluges which are not well-encapsulated from one another (Barrett & Kurzban, 2006; Marcus, 2008). As such, activation of psychological / neural architecture related to threats of one type should be anticipated to potentiate related systems, setting the stage for "fluid compensation" patterns wherein threats of various types can lead to biases of various types (Heine et al., 2006; Jonas et al., 2014; Proulx et al., 2012). This seems particularly likely to occur when the threat is processed in a highly subtle way, as impoverished depth of processing may entail less elicitation of domain-specific responses. Notably, in this regard, most of the fluid compensation effects recorded in the threat compensation literature follow subtle or subliminal manipulations, usually including a period of distraction and delay (Holbrook et al., 2011; also see Hart, this volume, for a similar proposal). Whether or not our speculation about the relationship between the subtlety of threat-induction and the activation of distinct systems is borne out, it does not follow from the fact that such cross-system glitches can be experimentally produced that there are no distinct systems. To the contrary, our serial homology account actually requires a certain degree of substitutability of input threats and output biases, due to kluge effects of shared structure.

Individuating threat management homologues

Theorists advocating for the radical unification of distinct threat management processes emphasize the substitutability of input threats and output biases. For instance, semantic or perceptual anomalies and mortality-salience inductions have equivalent effects on ideological biases such as the punishment of a fictional prostitute (Proulx & Heine, 2008; Randles, Proulx, & Heine, 2011). Such results have been taken as evidence that any sort of conflict can interchangeably elicit any sort of compensatory bias, from heightened implicit pattern detection to moral condemnation, calling into doubt theories limited to narrow classes of threats (e.g., Randles et al., 2011; Proulx et al., 2012). Indeed, one of us (CH) has previously advanced a similar argument (Holbrook et al., 2011; Holbrook & Sousa, 2013). However, gross equivalencies in the effects of disparate threats may reflect the activation of mental structures common to multiple threat management homologues, particularly to the extent that the target judgments are orthogonal to the proper domains of these underlying systems. In this section, therefore, we propose three specific criteria by which to discern threat management homologues. Threat management systems may be individuated according to differences in (i) the cues that activate the system, (ii) the cognitions or behaviors that follow system activation, and (iii) the processing algorithms that mediate these output biases.

With respect to the eliciting cues, distinct systems should be activated by threat categories that are thematically coherent, and are not redundantly encompassed by another system. For example, cues of being socially isolated, like cues of death, have been confirmed to increase group chauvinism; importantly, the isolation manipulation has also been shown not to increase the salience of death thoughts (Navarrete et al., 2004). Thus, to the extent that social isolation cues are confirmed to be unrelated to death thoughts, there are grounds to suppose that there might be distinct systems related to threats of social isolation and to threats of death, respectively, which can similarly influence intergroup bias. Evidence that threats from divergent domains can produce similar effects is not sufficient to infer the presence of multiple systems, however, as the more parsimonious assumption would be that there is only one threat system which can be activated by a broad class of triggers (for similar proposals, see Hart, this volume; Holbrook et al., 2011; McGregor et al., 2010; Proulx et al., 2012).

Truly distinct systems should produce distinguishable effects on cognition and behavior. For example, participants threatened by reminders of serious problems in valued interpersonal relationships have been shown to produce worldview defense reactions comparable to those evinced by participants who have been reminded of death (McGregor & Marigold, 2003). However, it remains to be seen whether relationship-problem and death manipulations would equivalently bias judgments differentially germane to each threat. Should future research determine that, for example, reminders of relationship problems bolster greater professed willingness to affiliate with cherished relationship partners than do reminders of death—and, conversely, that reminders of death bolster greater endorsement of beliefs in a pleasant afterlife than do reminders of relationship problems—then the strategic linkages between the respective threat and judgment categories would militate for the presence of homologous systems. A similar difference may hold between informational uncertainty (e.g., about the facts of a situation) and personal uncertainty (e.g., about one’s social prospects or moral character), which van den Bos and colleagues (this volume) argue invoke distinct psychological profiles and should not be conflated. Importantly, a homologous relationship between plural systems requires discernibly unique relations between their input elicitors and output effects, but is simultaneously compatible with findings that, due to their shared structure, the separate threat categories also influence similar judgment categories.

Finally, threat management homologues may be individuated according to differences in the processing algorithms by which the eliciting threats produce output biases. For example, consider cues of loss of personal control versus cues of death. Both topics have been demonstrated to enhance avowed religious belief (Kay, Gaucher, Napier, Callan, & Laurin, 2008; Jonas & Fischer, 2006; Norenzayan & Hansen, 2006), but may do so via differing pathways (Kay, Gaucher, McGregor, & Nash, 2010). In their research on control threats, Kay and colleagues found that cues of lack of control led to diminution of beliefs in order and structure, and that the magnitude of this perceived threat to order predicted the influence of the control manipulation on avowed belief in God. In still more direct evidence for a strategic connection between threats to control and belief in God as a means of attaining control, Kay et al. found that the threat to control significantly increased endorsement of belief in God when God was framed as a controller, but not when God was framed as a creator (2008; Study 1; for a full discussion of evidence that religious belief can specifically remediate threats to control, see Kay et al., 2009). Whereas cues of lack of control appear to heighten religiosity due to perceptions of God in these samples as a source of compensatory external control over events, death primes may motivate supernatural belief in an afterlife largely in an attempt to negate the problem posed by death as the end of one's existence (Jonas & Fischer, 2006: Norenzayan & Hansen, 2006). For instance, Norenzayan and Hansen (2006) found that reminders of death experimentally increased avowed belief in God without framing God explicitly as a controller. Moreover, reminders of death also increased avowed belief in supernatural agents that were relatively alien to the predominantly Christian participants, and hence do not appear likely to have been associated with providing an indirect means of control to them (e.g., shamanic ancestral spirits). The apparent dual motivational pathways by which threats to control and threats of death can lead to similar increases in avowed religious belief demonstrates the importance of taking processing algorithms—reflective of the functional reason that a threat produces a particular bias—into account when evaluating threat management homologues.

We have argued that the mind may contain multiple homologous systems relating threats of various categories to ideological reactivity of various kinds. We have further argued that, whereas some of these homologues may be expected to have evolved over deep time to become part of our panhuman heritage, others may be contingent on certain cultural and developmental conditions, yet no less rooted in evolved structures, and no less psychologically real. However, we stress that evidence adduced in support of the existence of any given serially homologous threat management system must compellingly rebuff more parsimonious explanations, and such systems should not be postulated unless the criteria for individuating threat management systems enumerated above are satisfied. Hypothesized threat management systems that do not evince domain-specificity, or are defined in terms so nebulous as to prevent disconfirmation, should be rejected a priori.

Advantages of homological synthesis over unitary synthesis

Both the homology approach advocated here, and the unitary proposals advocated elsewhere, aspire to coherently synthesize disparate literatures in a biologically plausible manner. In the most similar in spirit of these prior accounts to our own, Ian McGregor and colleagues' "reactive approach motivation" theory links the capacity for threats to exacerbate human ideological investments (e.g., moral conviction, jingoism, religiosity) to ancient, evolutionarily conserved brain circuits designed to mediate effective goal pursuit (McGregor, 2006; Jonas et al., 2014; Van den Bos et al., this volume). Building on literature from comparative neuroscience (e.g., Gray & McNaughton, 2000), McGregor et al. argue that when personal goals are threatened, feelings of anxiety deter active goal-pursuit, and organisms reflexively seek ways of attaining the threatened goals or alternative goals (for a detailed review, see Jonas et al., 2014). The hypothesized goal-pursuit system is ancient, with homologues extant in numerous vertebrate species whose lineages diverged hundreds of millions of years in the past. According to this model, when high-level goals are imperiled (e.g., to maintain satisfying romantic relationships; to attain status in one's career; to be morally consistent), anxiety ensues as goal-pursuit is halted to deal with the conflict. The goal-pursuit system is then thought to motivate strategic attempts to palliate the elicited anxiety (e.g., by reinforcing ideals, which are represented as high-level goals) and thereby resume sanguine goal-pursuit (also see Van den Bos et al., this volume). Thus, akin to the homology account we advance here, McGregor and colleagues argue that the human capacity for abstract thought co-evolved with the goal-pursuit system, such that worldview ideals are represented as high-level goals that "can be understood in terms of ancient goal-regulation processes that humans share with pigeons and fish" (McGregor, 2006, p. 299).

In contrast to the reactive approach motivation model sketched above, which relates all worldview defense effects to a shared, evolutionarily ancient goal-pursuit architecture, our homology approach highlights the likelihood that truly distinct threat management systems may exist and warrant recognition. According to the reactive approach motivation model, various threats can equivalently kindle goal-impedance anxiety, and hence initiate compensation strategies such as worldview defense. As discussed above, the shared structure common to psychological homologues is indeed likely to cause “bleed” between the activation of related systems, generating somewhat parallel responses to distinct threats. Nevertheless, the distinct strategies implicated in addressing conflicts in highly distinct domains (e.g., mate-acquisition, status-striving, pathogen-avoidance) militates for the existence of distinct, specialized threat management systems branching off of shared pathways.

Hart (this volume) proposes another theoretical integration, a general-purpose “security system” that manages threats of various types via the innate attachment mechanisms that motivate immature members of social species to maintain physical proximity to their caregivers (Bowlby, 1982). Noting that threat-anxiety motivates attachment behavior in children, that proximity to caregivers palliates anxiety, and that political or religious in-groups can function as sources of attachment in adult life (Bowlby, 1982), Hart argues that the attachment architecture is extended to incorporate abstract concepts such as ideological values. On this account, when threatened, adults cleave more fiercely to their cherished ideologies in a manner similar to anxious children cleaving to their caregivers. Space prohibits a detailed treatment of the theoretical relationships between the attachment system and the ancient threat-detection systems others have cited as at the root of worldview defense in humans. Rather, we simply note the thematic harmony between Hart’s co-optation account and the concepts of serial homology and neural recycling advanced here. Hart contends that the “scaffolding” provided by the caregiver attachment system redeploys in modified forms over the lifespan (e.g., romantic attachment, Hazan & Shaver, 1987) and plausibly extends to social groups and even abstract symbols. From our perspective, Hart might well have characterized the ideological attachment system he describes as a serial homologue of the phylogenetically ancient caregiver attachment system. However, in emphasizing the interchangeability of various threats and various compensatory reactions—from heightened group prejudice to seeking comfort food—the security motivation system model arguably obscures the potential existence of discretely specialized threat management homologues.

In perhaps the most sweeping bid to explain all worldview defense effects in terms of a single overarching process, Proulx and colleagues (2012) posit a single "inconsistency compensation" mechanism whose function is to palliate anxious reactions to any sort of emotional, semantic, or perceptual violations of expectations. Although the inconsistency compensation account acknowledges that a vast array of distinct stimuli can engender a broad range of distinct cognitive or behavioral biases, and that both the eliciting stimuli and the form of the biases that are engendered are moderated by individual and cultural differences, all of these complex relationships are attributed to a common prediction error / conflict monitoring mechanism. As in our analysis of the reactive approach motivation and security system models, we laud the effort to integrate disparate theories, but caution investigators not to inadvertently discard important functional and neuropsychological specializations in the pursuit of parsimony. After all, whale fins and bird wings share undeniably similar structure and function—and recognizing these similarities is valuable—but dismissing their differences would disastrously impoverish our understanding of their fascinating functional specializations.

Whereas the reactive approach motivation, security system, and inconsistency compensation models are all highly domain-general in approach, and hence inherently liable to conflate noteworthy specializations between threat management systems, domain-specific threat management theories that purport to explain all of the worldview defense data as mere tokens of "the one true threat system" potentially err by ignoring evidence favoring cousin theories. For example, terror management theorists have sometimes attempted to quell the growing tide of evidence that threats unrelated to death can induce parallel biases by insisting that these effects are indirectly related in some fashion to the death-anxiety-suppression architecture that they have postulated (e.g., Landau, Solomon, Pyszczynski, & Greenberg, 2007). Fortunately, the concept of homology frees threat management researchers not only to admit to the existence of cousin systems, but to welcome the study of such homologues as informative with respect to the distinct structure and functional origins of the system on which they have chosen to focus.

Conclusion

Our objective in this chapter has been to introduce the concept of psychological homology as a promising way of making sense of the sprawling patchwork of threat-and-defense theories and data, much of which is discussed in the four preceding chapters in this volume. We have not engaged with the far more formidable challenge of identifying the genuinely distinct systems, or taxonomizing their derivations from prior structures. Indeed, at the time of writing, there is insufficient evidence to make many of these determinations, as much of the comparative cross-cultural and neurobiological data required have yet to be collected. Hence, we invite investigators to bring these principles to bear in their own work, and, in particular, to craft studies capable of detecting special relationships between subtypes of input threats, output biases, and mediating processing algorithms. Going forward, the concept of homology provides a plausible middle trajectory between the Scylla (heterogeneous, largely disconnected approaches) and Charybdis (unitary, monolithic approaches) of current theoretical options dividing the threat compensation literature.

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Footnotes

[1] Note that serial homology can also describe a scenario in which two derived homologues, both of which have been modified, replace an initial trait (Clark, 2010). The important point for present purposes is not that initial traits persist without modification, but that multiple derived homologues may co-exist within an organism.

[2] The word “adaptive” is often used inconsistently. A trait is biologically adaptive to the extent that it promotes reproductive fitness; social psychologists and clinicians, by contrast, tend to equate “adaptiveness” with states of subjective well-being. However, many adaptive mechanisms are orthogonal to, or even bring about, suffering. For instance, anxiety is adaptive to the extent that it motivates individuals to resolve problems that may interfere with reproductive fitness (Marks & Nesse, 1994). Likewise, the emotion anger is thought to have evolved to motivate punishment to deter future transgression, and thereby (albeit indirectly) to enhance reproductive fitness (Fessler, 2010). In this chapter, we use the term adaptive in the evolutionary sense.

[3] This example is offered solely by way of illustration of a potential “exapted domain” in which disgust might exert coarse influence despite an overt lack of fit with the pathogen-avoidance function disgust evolved for. We are agnostic at present about whether political biases related to disgust would actually be *exaptive* in either the sense of arising without special selection, or in the sense of serendipitously increasing reproductive fitness. If real, such a link might exert a null or even a negative fitness effect.

Table 1. Theoretical perspectives relating threat to ideological adherence

Approaches to Worldview Defense	*Representative Publication*
Coalitional Psychology	Navarrete, Kurzban, Fessler, & Kirkpatrick, 2004
Compensatory Control Theory	Kay, Gaucher, McGregor, & Nash, 2010
Group-based Control Model	Fritsche et al., 2013
Inconsistency Compensation Theory	Proulx, Inzlicht, & Harmon-Jones, 2012
Meaning Maintenance Model	Heine, Proulx, & Vohs, 2006
Reactive Approach Motivation	McGregor, Nash, Mann, & Phills, 2010
Security System Model	Hart, Shaver, & Goldenberg, 2005
System Justification Theory	Jost et al., 2007
Terror Management Theory	Greenberg & Kosloff, 2008
Uncertainty Management Theory	Van den Bos, 2009
Unconscious Vigilance	Holbrook, Sousa, & Hahn-Holbrook, 2011