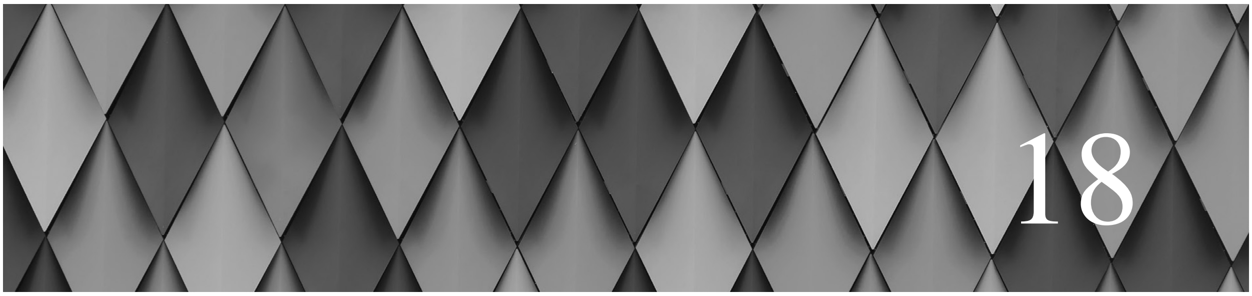

18

Threat of Infectious Disease

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Management of infectious disease represents one of the most fundamental selection pressures humans have confronted over their evolutionary history (Ackerman et al., 2012). To our ancestors, parasites and pathogens were ever-present and significant dangers (Gangestad and Buss, 1993; Low, 1990), with the impact of these infectious agents extending beyond hominids, potentially to the origins of sexual reproduction itself (Brockhurst, 2011). Even in contemporary society, contracting infectious disease is an everyday possibility. Colds and flus are some of the leading causes of workplace absenteeism (and general discomfort) in the United States (Japsen, 2012). Pathogenic agents infect hundreds of millions of people and cause approximately 9,500,000 deaths (over 16% of all deaths) worldwide per year (World Health Organization, 2008). And the annual mortality rate from infectious diseases outpaces the annual mortality rate from all twentieth-century wars combined (Pirages, 2005). Clearly, this is a big problem for human fitness.

Perhaps the best-known defense against invading parasites and germs is the physiological immune system. This complex system is often highly effective, allowing us to overcome both novel and familiar threats. However, engagement of the physiological immune system is also energetically costly and imperfect in that it must continually adapt to the co-evolution of germs themselves (Lochmiller and Deerenberg, 2000). Further, it fights only those germs that have already entered the body. As a complement to this system, researchers have proposed that humans also possess a behavioral immune system (BIS) through which activation of certain psychological responses reduces the probability of initial infection (Neuberg et al., 2011; Schaller, 2015; Schaller et al., 2015). These responses aid individuals in both the detection and avoidance of infection threats by attuning people to cues associated with disease and by motivating evasive or intervening responses against these cues. For example, many illnesses produce external symptoms such as sores and lesions (Kurzban and Leary, 2001) and, accordingly, perceivers' reactions to these features are often strongly negative (e.g., Park et al., 2003). Moreover, the BIS uses liberal criteria when identifying potential threats in order to minimize the probability of contracting disease, even though this liberal bias increases the rate of false alarms to non-existent threats (Haselton and Nettle, 2006; Nesse, 2005). Thus, just as a smoke detector will sound an alarm in response to benign cues such as cooking fumes, a number of non-contagious physical and mental features are treated as cues to the presence of pathogens in other people. Such features include disfigurements (Ackerman et al., 2009; Miller and Maner, 2011), disabilities (Park et al., 2003), obesity (Lund and Miller, 2014; Park et al., 2007), elderly appearance (Duncan and Schaller, 2009; Miller and Maner, 2012), mental illness (Lund and Boggero, 2014), and outgroup association or membership (Faulkner et al., 2004; Huang et al., 2011; Navarrete et al., 2007).

Much like the physiological immune system, the BIS includes a complex set of processes that meet the end goal of infection avoidance through a variety of means. Research indicates that the BIS draws on psychological mechanisms, including interpersonal attention (Ackerman et al., 2009), social categorization (Miller and Maner, 2012), preferences for mates and leaders (Lee and Zietsch, 2011; Murray et al., 2013; White et al., 2013), prejudicial attitudes (Faulkner et al., 2004; Huang et al., 2011), and behavioral activation (Mortensen et al., 2010). This system also interfaces with the physiological immune system in a functionally flexible manner, such that people or contexts conveying heightened vulnerability (or perceived vulnerability) to infection trigger stronger BIS responses (Schaller et al., 2015). For instance, situational factors indicating weakened physiological immunity – as occurs subsequent to fighting an actual infection (van der Sluijs et al., 2004) – can exaggerate BIS responses as a means of compensating for this increased vulnerability (Miller and Maner, 2011). Activation of the BIS in healthy people may even kick-start aspects of the physiological immune system in preparation for possible infection (Schaller et al., 2010; Stevenson et al., 2011).

Thus, not only would an infectious disease tracking and avoidance system be functionally useful in theory, evidence indicates that we have likely evolved such a system. In the current chapter, we consider whether individual differences might play an important role in this system's operation, and perhaps more critically, the implications such a system has for shaping human personality. To do so, we first highlight the theoretical reasons to expect variation in pathogen management mechanisms and the psychological models relevant to these mechanisms (e.g., BIS, disgust). Next, we review research on the direct impact of pathogen threats on specific personality attributes. Subsequently, we place relevant individual differences within a motivational structure in order to organize specific content domains of personality linked to pathogen threats. Finally, we propose some unanswered questions for the field that may be promising directions for future research.

WHY EXPECT INDIVIDUAL DIFFERENCES?

Individual differences reflect invariances or consistencies in behavior, cognition, affect, and so on. These are generally presumed to stem from some combination of genes and environment, often with early-life environments playing an especially important role (Simpson et al., 2011). We suggest that factors indexing potential exposure to pathogens and vulnerability to infection will predict the expression of individual differences in BIS-relevant sensitivities.

Consider variation in the environments that humans inhabit. Since early hominid migrations out of Africa, people have occupied a wide range of ecological niches. Some of these ecologies are more amenable than others to propagation and transmission of disease-causing agents. Climates that are warm and wet – such as those found near the equator – help to facilitate pathogen prevalence (Guernier et al., 2004) and threaten both subsistence cultures and industrialized nations. In such places, continual exposure (or threat of exposure) to infection may have acted as a selection pressure on the mental and cultural evolution of behaviors and practices that function to cope with disease hazards. Societies that inhabit more temperate, drier locations face less pressure to respond to pathogen threats in order to thrive. Indeed, as we review later, ecological pathogen prevalence is a key predictor of a range of individual and cultural differences (e.g., Gangestad et al., 2006). Thus, environmental variance may set the stage for the development of individual differences in BIS activity.

Variation between people can also play an important role in the management of infectious diseases. For instance, physiological immunity to germs is heavily influenced by personal factors such as genes, gut microbiota, fatigue, and psychological distress (e.g., Beck et al., 1999; Hickie et al., 1999; Round and Mazmanian, 2009). Relatedly, a life history perspective suggests that people reared in resource-limited and unpredictable childhood environments may suffer deficits in the growth and maintenance of their physiological immune systems (McDade, 2005), leaving people vulnerable to external pathogen threats. Such dysregulation can also result in hyperactive immune activity, as seen in allergic and autoimmune disorders. Therefore, people with dysregulated systems may compensate through relatively stronger or more frequent use of the BIS.

Individual differences in the BIS may present in one of two ways. First, people may express different chronic degrees of BIS activity, much as one person could be high in agreeableness and another low in agreeableness. Second, people may vary in responsivity to contextual information indicating the presence of potential germ threats. This sensitivity to context forms the basis of the ‘functional flexibility principle’, the proposition that the physical and cognitive costs of motivational activation led to the evolution of mechanisms that track when a cue (such as vulnerability to infection) is present or not (Schaller et al., 2015; Schaller and Neuberg, 2012). Thus, people may exhibit their given level of BIS response only when pathogens are especially prevalent or when personal susceptibility is relatively high (e.g., from fatigue). It is important to note that, because the BIS is psychological in nature, the types of individual differences being discussed here include personality characteristics that facilitate disease avoidance in addition to basic behaviors.

EMOTIONAL MARKERS OF THE BIS: DISGUST

Thus far, we have considered the role of disease avoidance from a primarily cognitive perspective, the BIS. A related perspective emphasizes the role of affective responses like disgust in promoting aversion to, and expulsion of, toxic and disease-causing substances. By many theoretical accounts, disgust emerged as an adaptation to the selection pressures posed by pathogens (e.g., Tybur et al., 2013). Evidence does suggest that disgust initiates behaviors that reduce the likelihood of pathogen exposure. Across cultures, people react with disgust to feces, rotting food, and body fluids, all of which reliably house pathogens. Simply seeing or imagining, as well as actually touching, such items can elicit a cross-culturally recognizable facial expression, increased salivation, vomiting, lowered blood pressure, increased galvanic skin response, active serotonin pathways, increased activation in the parasympathetic branch of the autonomic nervous system, increased immune response, reported nausea, and, ultimately, avoidance and/or withdrawal behavior (Curtis et al., 2011; Olatunji et al., 2012; Rozin and Haidt, 2013). Experiencing disgust also motivates decisions intended to reduce pathogen transmission risk (Tybur et al., 2011).

Yet, the story of disgust is not entirely straightforward. Many carriers of pathogens do not evoke this emotion. For instance, the thought of maggot-ridden meat may gross you out, but the thought of peanut butter laced with *Salmonella* likely will not produce the same response. Conversely, people often feel (or at least report feeling) disgusted by pathogen-free items, such as hotdogs threaded with pasta (think about it). Human behaviors that seem entirely irrelevant to pathogen transmission, such as learning that a colleague stole money from a children's charity or cheated on a romantic partner, can also elicit feelings of disgust. Existing models of disgust reflect a similar variation in which antecedents and functions of disgust are represented. For instance, Rozin et al. (2000) argue that, although disgust first evolved as a food rejection system, it was later re-purposed for motivating the cleansing, avoiding, and expelling of a broad array of contaminants. They claim that not only does disgust motivate pathogen avoidance, it also functions to help individuals avoid reminders of humans' animal (thus mortal) nature and to protect sacred values and objects. Kelly (2011) also makes use of disgust re-purposing; he argues that disgust evolved first to motivate pathogen avoidance and then to motivate moral judgments and intergroup attitudes. Curtis et al. (2011) argue that group-level hygienic behaviors supplement an imperfect disgust system through cultural rules about purity and pollution, which are responsible for social divisions (e.g., social class). Finally, Tybur et al. (2013) distinguish three motivational domains of disgust – pathogen, sexual, and moral. Their model posits that sexual disgust discourages engaging in low-value mating opportunities and that expressions of moral disgust signal to nearby conspecifics that certain actions deserve condemnation.

Despite the differences among these models, it is not obvious from existing data that disgust ever betrays its historical roots: pathogen avoidance. More often than not, disgust is associated with targets that pose some pathogen threat, real or perceived. Disgust undoubtedly plays an important role in more social domains, but it seems that it does so largely in service to a pathogen avoidance system (Inbar and Olatunji 2014). Because of this, the experience of disgust, and its consequences, can be integrated with the BIS system model to explain aspects of personality and individual differences. We consider several such examples next.

DIRECT IMPACTS OF PATHOGEN THREAT ON INDIVIDUAL DIFFERENCES

Perceived Vulnerability to Disease

As an individual difference, perceived vulnerability to disease represents chronic sensitivities involving detection and aversion of infectious disease cues as well as beliefs about the relevancy of these cues to the individual. A commonly used measure in the behavioral immune literature, the Perceived Vulnerability to Disease (PVD) scale, was developed by Duncan et al. (2009) to assess two types of sensitivities – Germ Aversion (GA), which refers to 'discomfort in situations that connote an increased likelihood for the transmission of pathogens' (p. 545), and includes items such as, 'I do not like to write with a pencil someone else has obviously chewed on', and Perceived Infectability (PI), which refers to 'beliefs pertaining to their susceptibility to infectious diseases' (p. 545), and includes items such as, 'In general, I am very susceptible to colds, flu, and other infectious diseases'. Duncan and colleagues (2009) characterize GA as a set of aversive affective responses geared specifically toward pathogen-relevant contexts, whereas they characterize PI as a set of cognitions about one's immune functioning and likelihood of being infected in the future.

The PVD scale is associated with, yet distinct from, other indices of health threat. For example, classic measures of hypochondria and beliefs about health (i.e., the Health Anxiety Inventory, Whitely Index, and Illness Attitude Scale) correlate positively with the PVD scale, particularly with the PI subscale (Duncan et al., 2009). The Disgust Sensitivity scale (Haidt et al., 1994) correlates most strongly with GA, as disgust is an emotion motivating avoidance or expulsion rather than an indicator of one's own vulnerability. Despite these associations, PVD is different from instruments designed to gauge health anxiety or hypochondria, which measure health concerns in general and may include health problems that are non-contagious (e.g., cancer, heart disease), as well as from disgust sensitivity, which assesses reactions to non-disease-relevant stimuli and situations.

PVD is also tied to traits and attitudes with more indirect relevance to pathogen transmission but which reflect the potential for exposure to, or changes in, infection susceptibility. As we expand upon in later sections, these constructs are tied to specific motivations associated with BIS activation, such as self-protection motives, as well as a preference for fixed norms. Indeed, GA positively correlates with Social Dominance Orientation (SDO), Belief in a Dangerous World (BDW), Need for Structure, Affect Intensity, and Faith in Intuition (Duncan et al., 2009). Here, social dominance aligns with self-protection motives, as higher scores on SDO reflect aggression toward outgroups (that may carry foreign germs). The connection with self-protection is also found in the (relatively weak) association with BDW, a measure of individual differences in perception of interpersonal hostility and danger. The relationship between GA and Need for Structure likely reflects a desire to follow traditions and norms, which serve to protect people from disease risks associated with deviating from established norms (e.g., hygiene, food preparation). Correlations between GA and Affect Intensity and Faith in Intuition are consistent with the affect-based (disgust) nature of the GA subscale.

The PVD scale is also tied to social judgments and inferences. Specifically, GA predicts anti-fat attitudes (Park et al., 2007), anti-immigrant attitudes (Faulkner et al., 2004), and Implicit Association Test (IAT) scores indicating a tendency to implicitly associate negative words with the physically disabled, whereas PI predicts negative implicit attitudes toward the elderly. Finally, both PVD subscales are negatively correlated with people's self-reported number of friends with disabilities (Park et al., 2003) and with Sociosexual Orientation Inventory scores, such that higher levels of either GA or PI are associated with weaker preferences for low-investment, short-term relationships.

Given the theoretical distinctions between GA and PI, one might expect that GA scores predict relatively stronger reactions to external cues in the environment and PI scores predict relatively stronger reactions to internal cues. If so, this could account for the greater association between GA and negative attitudes toward obese individuals, immigrants, and physically disabled individuals, but the link between PI and anti-elderly attitudes is surprising. It may be that seeing elderly people evokes a self-reflective sense of internal vulnerability associated with aging.

PVD represents a useful measure for testing the principle discussed earlier involving 'functional flexibility' – responsivity to infectious disease cues depends, in part, on people's chronic sensitivity to such cues, which often reflects susceptibility to, or concern about, infection (Schaller et al., 2015).

Indeed, some studies find that pathogen threat cues affect people differently as a function of their perceived vulnerability, usually showing that responses are strongest for those scoring highly on PVD factors (e.g., Huang et al., 2011; Mortensen et al., 2010). Yet, PVD does not always interact with situational disease threats (e.g., Ackerman et al., 2009; Murray and Schaller, 2012). It may be that, when the cues to pathogen threat are strong, people exhibit classic BIS responses regardless of their chronic sensitivities, real or perceived. In weaker or more ambiguous contexts, interaction effects may dominate, such that the effect of the prime depends only on GA or PI (e.g., Ackerman et al., 2017; Fessler et al., 2005). The contexts in which one subscale plays more of a significant role than the other have been inconsistent. Why and when such effects occur therefore remain important questions for future research (see Tybur et al., 2014).

Disgust Sensitivity

As discussed earlier, disgust plays an important role in managing infectious disease threats. Although many objects, people, concepts, and situations can evoke disgust in the moment, people vary in the extent to which they feel disgust; that is, disgust responses can reflect individual differences. Tybur et al. (2009) extended work on disgust by proposing that this emotion is comprised of three functionally specialized domains. The first is pathogen disgust, which motivates pathogen avoidance. Sexual disgust, the second domain, discourages sexual behavior with sexual partners who may threaten long-term reproductive success. Finally, moral disgust discourages interactions and behaviors that are socially costly to an individual or his/her group. In order to capture individual differences in these distinct disgust domains, they developed a self-report scale: The Three Domains of Disgust Scale (TDDS). These researchers predicted that each of the disgust-based motivations should share variability with other individual differences in domain-specific ways. Consistent with the prediction that chronic concern about pathogens should motivate avoidance, the Pathogen Disgust subscale correlated with relevant measures of Big Five personality traits (e.g., positively with neuroticism, negatively with openness to experience) and, unsurprisingly, correlated positively with PVD. In contrast, sexual disgust – which should impede sexual motivations and, ultimately, contact with low-quality mates – positively correlated with conscientiousness and agreeableness. Finally, moral disgust negatively correlated with psychopathy, a fundamentally antisocial aspect of personality. Armed with predictions that disgust should motivate domain-specific attitudes and behaviors, researchers in later articles describe a variety of confirmatory correlations. For example, pathogen disgust is positively associated with women's facial masculinity preferences, contamination fear, obsessive–compulsive tendencies, depression, anti-fat attitudes, behavioral avoidance, moral purity (moral disgust is instead correlated with Harm/Care and Ingroup Loyalty on the Moral Foundations Questionnaire), and increased galvanic skin response to pathogen cues (DeBruine et al., 2010; Lieberman et al., 2012; Olatunji et al., 2012; Tybur and de Vries, 2013).

Extreme responses, such as the contamination fears and washing behaviors that characterize Obsessive–Compulsive Disorder (OCD), also likely reflect trait variation in pathogen threat concerns. Researchers have observed positive correlations between individual differences in disgust – as measured by Pathogen Disgust from the TDDS and most subscales of the Disgust Sensitivity scale and its revised version (Haidt et al., 1994; Olatunji et al., 2007) – and self-reported washing and checking symptoms of OCD in clinical and non-clinical samples (Olatunji et al., 2012; Woody and Tolin, 2002). Moreover, in a series of studies, non-clinical participants reporting high contamination obsessions reported greater disgust in response to aversive videos (Woody and Tolin, 2002). High-contamination participants were also less willing to touch (or even approach) a variety of disgusting objects in a series of behavioral avoidance tasks. Thus, to the extent that OCD symptomology represents an individual difference, pathogen threat appears to elevate its manifestation.

Five-Factor Model of Personality

Although it may sometimes be beneficial for individuals to form social relationships and experience novel situations, engaging in these behaviors increases their risk for infection. To the extent that personality motivates behavior, the BIS model predicts that heightened pathogen risk should dampen personality traits associated with risky behavior. A variety of disease threat indicators have been linked to weakened expression of specific (Big Five) personality factors. One such indicator is ecological pathogen prevalence, which indexes the degree to which an individual is likely to become infected by pathogenic agents. As would be expected from a BIS perspective, greater pathogen prevalence appears negatively correlated with extraversion and openness to experience (as measured by the NEO-PI-R; Schaller and Murray, 2008). In other words, as the likelihood of contact with pathogens increases, people report less willingness to interact with others and less openness to novel experiences. These effects hold even controlling for GDP, life expectancy, and climate, and they are stronger with measures of historical as compared to current pathogen prevalence, suggesting that high levels of extraversion and openness may have been genetically selected against in pathogen-rich environments. In this particular study, the other three personality traits of the Big Five – neuroticism, agreeableness, and conscientiousness – did not have a consistent relationship with pathogen prevalence. Expanding on Schaller and Murray's analysis (2008), Thornhill et al. (2010) separated types of parasites in a region (parasite richness) into zoonotic (i.e., parasites that only infect animals), human-specific, and multi-host (i.e., parasites that infect both animals and humans) parasites. Distinguishing among parasites in this way affords a stricter test of the infection hypothesis: people should be sensitive primarily to those diseases that are transmittable to humans. Indeed, Thornhill and colleagues (2010) found that only human-specific and multi-host parasite-richness were negatively correlated with extraversion and openness. Parasite severity, the number of cases of infections per person, yielded a similar negative correlation with these traits.

At an individual level, chronic concerns about infection are associated with a broader range of personality traits. The GA subscale of the PVD correlates negatively with extraversion, agreeableness, and openness, and it correlates positively with neuroticism (Duncan et al., 2009). The PI subscale correlates negatively with agreeableness and conscientiousness, and it correlates positively with neuroticism. The findings with extraversion and openness here are consistent with the ecological data presented earlier. Correlations for the remaining traits are less consistent with findings from the ecological data. There have also been subsequent analyses attempting to link the TDDS with various instantiations of Big Five personality factors (Tybur and de Vries, 2013). These have yielded somewhat inconsistent results compared to the more consistent associations found between PVD and the Big Five. Controlling for sex and age, the pathogen disgust subscale of the TDDS correlates positively with extraversion, neuroticism, and orderliness on the Five-Dimension Personality Test (5DT). Controlling for sex and age again, the pathogen disgust subscale correlates positively with emotionality and conscientiousness, and negatively with agreeableness and openness to experience on the HEXACO model of personality. Together, it seems the pathogen disgust subscale consistently correlates with neuroticism and orderliness/conscientiousness. However, there are some divergent findings between the PVD and TDDS (e.g., differences in correlations with extraversion) suggesting that different personality scales may be tapping different behaviors or tendencies associated with each trait. These scales also may have different psychometric properties (e.g., the 5DT is measured using yes or no questions, the HEXACO uses five-point Likert-type scales), which could contribute to fluctuations in findings across studies.

Although personality traits can be stable within individuals, nonrandom fluctuations in how people judge their own personality traits can occur across time (Funder, 2006). One study investigated changes in personality dimensions as a result of situational disease cues (Mortensen et al., 2010). Following a slideshow designed to trigger pathogen threat concerns or a pathogen-irrelevant slideshow, participants completed both the Big Five Inventory (John and Srivastava, 1999) and the PVD scale. The pathogen threat prime led to overall lower levels of extraversion, similar to the pattern demonstrated in the chronic and ecological studies above. Additionally, interactions between situational cues and PVD emerged for agreeableness and openness, with highly disease-sensitive people reporting less agreeableness and less openness. No published experiments have tested whether the TDDS, or other measures of disgust sensitivity, moderate the relationship between immediate disease cues and the Big Five. Overall, the ecological, correlational, and experimental evidence does point to a connection between environmental pathogen cues and decreased extraversion and openness. In more specific terms, chronic and incidental concerns about disease lead people to adopt strategies of reducing social contact and avoiding novel experiences.

FUNDAMENTAL MOTIVES AS A FRAMEWORK FOR UNDERSTANDING THE INFLUENCE OF PATHOGEN THREAT ON INDIVIDUAL DIFFERENCES

Central to our discussion in the following section is the notion that individual differences (e.g., personality traits) can represent attunement to, predisposition to adopt, and chronic pursuit of goals (e.g., Dweck and Leggett, 1988; Funder, 2006). For example, a person high in threat sensitivity may pay more attention to stimuli perceived to indicate the presence of danger and be more likely to engage in protective actions. From this point of view, certain individual differences can reflect underlying motives to pursue and complete specific, often fundamental, goals (Neel et al., 2015).

A fundamental motives framework provides a comprehensive, theory-driven approach that has been successful in organizing situation-level phenomena and in generating new predictions about situational factors. This approach builds from the assumption that human cognition and behavior consists of many mental processes adapted to solve important, recurrent problems over the course of human evolution. These processes draw on inputs from local ecologies and cultures to motivate actions that are relevant to problem domains that include self-protection, affiliation, mating, management of status hierarchies, and parenting (e.g., Ackerman et al., 2012; Ackerman and Kenrick, 2008; Kenrick et al., 2003, 2010). In addition to advancing our understanding of situational forces, this framework can help to organize individual differences according to (1) domains likely to be influenced by infectious disease threats, and (2) response mechanisms to these threats, including the BIS. This organization is distinct from personality models like the Big Five, although it does help to identify types of content and action relevant to these models (see Neel et al., 2015, for an extended discussion of the similarities and differences in fundamental motives and traditional personality approaches). Next, we detail several motive domains in which pathogens and pathogen threat appear to have played a substantive role in shaping the psychology of individual differences.

Self-protection

Perhaps no fundamental motive is more closely tied to the management of infectious disease threats than that of self-protection. Survival is clearly important from both a personal perspective and an evolutionary perspective (in the service of differential reproduction). Physiological harm also saps energetic resources that could be used in the pursuit of other goals. Individual differences within the domain of self-protection are myriad, one of which – emotional (disgust) sensitivity – we have described earlier. Here, we focus on two major categories of action that afford possible injury to the self: food consumption and intergroup interaction. Both involve key vectors of infectious disease, and both can be represented through individual differences such as food preferences and stereotypic attitudes, respectively. Thus, behavioral immune responses should be specially tailored to manage such threats. Important for the following discussion, recall that pathogen management systems like the BIS use liberal detection criteria for potential threats. The costs of missing a real pathogen threat are likely greater than the costs of false alarming to a nonexistent threat (Haselton and Nettle, 2006; Nesse, 2005), and thus the selection pressures created by these differential costs have led to inherent bias in behavioral immune mechanisms.

Food choices

Not eating is difficult. People may struggle with individual diets, but avoiding food altogether does not make for a long or happy life. Yet, consumption of the wrong foods (e.g., those containing dangerous pathogens) can, in mild cases, cause digestive distress and, in severe cases, death. Food is unique in that we allow it to bypass our body's first line of physiological immune defense – our skin – and so people should prioritize psychological mechanisms that help us to choose the 'right' foods. Research does indicate we are particularly sensitive to food cues that connote the possibility of germ contamination, such as signs of spoilage. Not only do we readily detect such cues (even over-perceiving them), our chronic food preferences support avoidance of them. Given its association with bodily expulsion, disgust plays an important role in these preferences. Physiological disgust is a common reaction to the experience of eating contaminated or spoiled foods, even foods that only have the appearance of contamination (Rozin et al., 2000). Our preferences also reflect the fact that some foods are more pathogenically dangerous than others. Tybur and Lieberman (2016) found that pairing pathogen cues with images of meats led to less willingness to eat those meats, whereas pathogen cues paired with images of plants did not produce aversion. Over the course of our cultural evolutionary history, human groups have discovered means of inhibiting pathogen growth in foods, and the preferences of people in pathogen-rich ecologies reflect these discoveries. For instance, spices such as garlic, onion, and chili contain antimicrobial properties. People in climates that cultivate pathogens and parasites tend to use more spices in their recipes (Sherman and Billing, 1999), and the cultural normalization of these recipes becomes part of what it means to be an individual within those cultures.

Beyond clear indicators of contamination such as spoilage, individuals also differ in their preferences for novel or strange foods. This may be because novel food (particularly if the novelty is geographic or cultural in origin) is more likely to harbor germs to which one's body has not adapted immune defenses compared to commonly eaten food.

Indeed, food neophobia (i.e., the avoidance of unfamiliar foods) is predicted by pathogen stress (Thornhill and Fincher, 2014a). For instance, women who score highly on pathogen disgust tend to distrust novel foods (Al-Shawaf et al., 2015). People with high levels of GA also tend to hold more distrustful and negative attitudes toward genetically modified foods (Prokop et al., 2013). More generally, disease concern is associated with reduced openness to experience (Duncan et al., 2009), which is itself associated with reduced risk taking and increased preference for familiarity. This could account for the specific patterns of food preferences reviewed here, and it could also help explain broader aversions to novel stimuli (e.g., people), as we discuss next.

Stereotyping and prejudice

Just as unfamiliar foods may contain pathogens to which we have not been previously exposed, so might unfamiliar people. Our adaptive immune defenses are quite effective in developing targeted reactions (e.g., antibodies) to infection-causing germs, providing we survive the initial infection. Unfortunately, history shows that a lack of early exposure to pathogens (often due to differences in the ecologies societies inhabit) can result in extreme harm once those pathogens are introduced to naïve populations. Consider the epidemics that can result when societies first come into contact (e.g., smallpox and measles in the Americas; Diamond, 1997). Such diseases are often spread from person to person. Given such dangers, a BIS that is already tuned to overgeneralize the cues signaling threat (Schaller and Park, 2011) is liable to produce chronic suspicion and dislike of unfamiliar people, particularly those who harbor cues that have reliably indicated infection. Heuristically however, infection risk may be signaled by any deviation from typical morphology and behavior (e.g., facial disfigurement, rashes, convulsions) as well as foreign or outgroup markers (e.g., race, sexual orientation, cultural differences). From this perspective, a degree of the stereotypic attitudes and prejudices expressed toward others – and the corresponding pull toward a homogeneous ingroup – may stem from the threat of infectious disease.

Some existing evidence supports this conclusion. Fincher and Thornhill (2012) have demonstrated that philopatry (i.e., persistently residing in a familiar environment), ingroup favoritism, and outgroup dislike may have all emerged as beliefs, behaviors, and cultural practices serving to reduce the threat of local pathogens. Societal structures that serve to fraction people into groups, such as religions, appear more common in areas of high pathogen stress (Fincher and Thornhill, 2008). Chronic levels of pathogen concern also are associated with negative attitudes toward individuals bearing a variety of outgroup and non-normative features. For instance, people with strong GA and pathogen disgust report greater anti-fat prejudice, particularly after viewing images of obese people (Park et al., 2007). In one study, disgust-sensitive and disease-concerned people responding to postings on psychology and political websites expressed greater ethnocentrism, ingroup attraction, and outgroup negativity (Navarrete and Fessler, 2006). People with such concerns also report fewer numbers of family members and friends with disabilities (Park et al., 2003), suggesting that these prejudicial attitudes spill over into behavior. These reactions may be explicit, but they also can involve implicit reactions held as well. Studies show that people with greater PVD hold more implicit negative attitudes toward unfamiliar, foreign groups and people with disabilities, and they implicitly associate such groups with danger (Faulkner et al., 2004). In some contexts, implicit stereotypes emerge for chronically concerned people only when cued by situational pathogen threats, highlighting the functional flexibility principle of the BIS (e.g., participants reporting greater PI to disease showed stronger implicit associations between elderly adults and disease; Duncan and Schaller, 2009).

Finally, individual differences in disease vulnerability may also change according to the state of the perceiver. For example, American women in their first trimester of pregnancy – a period of increased risk for infection – revealed greater ingroup attraction and outgroup negativity (Navarrete et al., 2007). These women liked an American-born, pro-American author more and a foreign-born, anti-American author less. People also become more vulnerable to infection after having been sick recently. For these people, enhanced BIS reactions may protect from additional infection. Consistent with this idea, recently ill people show faster avoidant behaviors toward disfigured others (Miller and Maner, 2011).

Affiliation

People everywhere desire to form social groups (Baumeister and Leary, 1995; Caporael, 1997). Relationships with group members afford a number of benefits – safety, romance, direction in uncertain situations – and thus people attempt to manage those social connections using a variety of rules, incentives, and cognitive biases, from empathy to reciprocity. Behaviors such as cooperation and mutual provisioning of assistance would clearly be valuable in the context of infectious diseases where effective prevention and treatment of illnesses often require interpersonal care. Yet, active infection concerns can also lead to down-regulation of affiliative desires, at least with unspecified others (Sacco et al., 2014).

The establishment of social relationships typically involves separating people into ‘good’ and ‘bad’ coalitional partners, or ingroups and outgroups. Therefore, an affiliation motive draws on group formation processes and mechanisms that track conformity to, and violation of, group rules. In this section, we discuss several types of affiliation-relevant individual differences that have been linked to behavioral immune activity: individualism/collectivism, political orientation, and morality.

Individualism and collectivism

Individualism/collectivism represents one of the most widely researched psychological distinctions between cultures (see Hofstede, 2001, or Triandis, 1995, for reviews). A collectivistic culture is one in which the boundary between ingroup and outgroup is strong, whereas an individualistic culture is one in which the boundary between these is relatively weak. Collectivism is associated with relatively more social tightness – a strong emphasis on conformity and adherence to norms – compared to individualism, which is characterized by greater tolerance of norm violations (Gelfand et al., 2006; Murray et al., 2011). These cultural-level differences in group structures also extend to the individual, in turn affecting their self-concepts, personalities, chronic motivations, chronic experiences of emotions, and chronic ways of interpreting and reasoning about the world (Markus and Kitayama, 1991; Nisbett et al., 2001). For example, collectivists tend to form stronger ties with their ingroups than individualists. This means that the self-concepts of collectivists tend to include their group memberships, whereas the self-concepts of individualists do not. Thus, individualism/collectivism can be represented as both an individual difference as well as a cultural difference.

Several reasons have been proposed to explain why higher levels of pathogen prevalence predict greater levels of collectivism within individuals and cultures (Thornhill and Fincher, 2014b). As discussed in the section on stereotyping and prejudice, in the presence of pathogens, people are motivated to avoid outgroup members who display cues to novelty and may carry novel pathogens, leading people to more readily draw distinctions between ingroup and outgroup members. Second, the greater nepotism and ingroup altruism found in collectivistic groups help ensure that those ingroup members who fall ill are given care. Finally, stronger observance of certain ingroup norms (i.e., food preparation, cleaning, and hygiene practices) can serve as protective qualities against disease transmission.

These ideas have typically been examined at the level of culture, although a conceptual equivalency exists with individual cognition. Fincher and colleagues (2008) conducted one test using four separate multi-national surveys of individualism and collectivism (Gelfand et al., 2004; Hofstede, 2001; Kashima and Kashima, 1998; Suh et al., 1998) that included direct survey measurement of individuals and secondary examination of language-use within nations. Across cultures, pathogen severity (i.e., the number of cases of individuals with infectious diseases) was strongly negatively correlated with individualism and strongly positively correlated with collectivism. This was most prominently the case for measures of historical pathogen prevalence (i.e., incidence rates dating before the 1990s) rather than for contemporary prevalence (i.e., rates from June–August of 2007). This may be because of the slow rate of cultural change or the relatively slow action of natural selection in creating large-scale genetic shifts. Importantly, however, this helps to clarify any causal claims, as the ecological factor of prevalence preceded the cultural expression of collectivism. This link between historical pathogen prevalence and collectivism held even when controlling for alternative influences such as GDP, the GINI index (i.e., an index of income disparity), population density, and residual life expectancy (i.e., life expectancy variance not accounted for by pathogen prevalence).

An analysis was also performed separating human-host, multi-host, and zoonotic parasites (i.e., parasites that only infect animals), revealing that the collectivism effect is driven solely by the levels of human and multi-host parasites, but not zoonotic ones (Thornhill et al., 2010). This again helps to rule out alternative explanations, including ones tying collectivism and its consequents to increased levels of human–animal interaction (e.g., farming and fishing; Uskul et al., 2008). In another cultural-level analysis, Fincher and Thornhill (2012) looked at the strength of family ties as measured by five items in the World Values Survey (e.g., importance of family, respecting parents regardless of faults or qualities). Higher pathogen prevalence was positively related to the strength of family ties, even controlling for various economic indices and civil liberties. Within the United States, tests of association between broader measures of collectivism and family ties mirrored the cross-national data, particularly for analyses of human-host/mixed-host pathogens (Fincher and Thornhill, 2012).

As mentioned earlier, collectivistic cultures are typically tighter than individualistic cultures in their emphasis on conformity and adherence to norms (Gelfand et al., 2006). One might expect that, in areas where pathogen prevalence is high, deviations from norms that are designed to offer protection from pathogens could be costly. Murray and colleagues (2011) examined this link between pathogen prevalence and cross-national differences in conformity pressure, using four country-level measures. These included the number of left-handed people, personality variability, attitudes toward obedience as measured in the World Values Survey, and a meta-analysis of dozens of behavioral conformity experiments performed globally (Bond and Smith, 1996). Again, historical pathogen prevalence was a strong predictor of conformity pressure at both regional and national levels, such that greater levels of pathogens were associated with lower levels of left-handed people and less personality variability, as well as more positive attitudes toward obedience and greater behavioral conformity. The predictive power of historical pathogen prevalence held even when entering collectivism into the regression, suggesting that this is not a by-product of this cultural structure.

Cultural-level differences in conformity should be reflected in the products that cultures generate, as well as in their individual phenotypes. In fact, some evidence indicates that pathogen prevalence predicts lower levels of innovation, as indexed by the number of Nobel Prize Laureates per capita, the Global Innovation Index, the Technology Achievement Index, innovative capacity, and number of patent applications (Murray, 2014). Although these are national-level metrics, we can speculate that conformity pressures stemming from chronic ecological cues could lead to a decrease in individual creativity or a decreased willingness to express novel ideas. This possibility is supported by data that both replicate the negative relationship between patent applications and pathogen prevalence in US state data and show experimentally that pathogen threat reduces openness to innovation (Huang et al., 2016).

Finally, at the individual level, in a study by Murray and Schaller (2012), people who scored highly on the GA subscale of the PVD measure tended to also score highly on conformist attitudes (e.g., 'Breaking social norms can have harmful, unintended consequences'). People high in PVD-GA also expressed greater liking for people with conformist traits and were more likely to value obedience in their children. Together, these findings highlight how an affiliation motive can produce different types of cognitive and behavioral responses, dependent on the existing degree of pathogen concern.

Political orientation

By 2013, at least 24 studies had tested whether chronic motivations to avoid pathogens are related to factors underlying political orientation, in particular social conservatism and religiosity (Terrizzi et al., 2013). One prominent hypothesis is that socially conservative beliefs – which promote adherence to tradition, ingroup cohesion, and wariness of outgroup members – reflect a strategy that reduces the risk of pathogen exposure associated with foreign and unfamiliar people. Aggregating across these studies, Terrizzi et al. (2013) estimated a moderate relationship between political conservatism and BIS strength (*r*s = .23–.31).

Tybur et al. (2015) tested this connection with several large US samples and found no direct relation between multiple measures of pathogen disgust and social conservatism. However, they found that sexual disgust and sociosexuality – an index of openness toward uncommitted sex – mediated the association between pathogen disgust and social conservatism, suggesting that people who are chronically concerned with pathogen threat tend to follow a monogamous sexual strategy, and these same people tend to hold socially conservative political ideologies.

The lack of a direct connection between conservatism and pathogen disgust seems to conflict with evidence implying that intergroup attitudes can function to reduce the pathogen exposure risk associated with novel outgroup members. Fincher and Thornhill (2012) have demonstrated that philopatry (i.e., staying put in a familiar environment), ingroup favoritism, and outgroup dislike may have all emerged as beliefs, behaviors, and cultural practices serving to reduce the threat of local pathogens. Their results are consistent with those presented by Schaller and Murray (2008), who find that historical levels of pathogen prevalence negatively correlate with more promiscuous sexual strategies, openness to experience, and extraversion. Why then does social conservatism in the United States fail to correlate with chronic concerns about infectious disease?

The tendency toward social exclusivity and outgroup avoidance characteristic of conservatism in the United States might serve as a pathogen avoidance strategy, but emergence of associations between conservatism and pathogen threat may depend on the existence and salience of those threats. For instance, the United States is only slightly above average in non-zoonotic pathogen prevalence according to Thornhill and Fincher's (2014) data on pathogen prevalence in 147 countries. Moreover, even if infectious pathogens are prevalent, this fact may escape notice. For example, both young and White Americans (who comprise most psychology samples) are the least likely to agree (23% and 27%, respectively) that the widely reported Zika virus was a major health threat in the United States (Rainie and Funk, 2016). However, some evidence suggests that salient pathogen threats can strengthen traits associated with US conservatism. One study found that, when cued with pathogen threat, the chronic concern germ concerns of US undergraduates negatively correlated with agreeableness and openness (Mortensen et al., 2010), personality traits which negatively correlate with political orientation and party identification (Hirsh et al., 2010). Additional studies on Canadian and US participants have found that disease salience leads to greater conformist attitudes and avoidance tendencies (Mortensen et al., 2010; Murray and Schaller, 2012). Finally, when participants felt protected from infectious disease, they reported lower levels of prejudice (Huang et al., 2011). Taken together, these data suggest that the link between chronic pathogen concern and traits comprising US political conservatism (i.e., social exclusivity, outgroup avoidance) may depend on salient infectious disease cues.

Morality

Lay thinking has often connected aspects of moral thinking to disease. Empirically, recent research in the domain of situated cognition uses the embodied experience of dirtiness/cleanliness as a bridge between morality and pathogen threat (e.g., Lee and Schwarz, 2011). For example, committing (or recalling) immoral acts makes the act of cleaning more mentally accessible and desirable (Zhong and Liljenquist, 2006), whereas exposure to physical dirtiness heightens the desire to punish immoral others (Schnall et al., 2008b). This connection is quite specific to actions that mitigate infection risk. Lee and Schwarz (2010) found that immoral acts committed verbally heighten preference for mouthwash, but immoral acts committed with the hands heighten preference for hand sanitizer. Engaging in physical cleaning behavior also interrupts the typical downstream consequences for moral perception, as would be expected given a conceptual overlap. Thus, hand washing leads people to feel less guilty about past transgressions (Zhong and Liljenquist, 2006) and can reduce condemnation toward immoral others (Schnall et al., 2008a). Such experimental findings make the case for mental associations between morality and pathogen threat.

However, a recent meta-analysis of the effect of disgust inductions on moral judgments (Landy and Goodwin, 2015), coupled with certain replication problems (e.g., Johnson et al., 2016), raise doubts about a clear path from disgust to moral judgments. As suggested earlier, disgust is grounded in the service of pathogen avoidance, and so its influence may be specific to pathogen-related moral content. Inbar and Pizarro (2014) also argue that the relationship between disgust and morality can be explained by a motivation to avoid pathogens: if objects, acts, and/or concepts are judged both immoral and disgusting, it is because they are heuristically associated with pathogens.

This connection is perhaps best observed with moral questions in two domains – sexual acts and food. Studies commonly find that people perceive immorality in behaviors such as having sex with relatives (e.g., Lieberman et al., 2003) and eating dog or human meat (Haidt et al., 1993; Russell and Giner-Sorolla, 2011). Disgust is also positively correlated with religious attitudes about sex and negatively correlated with attitudes toward groups that threaten traditional sexual morality (Crawford et al., 2014; Tybur et al., 2015). Despite such findings, research examining the influence of disgust on pathogen-specific moral issues is relatively rare. This leaves open the question of whether disgust is associated with moral thinking in a domain-general fashion, or whether this association relates primarily to pathogen threat management.

Mating

From the perspective of evolutionary biology, no set of problems is as central to human existence as those involved in mating (Maner and Ackerman, 2015). It is clear why – differential reproduction represents the primary end of the evolutionary game. A mating motive relates to a number of specific goals, from selecting to attracting to retaining romantic partners. Information about pathogen threats is relevant to each of these goals, and should influence the criteria people use to evaluate potential mates as well as the style of romantic relationships people attempt to form. Indeed, sexual reproduction owes its existence to the co-evolutionary interplay between organisms and pathogens (Brockhurst, 2011; Hamilton, 1980; Hamilton et al., 1990; Morran et al., 2011). In the following sections, we detail these influences on individual differences in romantic selectivity and sociosexuality.

Selectivity

Sexual recombination is only one piece of the mating puzzle. In the evasion of infection, not only is the ability to create novel combinations important, but so too are individual differences in sexual selectivity. In ecologies where infection is prevalent, organisms should prefer mates that have strong pathogen resistance. How do organisms solve the problem of identifying cues that reliably signal pathogen resistance? The parasite theory of sexual selection posits that animals indicate inherent pathogen resistance through sexual signaling and costly displays (Hamilton and Zuk, 1982; Jacobs and Zuk, 2010). Supporting this proposal, Hamilton and Zuk (1982) found that high regional incidence of disease was positively associated with brightness of feathers and complexity of male vocals across 109 species of birds. In a separate study, Møller (2002) found that male barn swallows with longer tails were less likely to be infested with mites. A male swallow's reproductive success was also positively associated with the length of his tail, and his offspring were more likely to be resistant to mites. This was true even when relocating the chicks to other nests to be parented by other swallows, ruling out the possibility females were trying to avoid the spread of mites from the male to the offspring. These studies provide support for the idea that sexual signaling is a proxy for information about a mate's 'good genes', or their resistance to parasites, and that this resistance is indeed heritable. Such studies further suggest that organisms should be particularly swayed by costly or sexual signals in areas that are high in pathogen prevalence.

The same is true for people as well. High levels of pathogens in the ecology should evoke increased sensitivity to traits that confer high mate value. For example, people may become more selective about who they are willing to mate with and qualities of those people, such as physical attractiveness (Sugiyama, 2005). To test these predictions, Gangestad and Buss (1993) analyzed data from 37 societies on the importance conferred to physical attractiveness in mates during the selection process. They found a strong positive relationship between pathogen prevalence and importance of attractiveness ratings across countries. In a reanalysis of the same dataset, these effects were replicated even when controlling for gender inequality (Gangestad et al., 2006). For both men and women, pathogen prevalence was positively correlated with a preference for attractive mates, as well as a preference for health and good genes. For men, pathogen prevalence was negatively correlated with age of mate, indicating a preference for younger mates, where youth likely signals health. For women, pathogen prevalence was positively correlated with a preference for status and intelligence, traits which are also often associated with genetic fitness

(Miller, 2001). Similarly, women's preferences for masculine faces were also greater in nations and states with higher levels of pathogen stress (DeBruine et al., 2012). Such findings indicate that mate seekers use more selective criteria in areas marked by greater dangers of infectious disease.

Patterns of influence on costly and sexual signals are also found at an individual level of analysis. High scores on trait pathogen disgust predict women's preferences for more masculine faces, voices, and bodies (Jones et al., 2013a) and men's preferences for more feminine shapes in women's faces (Jones et al., 2013b). Similarly, pathogen disgust predicts men's preferences for low waist-to-hip female ratios and women's preferences for high shoulder-to-hip male ratios (Lee et al., 2015). Perhaps even more directly indexing behavioral immune influences on selectivity, GA (as measured with the subscale of the PVD scale) positively correlates with preference for facial symmetry (Young et al., 2011).

Pathogen threat appears to play a role not only on general selectivity, but also on individual differences in trade-offs relevant to mate selectivity. As the threat of infection increases, women should value genetic quality over and above other investments from mates, leading to a stronger preference for mate attractiveness compared to other features commonly associated with female romantic preference, such as a mate's resources. In essence, females should trade-off male parental investment for male genetic fitness, or proxies of fitness such as attractiveness (Gangestad and Simpson, 2000). To study this trade-off, Lee and Zietsch (2011) randomly assigned female participants to complete either a questionnaire related to resource scarcity, a questionnaire containing the PVD scale, or an unrelated questionnaire as the control. Then, people were given a limited amount of 'mate dollars' which they could allocate to a set of five 'good-genes' or five 'good-parent' traits. Intelligence, creativity, muscularity, social level, and confidence were the traits reflective of good genes, whereas earning potential, commitment, warmth, kindness, and a nurturing personality were traits reflective of good parenting. When participants were cued by disease, they tended to value the traits that signaled good genes over those that signaled good parenting. In contrast, participants cued with resource scarcity showed the opposite pattern, presumably because good parenting involves resource provisioning. Thus, pathogen threat appears to be tied to increased selectivity for genetic quality more than other types of mate qualities.

Sociosexuality

Romantic selectivity is commonly studied in terms of the traits or resources a potential mate brings to the table, but it is also reflected in the romantic behaviors of individuals. Sociosexuality (and its corresponding trait measure, the Sociosexual Orientation Inventory [SOI]; Simpson and Gangestad, 1991) refers to selectivity in the willingness to engage in sexual and romantic commitment behaviors. An unrestricted sexual strategy, as indicated by high scores on the SOI, reflects a preference for short-term, uncommitted, and novel sexual relationships. A restricted sexual strategy indicates a preference for long-term romantic relationships in which commitment is required for sex to occur. These strategies are chronic in nature and thus signify individual differences. Pathogen threat plays an important role in expressions of sociosexuality such that greater pathogen prevalence is associated with more sexual restrictedness in populations (i.e., a decrease in willingness to pursue short-term relationships of low-commitment; Schaller and Murray, 2008; Thornhill et al., 2010).

Specifically, Schaller and Murray (2008) analyzed SOI scores from 48 regions around the world and found that higher levels of pathogens predicted lower SOI values, indicating greater sexual restrictedness. This pattern was primarily found in females. This sex difference may have emerged because women face relatively higher obligatory parental investment costs than do men, and women are commonly more risk-averse in general (Byrnes et al., 1999), thus they may be more sensitive to cues that signal increased costs associated with unrestricted sexual behavior, in this case, pathogen transmission. These data were later reanalyzed after breaking down pathogen prevalence by type (i.e., zoonotic, multi-host, and human-specific; Thornhill et al., 2010). In 45 of the 48 regions, the same pattern for sociosexuality was found, with levels of multi-host or human-specific pathogens predicting sexual restrictedness. However, no such relationship was found for zoonotic pathogens (e.g., parasites that infect animals). Thus, it appears that only parasites that infect humans elicit threats that impact sexual strategies.

For chronic measures of pathogen threat sensitivity, both subscales of the perceived vulnerability to disease scale (GA and PI) have been shown to correlate negatively with SOI scores (Duncan et al., 2009). In one study, people who scored high on trait-level aversion to germs also scored lower on unrestricted sexuality and reported wanting fewer future sexual partners, and this effect was strongest when situational indicators of disease threat were present (Murray et al., 2013). This effect was strongest among women, again suggesting that women have more to lose in employing a sexually unrestricted strategy (Schmitt, 2005). Examining affective measures, Al-Shawaf et al. (2015) found that SOI correlated negatively with scores on the sexual disgust subscale of the TDDS, but not with the moral disgust or the pathogen disgust subscales. This failure to find a connection between SOI and pathogen disgust may be due to how the pathogen disgust subscale was constructed. That is, the original authors of the TDDS wanted to measure orthogonal constructs so the pathogen disgust subscale contains almost no content related to mating, perhaps isolating sociosexuality from this measure. Nevertheless, across a variety of studies and countries, individual differences in mating preferences (here, as reflected by sexual restrictedness) appear to serve as functional solutions to the dangers associated with infectious disease threats.

FUTURE DIRECTIONS

The three fundamental motives just discussed – self-protection, affiliation, and mating – are central to most of the extant BIS research. There are also two other domains included within the fundamental motives framework (Kenrick et al., 2010) which may help categorize reactions to infectious disease threats but have not as yet received much empirical attention. Next, we describe several predictions associated with each of these motives. Following these, we identify additional unanswered questions about the issue of psychological defenses against disease, which we hope might stimulate additional research.

Status

The drive for power and prestige within social groups is a hallmark of all societies, and in fact, all group-living primates (Barkow, 1989; Brown, 1991; Fiske, 2010). Indeed, one of the primary dimensions on which people categorize ingroup members is dominant–submissive (Wiggins and Broughton, 1985). Virtually no research has examined the role of pathogen threat on mental processes involved in status perception and seeking behavior, although some suggestive cross-national work ties political structures to ecological pathogen exposure. As discussed in the section on political orientation, pathogen prevalence is correlated with the tendency for societies to employ authoritarian governments (Murray et al., 2013; Thornhill et al., 2009). This suggests that people exposed to pathogen threats might prefer hierarchical systems where high status is held by a subset of group members rather than egalitarian social systems. If so, what kind of hierarchy might people prefer?

There are two pathways toward status (see Cheng and Tracy, 2014, for a review) – dominance and prestige. Dominance involves the procurement of status and rank through force, coercion, and intimidation. Dominant individuals essentially use fear to their advantage by threatening to withhold resources or physically harm someone else. This form of status is said to have evolved in response to conflict over resources or mates. In contrast, prestige is freely conferred deference or status granted to someone who is knowledgeable, skillful, or successful. Prestige relies on social learning, where there is a pressure to recognize and copy people who have skills and knowledge.

In attempting to link infectious disease threat responses to a status motive, prestige appears to be a promising pathway. If it is costly to acquire knowledge through direct experience (e.g., individual exploration and experimentation), then people should rely on cultural learning (e.g., the experiences of fellow group members; Henrich and McElreath, 2003). Prestige is a central cue to which people attend when seeking a person from which to learn (Henrich, 2015). Thus, in harsh ecologies characterized by high pathogen levels, people should be more likely to heed advice and copy behaviors of prestigious individuals in their groups. This suggests that skillful, successful, and knowledgeable people are more likely to gain status in pathogenic environments, and people should be particularly more willing to grant status to people in these environments by way of the prestige pathway. Alternately, dominance may be relatively more effective for certain pathogen-mitigating behaviors such as enforcing social norms and preventing contact with outgroup members.

Parenting

The study of how pathogen threats impact parenting will likely be a rich avenue for future research. From direct influences on child mortality, to social influences on decisions around vaccination, to quite indirect influences on the extent to which people invest in attachment relationships with children, pathogens have the potential to affect a wide range of behaviors. The existing work in this area focuses primarily on the role of ecological disease cues. As mentioned in the Individualism and Collectivism section of the chapter, such ecological cues are associated with stronger family ties. For example, in their cross-national analysis, Fincher and Thornhill (2012b) examined the link between parasite stress and familial beliefs, as measured in the World Values Survey (e.g., items concerning beliefs about the importance of family, parental love and connection, sacrifice for children, familial living situation). Pathogen stress correlated positively with family ties. That is, pathogen stress predicted the endorsement of unconditional love and respect for parents and of parents' duty to do their best for their children, as well as the importance of family, cohabitation with parents, and goals of making parents proud. These findings suggest that pathogen prevalence influences parents' investment in their children, but also children's investment in, and respect of, their parents. It is not clear whether this investment is characterized best by a supportive style of parenting or by an authoritative style, given that children are expressing unconditional respect.

In contrast to this positive association between pathogen prevalence and stronger family ties, the predictions made from a life history perspective seem, at first glance, to suggest different patterns of behavior. After all, life history theory predicts that ecological cues of mortality danger lead to the adoption of fast strategies, categorized partially by a decreased investment in parenting in favor of continued reproduction (Kaplan and

Gangestad, 2005). An explanation for this seeming inconsistency may lie in the intrinsic or extrinsic nature of disease threats. When the prevalence and severity of pathogens in an environment is high enough such that the threat becomes extrinsic (i.e., contact is unavoidable) and will likely produce serious consequences, a close family structure may yield few benefits. For example, a parent who invests copious time and energy into rearing a single child with a low chance of survival might garner a bigger genetic benefit from diverting that time and energy into further reproductive opportunities. Therefore, low investment in family members and offspring may become a better strategy in the face of extrinsic pathogen threat. Some evidence for this pattern exists. Quinlan (2007) analyzed a sample of 186 pre-industrial societies and found that, as pathogen stress increased, the time a mother spent nursing also increased. However, as pathogen stress became extreme, nursing duration decreased. Similarly, Thornhill and Fincher (2014a) found that an inverse curvilinear pattern provided the best fit for the relationship between pathogen stress and collectivism, such that, at extreme pathogen stress, nation-level scores on collectivism start to decrease. These findings suggest that, under extreme levels of pathogen threat, parenting styles may resemble those consistent with a fast life history strategy, with parents offering relatively little support and behaving in an insecurely attached manner with their children. As with our status motive discussion, these hypotheses are speculative and would benefit from further empirical investigation.

CONCLUSION

As one of the most significant dangers confronting humans over our history as a species, infectious disease has played a critical role as an evolutionary selection pressure. Adaptations that address this danger have therefore shaped not only our bodies, but also our cultures, our behaviors, and the personalities we exhibit as individuals. Perhaps the most common, lay understanding of this influence involves experiences and individual differences related to disgust and anxiety, but research on psychological constructs such as the BIS demonstrate the complex and widespread means by which the mind responds to pathogen-related threats. Many of the personality traits we consider foundational, from extraversion to openness, owe aspects of their exhibition and action to our history of managing infectious disease. Looking ahead, the relative infancy of the literature on comprehensive approaches to pathogen management, such as the BIS, ensures that much more research remains to be done. For instance, virtually all of the empirical work on psychological responses to pathogen threat has focused on externally oriented behavior and cognitions. Yet, might perceptions of the self and other inwardly directed responses also be susceptible to infectious disease cues? Additionally, as methodological and analytical techniques advance, integration of psychological with physiological activity likely represents one of the most needed next steps in furthering our understanding of how and when pathogen management systems function. We expect that empirical and theoretical attention to these issues will represent a large part of future research on the consequences of pathogen threat. We also hope that the current discussion has provided a window into the vast psychological landscape originating from our interactions with organisms as minute as germs.

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