



Contents lists available at ScienceDirect

Neuroscience and Biobehavioral Reviews

journal homepage: www.elsevier.com/locate/neubiorev



Review

Human threat management systems: Self-protection and disease avoidance

Steven L. Neuberg^{a,*}, Douglas T. Kenrick^a, Mark Schaller^b

^a Department of Psychology, Arizona State University, Tempe, AZ 85287-1104, United States

^b Department of Psychology, University of British Columbia, Vancouver, BC, Canada V6T 1Z4

ARTICLE INFO

Article history:

Received 8 March 2010
 Received in revised form 18 August 2010
 Accepted 18 August 2010

Keywords:

Self-protection
 Disease avoidance
 Threat management
 Precautionary psychology
 Evolutionary psychology
 Domain specificity
 Fear
 Disgust
 Prejudice
 Stigma
 Social cognition
 Motivation
 Error management

ABSTRACT

Humans likely evolved precautionary systems designed to minimize the threats to reproductive fitness posed by highly interdependent ultrasociality. A review of research on the self-protection and disease avoidance systems reveals that each system is functionally distinct and domain-specific: each is attuned to different cues; engages different emotions, inferences, and behavioral inclinations; and is rooted in somewhat different neurobiological substrates. These systems share important features, however. Each system is functionally coherent, in that perceptual, affective, cognitive, and behavioral processes work in concert to reduce fitness costs of potential threats. Each system is biased in a risk-averse manner, erring toward precautionary responses even when available cues only heuristically imply threat. And each system is functionally flexible, being highly sensitive to specific ecological and dispositional cues that signal greater vulnerability to the relevant threat. These features characterize a general template useful for understanding not only the self-protection and disease avoidance systems, but also a broader set of evolved, domain-specific precautionary systems.

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In the second half of the 20th century, cognitive scientists made great progress by thinking of the brain in computational terms. Although the brain is indeed an information-processing device, it is not a mere computer. Rather than being designed by engineers to process information in a dispassionate manner, the human brain has been designed by natural selection to be something of a motivational device to promote adaptive behavioral responses to critical challenges directly related to survival and reproductive fitness. The

result is not only a great number of cognitive and behavioral mechanisms for efficiently and effectively apprehending and interacting with the world, but also a set of predictable information processing errors and biases, including many related to the ways humans perceive and respond to other people.

Evolutionary models of human social cognition explicitly consider the cognitive and affective implications of different fitness-relevant threats faced by ancestral populations; in doing so, these models have been able to generate and parsimoniously explain a wide range of empirical discoveries about the links among motivation, cognition, and behavior.

Consider, for example, the following findings: prejudices against African American men are characterized by fear, whereas prej-

* Corresponding author. Tel.: +1 480 965 7845; fax: +1 480 965 8544.
 E-mail address: steven.neuberg@asu.edu (S.L. Neuberg).

udices against gay men are characterized by physical disgust (Cottrell and Neuberg, 2005). People who feel particularly vulnerable to disease have fewer friends with physical disabilities (Park et al., 2003). When Canadians (especially those who believe that the world is a dangerous place) find themselves suddenly in the dark, they judge Iraqis to be less trustworthy, but no less intelligent (Schaller et al., 2003a). Women are especially ethnocentric and xenophobic during their first trimester of pregnancy, compared to their second or third trimester (Navarrete et al., 2007). And, after seeing photographs that make germs and infections salient, people view themselves as less extraverted and less open to new experiences (Mortensen et al., 2010).

At first blush, these findings seem like a list of interesting, but largely disconnected, curiosities in the realm of social cognition. In fact, however, the implications of these findings are much broader. When viewed within an integrative conceptual context spanning the cognitive, social, and biological sciences, they contribute to a growing scientific literature documenting the existence of two functionally distinct threat management systems, one devoted to self-protection and the other to disease avoidance. We review this literature to draw inferences about the core features of these two systems. In addition, we suggest that these core features also characterize other neurocognitive systems that evolved in response to additional ancestral threats to survival and reproductive fitness.

1. Introduction and overview

From an evolutionary perspective, an organism's ultimate goal is reproductive fitness. For *Homo sapiens*, reproductive fitness has historically been enhanced by success in attaining a recurrent set of "fundamental" behavioral goals that have clear implications for survival and reproduction (e.g., resource acquisition, self-protection, disease avoidance, social affiliation, status, mate acquisition, mate retention, kin-rearing; Kenrick et al., 2010). In keeping with this evolutionary logic, contemporary human psychology is characterized by functionally distinct cognitive and behavioral systems that effectively address these fundamental challenges (Bugental, 2000; Kenrick et al., 2003).

Many of these fundamental goals are fundamentally *social*, in that the attainment of the goal depends necessarily on the presence and actions of other people. Furthermore, even goals that are not necessarily social by definition (e.g., resource-acquisition, self-protection) are more effectively attained within a cooperative social ecology. By promoting the successful accomplishment of fundamental fitness-relevant goals, the suite of adaptations that characterize the highly interdependent, "ultrasocial" form of human group living has also enhanced human reproductive fitness (Brewer, 2001; Campbell, 1982; Richerson and Boyd, 1995).

Although such sociality provides many benefits, it also introduces a set of potential threats. Other people possess the capacity, and often the inclination, to do harm. Mere proximity to others exposes individuals to potential physical attack and contagious disease. When people enter into cooperative alliances with others, they become vulnerable to exploitation by "free-riders" who take group benefits without contributing their fair share. And so on. Because enduring threats such as these have imposed costs on reproductive fitness, evolutionary pressures likely favored not just mechanisms to dispose people toward a life lived in close, interdependent proximity to others, but also cognitive and behavioral mechanisms designed to (a) attune individuals to the potentially-threatening features of other people and, when perceived (b) respond to these features in functional, threat-reducing ways.

Thus, just as ancestral humans evolved sensory, affective, cognitive, and behavioral mechanisms that respond in adaptive ways to fitness-relevant features in the physical ecology (e.g., visual

and olfactory cues that distinguish between edible and poisonous fruits), ancestral humans also evolved sensory, affective, cognitive, and behavioral mechanisms that respond functionally to fitness-relevant features in the *social* ecology. Some of these mechanisms are designed to promote affiliative and/or nurturant behaviors toward specific categories of individuals, such as potential mates or apparent offspring (Kenrick et al., 2001; Lieberman et al., 2007; Park et al., 2008). But other mechanisms are designed to facilitate avoidance of or protection against other specific categories of individuals (i.e., people who, either intentionally or unintentionally, pose some threat to one's reproductive fitness). We focus here on two of these precautionary systems—*self-protection* and *disease avoidance*.

Our review reveals that the self-protection and disease avoidance systems are functionally distinct psychological systems. Each system is characterized by a coordinated suite of mechanisms adaptively attuned to the perception of specific kinds of threat-signaling cues (e.g., angry facial expressions, skin rashes). When perceived, these cues arouse specific kinds of emotional reactions (fear, disgust) and activate specific kinds of cognitive associations into working memory (e.g., inferences about hostile intent, inferences about contamination). Consequently, they motivate specific forms of behavioral response (e.g., escape, avoidance of contact). Moreover, each system is rooted in a somewhat distinct set of physiological structures and neurochemical processes.

An important conclusion is that human threat detection and threat management is defined not by any singular system, but instead by a set of functionally distinct domain-specific systems, each of which was designed by evolutionary processes to respond in particular ways to particular kinds of perceptual cues that connote a particular form of threat. The psychology of threat is most aptly characterized as the evolved *psychologies* of threats (plural).

In addition to the domain-specificity characteristic of evolved precautionary systems (and evolved cognitive systems more generally; Barrett and Kurzban, 2006), our review also emphasizes several other features that the self-protection and disease-avoidance systems have in common. Each system is functionally coherent, in that perceptual, affective, cognitive, and behavioral processes work together to reduce fitness costs of potential threats. Each system is biased in a risk-averse manner, erring toward precautionary responses even when available cues only heuristically (and often wrongly) imply threat. Each system is highly sensitive to fluctuating ecological circumstances, and is more likely to be engaged when environmental cues signal that individuals are temporarily more susceptible to the specific threat. Each system is also sensitive to the perceiver's dispositional perceptions of vulnerability, and is more likely to be engaged among individuals who (for any reason) feel chronically susceptible to the specific threat.

These features are not only characteristic of the self-protection and disease avoidance systems; they are also likely to characterize other evolved, domain-specific precautionary systems as well.

2. The self-protection system

In the United States in 2008, there were over 16,000 murders and over 830,000 aggravated assaults serious enough to come to the attention of law enforcement (Crime in the United States, 2009). Among hunter-gatherer populations who occupy ecologies similar to those within which our ancestors evolved, homicide rates are at least as high (Chagnon, 1988). In addition to threats from individuals within one's group, there are serious threats from other groups, and violent intergroup conflict appears to have been common in ancestral populations of humans and other primates (Haas, 1990; Schaller and Neuberg, 2008). In short, the threat of intentional physical harm at the hands of conspecifics has been a recurrent feature of our evolutionary landscape. As a result, it seems likely that there

evolved a precautionary self-protection system that (a) is attuned to detect features in others that connote the possibility of such intentional harm, and (b) responds to the perception of those features with the activation of affective and cognitive responses that facilitate escape from or removal of the implied threat.

What social cues connote the potential for intentional harm? Several kinds of cues are likely to have reliably predicted the threat of violence in ancestral times. Physical aggression is often preceded by anger, which itself is typically accompanied by readily identified facial expressions and nonverbal postures (e.g., Ekman and Friesen, 1975; Zebrowitz et al., 2010). The perception of angry facial expressions thus heuristically implies an impending threat to one's physical safety. Consequently, people are very quick to detect and identify angry faces in their perceptual environment (Becker et al., 2007; Fox et al., 2000; Schupp et al., 2004).

The physical threat implication of an angry facial expression is greater when expressed by individuals who have the more general inclination and ability to do harm. Young men and women have historically differed both in their capacity to do physical harm and in their tendencies to do so. Men are especially likely to be, and to have been, perpetrators of interpersonal violence (e.g., Daly and Wilson, 1994). This sex difference is not peculiar to humans. Intergroup aggression, especially by and against males, is also a significant feature of primate species most closely related to humans (Carpenter, 1974; Cheney, 1986; Goodall, 1986; Wilson and Wrangham, 2003).

One implication of this sex difference is an adaptive (if imperfect) bias toward detecting anger more readily in the faces of men (compared to faces of women). Indeed, perceivers more rapidly and accurately identify male faces as angry; similarly, the perception of an angry facial expression facilitates the identification of that face as male (Becker et al., 2007; Zebrowitz et al., 2010).

Not all men are equally likely to pose a threat. Given the long history of intergroup conflict in ancestral populations, members of coalitional *outgroups* are especially likely to be viewed as potential threats to physical safety. One implication of this is that, just as it is especially easy to acquire and maintain a fearful response to non-social objects that posed significant threats throughout humans' evolutionary history (e.g., snakes; Öhman and Mineka, 2001), it is also especially easy to acquire and maintain a fearful response to people who belong to an ecologically meaningful outgroup. Consistent with this hypothesis, non-Black individuals in the United States are especially slow to unlearn fearful responses to the faces of Black strangers (Olsson et al., 2005). Moreover, this effect appears to be specific to male faces (Navarrete et al., 2009).

An additional recent line of research reveals unique cognitive responses to faces that are simultaneously angry, male, and outgroup. As context, there have been many studies demonstrating a cross-race recognition bias, such that White perceivers are much more adept at accurately identifying previously-encountered White faces than Black faces (e.g., Anthony et al., 1992; Chance and Goldstein, 1996). Recent research reveals, however, that this classic effect entirely disappears, and even reverses, when perceiving angry faces. Consistent with the rationale that there are especially profound threats implied by angry male outgroup members, White individuals appear to be especially likely to encode identifying information about angry Black male faces—with the consequence that White perceivers are sometimes even *better* at recognizing angry Black male faces than angry White male faces (Ackerman et al., 2006).

This illustrative set of findings suggests the operation of an adaptive self-protection system specifically attuned to perceive potential physical safety threats in the immediate environment. For such a system to adequately provide fitness-relevant benefits, however, it must not only perceive threats but also trigger an integrated set of functionally-relevant responses – emotions, inferences, and actions – that help to mitigate the apparent threat.

Emotions are a core feature of any precautionary system; they alert individuals to circumstances that threaten important goals and they coordinate cognitive and behavioral reactions so the organism might respond more effectively to the threat (e.g., Carver and Scheier, 1990; Cosmides and Tooby, 2000; Ekman, 1999; Nesse, 1990; Plutchik, 1980, 2003; Simon, 1967; Tooby and Cosmides, 1990). One influential model, widely accepted by psychologists for several decades, presumed that all emotions are physiologically interchangeable (Schachter and Singer, 1962). This viewpoint was associated with a more general tendency for psychologists to conceptualize cognition and emotion in domain-general terms. But several decades of research have challenged that view (Kenrick and Shiota, 2008; Sherry and Schacter, 1987). Instead, emotions are functionally specific: different emotions are evoked by different events and are associated with different, functionally specific responses (e.g., Frijda, 1986; Izard, 1991; Keltner et al., 2006; Plutchik, 1980; Roseman et al., 1994; Tomkins, 1963). Threats to physical safety not only elicit a negative (rather than a positive) affective response, they elicit a very specific form of negative affective response: fear (not disgust, not sadness, not pity). This very specific affective response is associated with the activation of specific kinds of cognitions into working memory (e.g., cognitions connoting aggression and intentional harm), and typically encourages a very specific form of action: escape.

Consistent with this analysis, the specific affective response (fear) associated with the self-protection system is diagnostic of a specific form of prejudice directed toward individuals who trigger the system (Schaller and Neuberg, 2008). More generally, recent research reveals that individuals and groups who are perceived to pose qualitatively different kinds of threats also evoke qualitatively different emotions that are associated with distinctly different forms of prejudice (Cottrell and Neuberg, 2005). Groups that trigger the self-protection system (e.g., for example, African Americans or Arabs, as perceived by European American perceivers) elicit a pattern of emotional reactions characterized by fear, whereas other groups (e.g., gay men) elicit emotional reactions that, while just as highly negative, are not characterized by fear at all, but are instead characterized by different emotions (and different behavioral tendencies as well). This result challenges a long tradition of research within the social sciences. Historically, social psychologists, political scientists, and sociologists have conceptualized prejudice very broadly as a “negative evaluation” of a group and its members. That perspective now appears simplistic. An accurate understanding of the psychology of prejudices (plural) requires attention to the specific threat that is perceived to be posed by any group, and the specific emotional reaction that is triggered in response.

Flight may be the predominant behavioral response to fear-inducing threats to one's physical being. Distancing oneself from the threat, however, is not always possible. An individual may be cornered, may anticipate being overtaken while fleeing, or may be compelled to defend kin or group mates unable themselves to escape the threat. In cases of perceived imminent and severe safety threat, marshalling one's resources to take the fight to the aggressor may become the higher-payoff response option (Blanchard et al., 2011; Blanchard et al., 2001; Eilam et al., 2011; Parker, 1974; Ydenberg and Dill, 1986). For instance, in one set of experiments, research participants believing Black men to be dangerous (relative to White men) exhibited opposing cognitive and behavioral responses to photos of Black men, depending on their immediate context: participants for whom cues to easy escape were made salient (e.g., when the study was administered in a large, outside field) reacted to Black male faces with increased cognitive accessibility of “flight” thoughts and distancing behaviors. In contrast, participants for whom escape appeared impossible (e.g., when the study was administered in a small, closed-in laboratory room)

reacted to these same faces with increased cognitive accessibility of “fight” thoughts and approach behaviors (Cesario et al., 2010).

Under some circumstances, defensive attack may also become a likely strategy of coalitions for addressing aggressive threats from others: by marshalling coalitional resources in the face of a physical safety threat, one may turn a position of relative weakness to a position of equality or strength, thereby increasing the payoff of defensive attack. Indeed, human history is replete with examples of intergroup conflict driven by coalition-supported anticipatory attack against potential aggressors (e.g., Ferguson, 1984; Haas, 1990).

Self-protection is adaptive, but it can be costly as well. Caloric resources are consumed by emotional, cognitive, and behavioral responses to perceived threats. Moreover, to the extent that an organism is actively engaged in self-protective behavior (e.g., escape), the satisfaction of other fitness-relevant goals (e.g., resource acquisition, mate-retention, kin-rearing) may be delayed, or even denied. Because humans have multiple goals that must be accomplished, and limited resources with which to do so, it would be functionally disastrous for any threat management system to be actively engaged at all times. Instead, threat management systems evolved to be “functionally flexible” (Schaller et al., 2007): they are less likely to be engaged under circumstances in which the baseline likelihood of threat is minimal, and most likely to be engaged under circumstances in which the likelihood of threat is greatest.

Thus, one would expect the self-protection system to be engaged primarily under conditions in which individuals perceive themselves to be especially vulnerable to physical harm. This subjective sense of vulnerability may be elicited by the perception of danger-connoting features in other people (e.g., angry facial expressions; Ackerman et al., 2006). This subjective sense of vulnerability may also be elicited by specific features in the local ecological context. For example, because of humans' relatively poor night vision and ancestral susceptibility to nocturnal predators, ambient darkness is a potent cue connoting enhanced vulnerability to physical harm. Therefore, the self-protection system is likely to be activated especially strongly under conditions of ambient darkness. Consistent with this logic, sudden noises produce especially exaggerated fear responses in people when they are in the dark (Grillon et al., 1997).

Other temporary events within one's immediate environment may also activate the self-protection system, with predictable consequences for social cognition. In one experiment, White participants watched a brief excerpt from a movie (*The Silence of the Lambs*) that was designed to elicit self-protection concerns, and then attempted to identify emotional expressions on the faces of other individuals (Maner et al., 2005). Results revealed that, compared to control participants, when the self-protection system was activated participants erroneously “saw” anger in the neutrally expressive faces of Black men—but not in the neutrally expressive faces of Black women or White men or women. Moreover, this effect was specific to the misperception of anger (i.e., activation of the self-protection system did not enhance perceptions of other negative emotions, such as fear, on the faces of the Black men). The highly focused functional specificity of these emotion-recognition errors suggests a system designed adaptively to err in the direction of precaution (cf. Haselton and Nettle, 2006; Nesse, 2005).

The specific perceptual, emotional, cognitive, and behavioral phenomena characterizing the self-protection system are also especially likely to be observed among people who chronically perceive themselves to be vulnerable to physical harm. Consistent with this analysis is evidence that people who are dispositionally anxious are especially likely to have their attention held by angry faces (Fox et al., 2001).

Furthermore, dispositional variables may interact with temporary contextual variables to produce exaggerated self-protection biases. For example, whereas some evidence indicates that ambi-

ent darkness leads people to be more prejudiced against ethnic outgroups, further evidence reveals that this effect holds primarily among individuals who chronically worry about their safety. Specifically, among individuals who perceive the world to be a dangerous place (but not among individuals who perceive the world to be benign), ambient darkness is especially likely to activate into working memory threat-connoting stereotypes of ethnic outgroups (Schaller et al., 2003a,b). Importantly, this effect is specific to the activation of stereotypic traits connoting the threat of intentional harm (e.g., *aggressive*), but does not obtain for stereotypic traits that are equally negative but threat-irrelevant (e.g., *ignorant*). Such a finding, again, reveals the functional specificity of the self-protection system.

We have briefly reviewed evidence suggesting the presence of a functional psychological system focused on protecting the self from physical harm. This psychological system necessarily exists within the context of a neurobiological substrate, and is mediated at least partially by specific neuroendocrinological processes. Thus far, there is very little research identifying specific anatomical structures and neurochemical processes that are implicated in the specific findings we have reviewed—although some clues are suggested by existing research on neural systems pertaining more generally to threat-identification (which implicates the amygdala; e.g., Johansen et al., 2010; LeDoux, 2000) and motor-preparation (which implicates the primary motor cortex and dorsal basal ganglia; e.g., Butler et al., 2007). Moreover, other research focusing on the precautionary processing of potential, less immediate threats implicate the cingulate cortex and insula (Fiddick, 2011), and research by Woody and Szechtman (2011) on a more general security motivation system suggests a neurobiological-circuit model consisting of a cascade of cortico-striato-pallido-thalamo-cortical loops with brainstem-mediated negative feedback. That said, much future work is needed to better articulate the linkages between the specific psychological phenomena reviewed here and their underlying neurophysiology.

3. The disease avoidance system

Other people not only pose direct threats to human survival via their potential for violence, but also pose indirect threats via their role in transmitting disease. The World Health Organization (2004) estimates that 15 million humans die per year from infectious diseases, predominantly involving those transmitted from humans to humans (e.g., influenza, tuberculosis, HIV/AIDS). These numbers pale, however, compared to the impact of a number of pandemics over the past thousand years. In the 1300s, plague is estimated to have killed between 25% and 50% of the populations of Europe, Asia, and Africa (Gottfried, 1983). And in the 1500s, European travelers introduced exotic diseases (e.g., smallpox, measles, and typhus) into the Americas that, by some estimates, killed over 75% of the population of Mexico (Dobson and Carter, 1996). As these percentages indicate, infectious diseases can place enormously strong selection pressures on human populations.

Nor is the threat of infection from communicable pathogens a new challenge for humans. Although the magnitude of this threat is likely to have increased with the advent of large group settlements and animal domestication around 11,000 years ago, many pathogens are of considerable antiquity and are likely to have imposed selection pressures on ancestral populations for tens of thousands of years (Ewald, 1994; Wolfe et al., 2007). One result has been the evolution of a highly sophisticated immune system. Another result has been the evolution of a *behavioral immune system*—a system designed not to fight pathogens post-infection but rather to avoid infection in the first place (Schaller and Duncan, 2007; Schaller and Park, in press).

The existence of an adaptive disease avoidance system is implicated by a diverse body of evidence on the behavior of humans as well as other animal species. For instance, just as sheep selectively avoid grazing in areas contaminated with their own fecal waste (Cooper et al., 2000), humans are disgusted by, and behaviorally reject, foods that are potentially contaminated by parasites (Rozin et al., 1986). Aversive behavioral responses are also shown toward conspecifics that, based on sensory cues, appear to pose some threat of pathogen infection. When animals exhibit even subtle symptoms of disease, they tend to be avoided and rejected by their fellow – to name a few – spiny lobsters, chimpanzees, mice, and bullfrog tadpoles (e.g., Behringer et al., 2006; Goodall, 1986; Kavaliers et al., 2003; Kiesecker et al., 1999). As the review below illustrates, this is the case for humans as well.

The first step toward mitigating a threat is to identify it. The human disease avoidance system should thus be specially attuned to individuals exhibiting perceptible cues that connote possible infection. Although most disease-causing pathogens are not visible to the human eye, their effects on the human body often manifest in visible cues, such as morphological changes from the physical norm (e.g., rashes, skin lesions) and unusual, non-normative actions (e.g., vomiting, diarrhea, ill-coordinated movements). It follows that humans are likely to be highly vigilant for such cues.

Inferring pathogen threat from such cues will necessarily be an imperfect process. There is great variability in the visually accessible manifestations of pathogens: different pathogens produce different symptoms, different individuals respond differently to the same kind of parasitic infection, and pathogen species themselves evolve at an exceptionally rapid pace (Ewald, 1994). Hence, although a disease avoidance system needs to be focused on a constrained class of cues, it cannot be calibrated too tightly on the low-level specifics of any of them lest it miss somewhat dissimilar, albeit diagnostic, signals of pathogen presence. A system designed to respond to a more crudely-defined range of cues is likely to have been more adaptive (Kurzban and Leary, 2001; Schaller and Duncan, 2007; Zebrowitz and Montepare, 2006). This has an important consequence: just as the physiological immune system sometimes misidentifies harmless “invaders” as pathogenic threats, the behavioral immune system sometimes misidentifies objectively harmless features of others as implying the threat of infectious disease.

This disease avoidance system is thus likely to be responsive to a wide range of unusual appearances and behaviors. This is the case. For instance, people are attentionally sensitive to disfigured faces: such faces “hold” attention (Ackerman et al., 2009). Other studies have identified a variety of additional physical features that serve as cues connoting the threat of disease; these include obesity, physical disability, and the facial manifestations of aging (Duncan and Schaller, 2009; Park et al., 2003, 2007). The emerging implication is that the disease avoidance system is perceptually sensitive to a broad set of anomalies – deviations from species-typical norms – in physical morphology and motor behavior. Other research suggests that the perception of culturally anomalous behavior – the tendency to act in ways that violate local cultural rituals and norms – may also trigger the disease-avoidance system (Faulkner et al., 2004).

As with the self-protection system, the disease avoidance system can only serve its adaptive ends if it engages an integrated suite of emotional and cognitive responses that promote the functionally adaptive behavior of physical avoidance. In contrast to the self-protection system (which is characterized by a fearful emotional response) the disease-avoidance system is characterized by a rather different emotion: disgust. There is a growing body of evidence indicating a functional linkage between disgust and disease avoidance (for a comprehensive review, see Oaten et al., 2009). Disgust is triggered by the visual perception of skin lesions, runny

noses, and other obvious symptoms of pathogenic infection (Curtis et al., 2004; Curtis and Biran, 2001). Disgust is also more likely to be elicited by the categories of people who, historically, were more likely to carry exotic pathogens, which pose a more acute threat to fitness (e.g., strangers, foreigners; Case et al., 2006; Curtis et al., 2004; Stevenson and Repacholi, 2005), or who are stereotypically associated with specific kinds of infectious diseases (e.g., gay men; Cottrell and Neuberg, 2005). These psychological reactions have implications for public policy (e.g., individuals who feel disgusted by gay men also tend to oppose gay rights; Cottrell et al., 2010).

As one functional consequence of disgust and its associated cognitive associations, people demean and behaviorally distance themselves from other individuals who possess diagnostic cues of contagious illness (e.g., leprosy; Plageron, 2005). This tendency is greater when the disease is perceived to be more highly contagious (Crandall and Moriarty, 1995). Moreover, consistent with the finding that the disease avoidance system responds to a broad range of superficial cues, people show a similar tendency to behaviorally avoid individuals who are characterized by objectively non-contagious physical anomalies (e.g., physical disabilities; Park et al., 2003).

Just as fear-driven self-protection may, under some circumstances, call for defensive attack, disgust-driven disease-avoidance may, under some circumstances, call for the proactive strategy of approaching a presumed contaminant and destroying it. Disease-minded, precautionary homeowners may aggressively seek, with Lysol and scrub brush in hand, potential sources of germs and molds throughout the home; individuals and coalitions may aggressively seek, lethal weapons in hand, members of other groups perceived as contaminating—for example, ethnic and religious outgroups labeled as “cockroaches” or “vermin.” We suspect this behavioral strategy becomes more likely as those confronted by the threat perceive themselves to have a significant upper-hand—when they believe they can effectively remove the contaminant without becoming infected in the process.

Just as self-protective responses are both adaptive and metabolically costly, disease avoidant responses are also both adaptive and metabolically costly. Therefore, the principle of functional flexibility also applies to the disease avoidance system. Disease-avoidant psychological responses are likely to be observed particularly strongly under circumstances in which individuals perceive themselves to be especially vulnerable to infection. This adaptive flexibility is evident in context-contingent variability in the tendency for prototypically disgusting stimuli to actually elicit disgust. For example, women show more exaggerated disgust responses during the first trimester of pregnancy—a time in which their body’s natural immunological defenses are temporarily suppressed (Fessler et al., 2005; see Hahn-Holbrook et al., 2011, and Lienard, 2011, for reviews of these and related findings). Perceived vulnerability to disease also influences behavioral responses to social cues that heuristically connote pathogen infection. For instance, people who feel more chronically vulnerable to disease are relatively less likely to have friends and acquaintances with physical disabilities (Park et al., 2003). And there is now a large body of evidence documenting more exaggerated disease-avoidant cognitive biases under conditions in which individuals are (or merely perceive themselves to be) more vulnerable to infection. For example, although it is common for aversive cognitions to be automatically activated into working memory upon the perception of morphologically anomalous individuals, this effect is especially pronounced among perceivers for whom the potential threat of infectious diseases is especially salient—a set of findings with implications for prejudices against people who are disabled, obese, or elderly (Duncan and Schaller, 2009; Park et al., 2003, 2007).

Another example of functional flexibility builds on the history of intergroup contact, which has historically been associated with

increased exposure to novel pathogens (Diamond, 1997). Consistent with this historical background and its implications for the disease avoidance system, xenophobic reactions to foreign peoples are especially pronounced under conditions in which perceivers feel especially vulnerable to infection (Faulkner et al., 2004). Similarly, among pregnant women, ethnocentric and xenophobic attitudes are exaggerated during the first trimester of pregnancy, when the body is temporarily immunosuppressed (Navarrete et al., 2007).

Several new lines of inquiry reveal additional implications of the disease avoidance system. One set of studies reveals implications for individuals' self-concept and general social disposition: when the threat of infectious disease is made temporarily salient, people subsequently view themselves as less extraverted and as less open to new experiences, and also exhibit more avoidant motor movements in response to social stimuli (Mortensen et al., 2010). Each of these effects serves to reduce an individual's likelihood of entering into novel, and thus potentially pathogenic, social interactions.

The disease avoidance system may also help account for a wide-ranging set of cross-cultural differences in human behavior. Worldwide regional differences in pathogen prevalence are associated with different norms for food preparation, such that people who live in pathogen-dense environments habitually use more culinary spices—which just happen to be natural antibiotics (Sherman and Billing, 1999). Regional variability in pathogen prevalence also predicts worldwide differences in basic dispositional tendencies such as extraversion and openness to experience (within ecologies characterized by high pathogen prevalence, people report lower levels of extraversion and openness; Schaller and Murray, 2008), as well as in cultural value systems (within ecologies characterized by high pathogen prevalence, cultures are more collectivistic; Fincher et al., 2008). The emerging body of evidence is consistent with a conclusion that these different societal patterns of cognition and behavior represent adaptive responses to the different levels of threat posed by pathogens in the local ecology (for a comprehensive review, see Schaller and Murray, *in press*).

There has also been recent speculation that, when activated, the disease avoidance system may have causal implications for actual immunological responses to pathogenic intruders (Rubio-Godoy et al., 2007; Oaten et al., 2009). Consistent with this speculation is recent evidence that the mere visual perception of other people's disease symptoms causes perceivers' white blood cells to respond more aggressively to bacterial infection by producing greater quantities of the pro-inflammatory cytokine interleukin-6 (Schaller et al., 2010).

This new line of inquiry suggests that there are important physiological linkages between two functionally related systems—one designed for disease avoidance and the other for disease elimination. Oaten et al. (2009) review empirical findings suggesting that the human insular cortex is involved in the processing of disgust-eliciting stimuli, in the visceral sensation of nausea, and in the conditioning of the immune system's eliminative response to pathogens. This evidence suggests an organized physiological substrate that facilitates not only the identification of disease-relevant cues but also facilitates a coordinated suite of functional responses (i.e., expulsion facilitated by nausea, destruction via immune system reactions).

Other lines of research have identified additional physiological substrates of the disease avoidance system. For instance, many animals employ olfactory cues to identify and remember infected conspecifics, and to facilitate avoidance. Some of the roots of these precautionary processes have been identified at genetic and neurochemical levels of analysis, in the form of specific genes coding for neuropeptide, oxytocin, and estrogenic mechanisms (Kavaliers et al., 2005). Further research is likely to reveal a more complete portrait of the structural and neurochemical foundations of the

disease avoidance system, and of its linkages to other systems designed for anti-pathogen defense.

4. Features common to the self-protection and disease-avoidance systems

The review above suggests that the self-protection and disease-avoidance systems share (at least) four common features:

(1) *Threat-management systems are domain-specific and focused.* Adaptive problems require solutions that are responsive to the specific nature of those problems. Evolved threat-management systems are characterized by this kind of specificity. The self-protection system focuses attention on specific kinds of sensory cues in the social ecology (e.g., angry facial expressions); the disease-avoidance system focuses attention on a rather different set of specific sensory cues (e.g., facial disfigurements). The two systems are associated with different emotional responses (fear versus disgust; Cottrell and Neuberg, 2005), and they also activate somewhat distinct kinds of knowledge structures and cognitive associations into working memory (Park et al., 2007; Schaller et al., 2003a,b). The affiliated neurobiology of the two systems differ as well (LeDoux, 2000; Oaten et al., 2009).

This kind of functional specificity is evident in the other animal species as well. Whereas humans are a highly visual species (and so are especially attentive to visual cues connoting threat), many nonhuman animals rely substantially on olfactory cues connoting threat. Different olfactory cues are typically used to identify predators (who pose a threat of intentional harm) and parasitized conspecifics (who pose a threat of disease transmission). Different neurobiological systems – and different genomic correlates – are associated with the recognition of, and behavioral responses to, these different olfactory cues (Kavaliers et al., 2005).

This principle of domain-specificity is consistent with a much broader range of findings about humans and other animals. Birds employ distinct neuropsychological systems for learning and remembering information about poisonous foods, the song of their species, and the location of their food caches. Similarly, humans employ distinct neuropsychological systems for learning and remembering words, faces, and nausea-inducing foods (e.g., Sherry and Schacter, 1987). Research on associative learning of nausea reveals that these associations depend on an organism's evolutionary history and typical ecology. Rats, which have relatively poor vision and rely on smell and taste to find food at night, condition nausea to novel tastes but not to novel visual stimuli (Garcia and Koelling, 1966). Quail, in contrast, have excellent vision and rely on visual cues in food choice, and they condition nausea to visual cues but not to taste (Wilcoxon et al., 1971). Within the cognitive and behavioral sciences, a large body of literature now implies the existence of similarly domain-specific systems that promote adaptive responses to a wide variety of specific fitness-relevant threats, and to a wide variety of specific fitness-relevant opportunities as well (Ackerman and Kenrick, 2009; Barrett and Kurzban, 2006; Kurzban and Aktipis, 2007; Pinker, 1997; Schaller et al., 2007; Tooby and Cosmides, 1992).

(2) *Threat-management systems promote coordinated cascades of adaptive responses.* Perceptual, affective, cognitive, and behavioral processes work together in an organized, coherent manner to reduce the fitness costs of potential threats. Once engaged by cues implying a physical safety threat, the self-protection system focuses attentional and cognitive resources on people who are stereotypically judged to be especially dangerous (Ackerman et al., 2006); it activates danger-connoting cognitive associations and guides inferential processing in such a way that those individuals are indeed judged to be especially dangerous (Maner et al., 2005; Schaller et al., 2003b); and it elicits an emotion – fear – that typically

facilitates behavioral escape from the perceived danger (Cottrell and Neuberg, 2005). Similarly, once engaged by cues implying a pathogen threat, the disease avoidance system focuses attentional resources on individuals characterized by features implying increased infection risk (Ackerman et al., 2009); it activates disease-connoting cognitive associations and guides inferential processing in such a way that those individuals are judged more harshly (Navarrete et al., 2007; Park et al., 2007); and it elicits an emotion – disgust – that typically facilitates behavioral avoidance of contact with these perceived threats (Curtis et al., 2004).

Indeed, recent evidence on disease avoidance suggests that evolved threat management systems not only promote adaptive consequences at the level of individual behavior (i.e., the inhibition of approach-oriented motor movements; Mortensen et al., 2010), but at additional levels of analysis as well. These consequences may range from cellular-level responses (e.g., the immunological phenomenon reported by Schaller et al., 2010) to population-level cultural strategies (Schaller and Murray, in press). All these consequences reduce individual susceptibility to perceived threats. The breadth of these adaptive consequences illustrates a fundamental point about both the self-protection and disease avoidance systems: their adaptive design integrates multiple distinct processes that work in a coordinated fashion to respond functionally to the focal threat, and thus to enhance reproductive fitness.

(3) *Because threat cues are not perfectly diagnostic, errors of interpretation are biased toward inferring threat.* Effectively managing threat requires that a perceived stimulus (e.g., a noxious smell, an angry facial expression) be quickly translated into a fitness-relevant inference (e.g., a threat to health, a threat to physical safety). Even when cues are reasonably diagnostic – rotting food contaminated by dangerous pathogens indeed often smells bad, and men who are about to physically attack often do look angry – this translation process is inherently imperfect. Malodorous foods are sometimes safe (and even healthy), and angry-looking men are sometimes merely posing. This signal detection problem inevitably produces errors, but the errors people make are not random. Instead, they tend to be predictably biased in a direction that, on average, is associated with reduced costs to reproductive fitness (Haselton and Nettle, 2006; Nesse, 2005). In the domains of threat-detection, these biases are risk-averse. It may be costly to mistakenly infer that a perfectly safe and nutritious food is contaminated, but the costs are typically small. In contrast, it can be very costly indeed to mistakenly infer that a pathogen-rife food is safe. Whereas the former error reduces the opportunity to acquire nutrition (an opportunity that will, usually, avail itself again), the latter error may cost one's life (and we get only one of these). In the long run, it has proven to be evolutionarily adaptive to err on the side of avoiding the latter kind of error, a bias that inevitably results in many errors of the former kind. This adaptive bias in error-management is characteristic of both the self-protection and disease avoidance system.

We have seen, for instance, that even when male outgroup members display objectively benign facial expressions, activation of the self-protection system causes perceivers to erroneously perceive anger in those facial expressions (Maner et al., 2005). And when the disease avoidance system is activated, people erroneously infer the threat of disease from individuals who are objectively healthy, but who just happen to have morphologically anomalous characteristics (e.g., benign facial birthmarks; Schaller and Duncan, 2007).

Such biases are sensible in the context of the ancestrally “deep” logic of evolutionary theory (Kenrick et al., 2009). Nonetheless, these biases can cause problems in the here-and-now. Recent work, for instance, suggests that an extreme lowering of thresholds for identifying cues and events as threats, or a difficulty “turning off” precautionary systems, may contribute to psychological disorders

such as post-traumatic stress disorder (linked to the self-protection system), some forms of obsessive–compulsive disorder (e.g., hand-washing, linked to the disease-avoidance system, and post-partum obsessive–compulsive disorder, linked to aspects of the kin-care system), social anxiety disorder (linked to the social affiliation system), and the like (e.g., Boyer and Lienard, 2008; Eilam et al., 2011; Hahn-Holbrook et al., 2011; Szechtman and Woody, 2004; Woody and Szechtman, 2011).

(4) *Threat-management systems are sensitive to contexts that connote enhanced vulnerabilities to particular threats.* For most psychological adaptations, there are no “hardwired” connections that necessarily and inevitably link a threat-connoting stimulus to a threat-managing response. Moreover, there are costs as well as benefits associated with any threat-managing response. Consequently, although threat-managing responses have the potential to be triggered by the sensory perception of a threat-connoting stimulus, that potential is not always realized. Threat-managing emotions, cognitions, and behaviors emerge more reliably and more strongly when circumstances suggest they are needed.

Thus, for instance, although the perception of male outgroup members is likely to activate danger-connoting cognitions into working memory, these cognitions are especially likely to be activated into working memory under ecological circumstances that make perceivers feel vulnerable to physical harm (e.g., ambient darkness; Schaller et al., 2003a). And, although disease-avoidant cognitions are likely to be produced upon the perception of people who appear to pose some threat of infection, these cognitions are especially likely to be produced under circumstances that make perceivers feel especially vulnerable to disease transmission (Faulkner et al., 2004; Park et al., 2007).

Threat-management systems are not only sensitive to vulnerability-connoting cues in the immediate ecological context, but are also sensitive to perceiver's chronic dispositional beliefs about specific forms of vulnerability. Consequently, these threat-managing responses are more readily engaged in some individuals than in others. Snakes and angry faces are likely to command attention, but they are especially likely to do so among people who are chronically anxious (Fox et al., 2001; Öhman et al., 2001). Similarly, people who chronically view the world as a dangerous place are especially likely to perceive outgroup men as posing some threat of intentional harm (Schaller et al., 2003b; Maner et al., 2005), and people who chronically worry about disease transmission are especially likely to respond aversively to people who are disabled, obese, or foreign (Faulkner et al., 2004; Park et al., 2003, 2007).

The evolutionary perspective predicts that humans should develop precautionary systems to address threats to physical safety, health, and other domains closely tied to reproductive fitness (e.g., Boyer and Bergstrom, 2011; Neuberg et al., 2010). Where, however, do individual differences in vulnerability, such as those discussed above, come from? Genetic differences in thresholds for identifying or experiencing events as threats clearly play a role, as do previous confrontations with threatening stimuli. How such confrontations translate into threat-identification threshold changes has been explored in the non-human animal literature (see Kavaliers and Choleris, 2001, for a review); these issues remain, however, an open question when applied to humans. Barely escaping an attack may sensitize an individual to cues of potential future attacks, and may lower the threshold for interpreting threat-associated cues – for example, the sound of another's approach – as an indicator of impending attack. In contrast, having survived a previous attack, or having learned that the cues associated with impending attacks are only minimally diagnostic, one may habituate to these cues and raise one's threshold for identifying others' approaches as threatening. The ways in which previous threat con-

frontations, in conjunction with genetic predispositions, work to alter how humans set threat-identification thresholds would seem a ripe area of research.

In sum, threat-management systems are especially likely to be activated among those individuals confronting threat-relevant ecological contexts or those with dispositional vulnerabilities to the particular threats. Such findings speak to the functional nature of these systems.

5. Final comments

In considering the adaptive nature of human threat management, we have focused on the self-protective and disease-avoidance systems. Threats to physical safety and health pose a significant challenge to reproductive fitness, and these systems evolved to manage these threats. Our review has revealed that these systems are functionally distinct: they are sensitive to different signaling cues, they come into play under different ecological and intrapersonal circumstances, they respond to perceived threats with distinct patterns of affect, cognition, and behavior, and they are linked to somewhat distinct neurobiological substrates and systems.

Our review has also revealed that these systems share several foundational features. Each is functionally coherent: cognitive, affective, and behavioral processes work in concert to reduce the fitness costs of potential threats. Each system is risk-averse—responsive to cues that merely heuristically imply threat and biased toward generating precautionary actions. Each system is highly sensitive to changes in the ecological context, and is especially likely to be engaged when environmental cues signal enhanced vulnerability to the specific relevant threat. And each system is sensitive to the perceiver's own dispositional sense of vulnerability, and is especially likely to be engaged in those who feel chronically susceptible to the specific, relevant threat.

Of course, self-protection and disease avoidance are only two of the long-recurring challenges faced by humans. Reproductive fitness also required that people solve problems associated with acquiring resources, forming productive and tangibly rewarding social relationships and coalitions, gaining status, acquiring and retaining mates, and rearing and protecting kin (Kenrick et al., 2010). Given the highly interdependent nature of human sociality, others have the ability (and sometimes the inclination) to threaten these goals as well—to threaten one's status within a social hierarchy, one's attractiveness as a potential mate, the payoff in resources from one's efforts, etc. To the extent such threats imposed selective pressures on ancestral populations, they too are likely to have resulted in the evolution of psychological mechanisms designed to mitigate and manage the specific threat. Indeed, there is a growing body of theory and evidence attesting to the existence of these additional kinds of functionally distinct threat-management systems, and of their implications for human cognition and behavior (e.g., Buss and Duntley, 2008; Kurzban and Leary, 2001; Cosmides and Tooby, 2005).

We expect that these systems, too, will be characterized by the adaptive features discussed here; these features thus provide a more general template for the deduction of many specific hypotheses pertaining to each threat-management system. Consider, for instance, the expectation of domain-specificity. The hypothesized domain-specificity of one of these systems – designed to facilitate the detection of people who “cheat” within the context of social exchange relationships – has received considerable research attention (Cosmides and Tooby, 2005), but the same is not yet true of research on other hypothesized threat-management mechanisms (e.g., Buss and Duntley, 2008). Similarly, consider the feature

of functional flexibility and the tendency for threat-management systems to be sensitive to the extent to which perceivers feel vulnerable to particular threats. Whereas this principle has guided much research on self-protection and disease avoidance, its implications have not yet been explored much in the context of other threat-management systems. The same is true regarding the error-management biases characterizing precautionary systems (Haselton and Nettle, 2006; Nesse, 2005). The implications of these biases – in which perceivers treat objectively benign objects as though they are threats – have guided much recent research on self-protection and disease-avoidance systems, as seen here, but generally remain to be studied with respect to other threat-management systems. The general framework outlined here is thus likely to prove valuable as researchers seek to understand the psychology of how people manage the other fundamental threats they encounter, as well.

Human information processing is often decried as being hopelessly irrational. The research reviewed here suggests, instead, that the mind serves a deeper form of rationality. Designed by natural selection to enhance reproductive fitness by addressing the fundamental challenges that have long confronted our ancestors, threat-management systems move contemporary individuals toward the kinds of functionally-focused decisions and actions that address their pressing challenges of the moment.

Acknowledgements

The contributions of Steven L. Neuberg and Douglas T. Kenrick were supported by grants from the National Institute of Mental Health (MH064734) and National Science Foundation (#0642873); the contributions of Mark Schaller were supported by the Social Sciences and Humanities Research Council of Canada.

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