Behavioral Immune System Theory and Its Research: A Re-examination from a New Perspective

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Abstract

Behavioral Immune System theory posits that in response to pathogenic threats, humans have evolved a specialized set of behavioral response tendencies, including vigilance toward and disgust for disease cues, preference for healthy mates, rejection of out-groups, endorsement of collectivism, and so forth. Existing research has primarily been conducted at two levels: macro (group) and micro (individual). While numerous findings support this theory, there also exist many inconsistent or even contradictory results. Deficiencies in research methodology, theoretical underpinnings, and modern applicability may account for this situation. Future research should address these issues, further expand the theoretical scope, examine the boundaries of the theory and related research, and investigate the physiological mechanisms underlying behavioral immunity, among other directions.

Full Text

The Behavioral Immune System Theory and Its Research: A Re-examination from a New Perspective

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Abstract

The theory of Behavioral Immune System (BIS) posits that to cope with pandemic stress, human beings have evolved a series of behavioral response tendencies, including vigilance toward and disgust of disease cues, preference for healthy mates, rejection of outgroups, and endorsement of collectivism. Existing research has primarily been conducted at two levels: macro (group) and micro (individual). While numerous studies have produced supportive evidence for the theory, many inconsistent or even contradictory findings have also emerged. Deficiencies in research methods, theoretical foundations, and modern applicability may account for these discrepancies. Future research should address these issues, further expand the scope of the theory, examine the boundaries of the theory and related research, and explore the physiological mechanisms underlying behavioral immunity.

Keywords: pandemic; behavioral immune system; infectious disease

Human history is a chronicle of struggle against various threats. Among these threats—including natural disasters and war—disease, particularly pandemics, ranks foremost. Statistics show that throughout human history, pandemics have claimed more lives than all other catastrophes combined (WHO, 2015). As an invisible yet devastating threat, pandemics have profoundly shaped human history and cultural psychology. Since the 1940s, pandemic outbreaks worldwide have been increasing (Jones et al., 2008). Even in the technologically advanced 21st century, pandemics continue to pose grave threats. Coronaviruses (e.g., SARS-CoV, MERS-CoV, COVID-19), Nipah virus, Ebola virus, and influenza have caused immense loss of life and property. The COVID-19 outbreak that began in late 2019 evolved into a rare global pandemic in 2020.

To combat pandemic threats, humans have developed a suite of defensive behaviors over our long evolutionary history, such as disgust toward disease cues, rejection of outgroups, and adherence to social norms. To understand these behaviors, researchers have proposed the Behavioral Immune System theory (Murray & Schaller, 2016; Schaller, 2006; Schaller & Park, 2011).

Over the past decade, researchers have conducted numerous studies on the behavioral immune system. While these studies have generated substantial supportive evidence, many findings are inconsistent with or even contradictory to the theory. Moreover, many scholars have questioned the theory' s theoretical foundations, physiological mechanisms, modern applicability, and ecological validity (Ackerman et al., 2018; De Barra & Curtis, 2012; Hruschka et al., 2014; Shakhar, 2019; Tybur et al., 2014).

Several review articles and chapters have summarized the behavioral immune system theory and its supporting evidence, both in English (Ackerman et al., 2018; Murray & Schaller, 2016; Shook et al., 2017) and Chinese (吴宝沛, 张雷, 2011). A common feature of these reviews is that they organize past research by content or theme, such as attention, facial preferences, mate preferences, in-

tergroup relations, and cultural values. However, these categorizations overlook a crucial point: studies under each theme include both micro- or individual-level research and macro- or group-level research. These two levels of research are often treated as equivalent, creating the impression that patterns at the group level can be generalized to the individual level and vice versa. In reality, however, patterns at the individual and group levels are theoretically and empirically independent. Findings at the individual level may not generalize to the group level, and vice versa (Tybur et al., 2014; Na et al., 2010). Otherwise, researchers risk committing ecological fallacy or individualistic fallacy (Eckersley, 2010; Eckersley & Dear, 2002; Robinson, 1950). Furthermore, previous reviews have focused primarily on evidence supporting the behavioral immune system theory, paying little attention to findings inconsistent with the theory and even less to the possible reasons behind such inconsistencies.

In light of these limitations, this paper breaks free from thematic and content constraints to organize existing literature from both group and individual perspectives. Our goal is to clarify: (1) which findings are at the individual level and which are at the group level; (2) which studies are cross-level; (3) which findings at each level are consistent or inconsistent with the behavioral immune system theory; and (4) which findings are consistent or inconsistent across the two levels. Based on this novel organization and the identified inconsistencies, we explore potential reasons for these discrepancies and point out directions for future research. Below, we first provide a brief introduction to the behavioral immune system (for more details, see Murray & Schaller, 2016; Schaller, 2006; Schaller & Park, 2011).

2. Behavioral Immune System Theory

Pandemics pose a tremendous threat to humans and represent one of the important selective pressures in human evolution. To combat pathogen threats, humans have evolved a behavioral immune system over our long evolutionary history. Unlike the physiological immune system, which reacts passively after pathogens invade the body, the behavioral immune system is a preventive immune response aimed at blocking pathogen entry through various means. This behavioral immune response has two main forms: reactive and proactive behavioral responses. When individuals perceive immediate contagion risk in their environment (e.g., smelling foul odors or seeing others' suffering), they immediately exhibit reactive avoidance behaviors, such as stricter sexual attitudes (Duncan et al., 2009; Murray, Jones, & Schaller, 2013; Schaller & Murray, 2008), greater willingness to use condoms (Tybur, Bryan, Magnan, & Hooper, 2011), and avoidance of sick individuals (Park et al., 2003; Park et al., 2007). Reactive behaviors aim to reduce current infection risk, whereas proactive responses aim to reduce long-term disease threats. For example, when facing long-term pathogen threats, people place greater value on physical attractiveness, symmetry, and secondary sexual characteristics in mates as health signals (Gangestad & Buss, 1993; Hill et al., 2015; Lee et al., 2015; Young et al., 2011), because

these health indicators not only reduce one's own risk of infection but also confer more robust immune genes to offspring (Tybur & Gangestad, 2011). Thus, both forms of behavioral immune responses can reduce infectious disease threats to individuals, their offspring, and ingroup members.

Because pathogens are invisible, the behavioral immune system has two key characteristics to maximize identification and avoidance of pathogen threats: overgeneralization and functional flexibility. Overgeneralization refers to the tendency of the behavioral immune system to be overly sensitive to or overgeneralize disease-related signals. Some researchers have aptly termed this the smoke detector principle (Haselton & Nettle, 2006; Nesse, 2005): just as smoke detectors may sound alarms in response to minor cooking fumes, the behavioral immune system may treat all contagious and non-contagious physical and psychological abnormalities as pathogen signals, including disfigurement (Ackerman et al., 2009; Miller & Maner, 2011; 2012), disability (Park et al., 2003), obesity (Lund & Miller, 2014; Park, et al., 2007), and aging (Duncan & Schaller, 2009; Miller & Maner, 2012), subsequently triggering psychological and behavioral responses. Although these signals may trigger false alarms, the cost of such errors is much smaller than the cost of missing genuine disease threats.

Functional flexibility means that the activation of the behavioral immune system is regulated by both environmental cues and individual pathogen susceptibility (e.g., Schaller, 2015; Schaller & Neuberg, 2012). Because not all environments pose the same level of infection threat and not all individuals have the same susceptibility, and because behavioral immunity carries costs, the behavioral immune system requires flexibility in weighing the costs and benefits of pathogen avoidance to maximize benefits and minimize costs. When environmental cues suggest greater pathogen threat, such as dirty environments or regions with high pandemic incidence, individuals are more likely to activate their behavioral immune system. For the same environmental cues, individuals with higher pathogen susceptibility are more likely to perceive them as pathogen signals. In other words, when individuals have higher susceptibility to disease, even relatively weak pathogen cues can activate their behavioral immune system.

3. Empirical Research and Findings

Based on behavioral immune system theory, researchers have conducted numerous studies over the past two decades. These studies have primarily been carried out at two levels: macro or group level (country and region), and micro or individual level. The former mainly examines relationships between historical pandemic incidence or stress at the group level and social, cultural, psychological, and behavioral variables (e.g., dietary habits, mate preferences, intergroup attitudes, individualism-collectivism values). The latter mainly examines relationships between objective disease cues or subjective disease concerns and various psychological and behavioral outcomes (e.g., attention, cognition, emotion, attitudes, values, behaviors). Below, we introduce research at these two levels separately, highlighting findings inconsistent with behavioral immune system

theory.

3.1 Macro or Group-Level Research

These studies primarily use publicly available archival data to examine relationships between historical pandemic incidence or stress at the group level and group psychology and behavior. Researchers have assessed pandemic incidence or stress through three main methods: (1) summing scores of various pandemic impact magnitudes present in a country or region (e.g., Fincher & Thornhill, 2008; Schaller & Murray, 2008); (2) summing the number of infectious disease outbreaks in a country or region (Thornhill et al., 2010), or using infectious disease incidence and mortality data recorded by the World Health Organization or local disease control centers (e.g., Fincher & Thornhill, 2012); and (3) using infant mortality rates and overall life expectancy as indirect indicators of pandemic stress (e.g., White et al., 2013). For various group psychological and behavioral indicators, researchers primarily use publicly available data, such as previously published data (e.g., on individualism and collectivism, Fincher et al., 2008), government-released data (e.g., U.S. election voting data, Beall, Hofer, & Schaller, 2016), and internet data (e.g., Google pandemic search data, Beall et al., 2016).

To date, group-level research findings consistent with behavioral immune system theory mainly show that in regions with high pandemic stress or threat: (1) people adhere more to collectivist values and obey group norms (Fincher et al., 2008; Murray et al., 2011; Thornhill et al., 2010); (2) people' s political ideology is more conservative, they exhibit more authoritarian personality traits, and they support authoritarian governments (Murray, Schaller, & Suedfeld, 2013; Terrizzi et al., 2013; Tybur et al., 2016); (3) people are more prejudiced against outgroups and trust outgroup members less (Fincher & Thornhill, 2012; Fincher, et al., 2008; O' Shea et al., 2020; Zhang, 2018), while ingroup relationships are tighter (Fincher & Thornhill, 2012); (4) people show lower extraversion and openness but higher conscientiousness (Schaller & Murray, 2008; Thornhill et al., 2010); (5) people prefer more attractive, symmetrical, and healthy faces and bodies (De Barra et al., 2013; DeBruine, Jones, Crawford et al., 2010; Gangestad, & Buss, 1993; White et al., 2013); (6) people have lower preference for second-hand items and higher valuation of new products (Huang et al., 2017); and (7) there are more religious or religious institutions (Fincher & Thornhill, 2008, 2012). In summary, people in high pandemic incidence regions tend to be more conservative, obedient, xenophobic, traditional, and collectivist.

However, some studies have found results inconsistent with behavioral immune system theory. For instance, Ross and Winterhalder (2016) followed Fincher and Thornhill' s (2012) research approach, and after controlling for archival data on epidemics and individual-level socio-cultural variables, used Bayesian models for reanalysis. They found results opposite to Fincher and Thornhill (2012): higher pathogen prevalence was associated with greater support for democratization, less endorsement of collectivist values, and lower religiosity. Cashdan

and Steele (2013) recoded pandemics across 186 countries and analyzed relationships between pandemics and cultural values and outgroup bias. Their results supported greater collectivism in high-pathogen regions but failed to replicate the relationship between pandemics and outgroup bias. Pollet (2014) reanalyzed data from Murray, Schaller, and Suedfeld (2013) and found that infectious disease stress was not a predictor of authoritarianism. Walter et al. (2020) surveyed 14,399 participants across 45 countries regarding mate preferences (e.g., importance of physical attractiveness, intelligence) and collected data on these countries' pathogen stress indicators, economic indicators (GDP), gender equality, and religiosity. Using multilevel models, they found no significant relationship between pathogen stress and mate preferences. Grossmann and Varnum (2015) conducted a dynamic analysis of the relationship between pandemics and individualism-collectivism in the United States over more than a century, finding that pandemics positively predicted increased individualism among Americans. Zhang (2018) analyzed pandemic indices from 80 countries and regions alongside data on ingroup and outgroup trust from the fifth and sixth waves of the World Values Survey. The results showed a curvilinear relationship between pathogen stress and trust in outgroup members: people in regions with moderate pathogen stress trusted outgroup members less than those in low- and high-pathogen stress regions.

3.2 Micro or Individual-Level Research

Micro or individual-level research consists of two main types. The first is experimental research conducted in laboratories, which can reveal causal relationships between disease-related factors and psychological and behavioral responses. These studies examine changes in psychological and behavioral reactions after individuals are exposed to pandemic-related threat manipulations or primed with disease-related stimuli (Tybur et al., 2014). The second is correlational research based on individual differences, focusing on relationships between disease-related factors and psychological and behavioral tendencies. These studies mainly examine relationships between subjective disease susceptibility, disgust sensitivity, perceived disease threat, disease avoidance motivation, and other psychological and behavioral tendencies. Below, we introduce the main findings of these two types of research.

3.2.1 Experimental Studies Findings from experimental studies consistent with behavioral immune system theory mainly include: (1) Pathogen cues affect cognition. Specifically, after being primed with pathogen threat, participants become more sensitive to disease-related people or objects, pay more attention to disfigured faces (Ackerman et al., 2009; Stone & Potton, 2017), show more accurate memory for disease-related items (Ganesan & Dar-Nimrod, 2019; Ganesan et al., 2019; Gretz & Huff, 2019), have better recognition ability for infectious disease faces (Tskhay et al., 2016), show higher resolution ability for graphics (Nussinson et al., 2018), and prefer opposite-sex individuals with more sexual characteristics and symmetrical faces (Little et al., 2011; White et al.,

2013). (2) Disease threat affects ingroup and outgroup attitudes. Specifically, after pathogen threat priming, participants show higher ethnocentrism (Navarrete & Fessler, 2006), higher outgroup prejudice (Faulkner et al., 2004; O' Shea et al., 2020), and prejudice against certain special groups such as immigrants, homosexual individuals, and obese people (Buckels & Trapnell, 2013; Faulkner et al., 2004; Huang et al., 2011; Inbar, Pizarro, & Bloom, 2012; Park et al., 2007; Tybur & Lieberman, 2016). (3) Disease threat affects moral judgment. Specifically, after disgust emotion priming, participants more strongly condemn moral norm violations (Erskine et al., 2011; Murray & Schaller, 2012), especially violations related to sexual purity (Horberg et al., 2009). (4) Disease threat affects sexual attitudes and strategies. Specifically, after disease threat priming, participants report greater willingness to use condoms in future sexual behavior (Tybur, Bryan, Magnan, & Hooper, 2011) and significantly decreased desire for short-term mating (Al-Shawaf et al., 2018). (5) Disease threat affects social values. Specifically, after pathogen threat priming, participants are less willing to take risks (Prokosch et al., 2019), show higher conformity attitudes and behavioral tendencies (Murray & Schaller, 2012; Wu & Chang, 2012), and more strongly support collectivist social strategies and conservative political ideology (Brown et al., 2016; Oosterhoff, Shook, & Ford, 2018). (6) Disease threat also affects personality, with participants reporting lower extraversion, openness, and agreeableness under pathogen threat conditions (Mortensen & colleagues, 2010).

However, some studies have found results inconsistent with behavioral immune system theory. For example, some research found that priming disease threat does not affect participants' facial preferences (Brown & Sacco, 2016). When expecting greater future disease threat, female participants showed stronger desire for new partners and more partners compared to control conditions (e.g., expecting future economic recession) (Hill et al., 2015). Olatunji and Puncochar (2016) found that participants'germ disgust tendency was significantly positively correlated with evaluations of severe moral violations but not with evaluations of mild or moderate moral violations. After priming disgust or neutral emotions, participants in the disgust condition actually evaluated moderate moral violations less harshly than those in the neutral condition.

3.2.2 Correlational Studies Main findings from this type of research include: (1) Individuals with higher disgust and sensitivity to pathogen-related cues show greater support for collectivist values (Terrizzi et al., 2014; Terrizzi et al., 2013), more xenophobia (Aarøe et al., 2017; Navarrete & Fessler, 2006; O' Shea et al., 2019), less preference for novel or foreign foods (Al-Shawaf et al., 2015), stronger obedience (Murray & Schaller, 2012; Wu & Chang, 2012), and more conservative political attitudes and religious beliefs (Aarøe et al., 2017; Beall et al., 2016; Brenner & Inbar, 2015; Smith et al., 2011; Terrizzi et al., 2010, 2012; Terrizzi et al., 2014). (2) Individuals with high disease susceptibility or who perceive themselves as highly susceptible prefer more symmetrical and healthy opposite-sex faces and bodies (DeBruine et al., 2010; Jones et al., 2013; Lee et al., 2013; 2015; Little et al., 2011; Nussinson et al., 2018; Tybur

& Gangestad, 2011; Young et al., 2011) and hold more conservative sexual attitudes, rejecting promiscuity more strongly (Duncan et al., 2009; Murray, Jones, Schaller et al., 2013). A study during the Ebola outbreak found that higher perceived susceptibility to Ebola virus was associated with more reported outgroup rejection reactions, with collectivism (or individualism) playing a moderating role: the relationship between perceived Ebola susceptibility and xenophobia was stronger among those with lower collectivism (or higher individualism) (Kim et al., 2016). (3) Individuals with high disease avoidance motivation or tendency show lower extraversion and openness but higher neuroticism and conscientiousness (Oosterhoff, Shook, & Iyer, 2018). (4) Higher anxiety and worry about influenza are associated with greater likelihood of adopting self-protective behavioral strategies such as reducing contact with others, hand disinfection, and mask-wearing (Puterman et al., 2009; Wheaton et al., 2012), and with greater implicit prejudice against homosexual individuals (Inbar et al., 2016).

However, some findings are inconsistent with behavioral immune system theory. For example, some research found that the relationship between disgust sensitivity and conservatism is contextual and depends on disgust elicitors, with no significant overall relationship between disgust sensitivity and political orientation (Elad-Strenger et al., 2020). Other studies found that disease avoidance motivation cannot predict individuals' mate preferences (Hadley & Hruschka, 2017) or personality traits such as extraversion, openness, neuroticism, and agreeableness (Olatunji et al., 2012; Tybur et al., 2009; Tybur, & de Vries, 2013), suggesting that the relationship between pandemics and personality may be moderated by other variables. Indeed, some studies have found consistent results with theoretical predictions only in specific populations (e.g., older adults) and for specific personality traits (e.g., openness) (Mullett et al., 2019).

3.2.3 Cross-Level Research Because collecting large-sample data at both group and individual levels simultaneously is extremely difficult, studies examining both levels are rare (e.g., Ross & Winterhalder, 2016; Tybur et al., 2016). Ross and Winterhalder (2016) used hierarchical Bayesian linear models to examine relationships between pandemic incidence and individual-level sociocultural outcome variables. They found that pandemic incidence positively predicted preference for democracy and negatively predicted collectivism, with no significant relationships with crime rates or gender inequality. Although they found positive correlations between pandemic incidence and religiosity and negative correlations with education, these relationships became non-significant after controlling for other variables. These results are inconsistent with classic pandemic theory findings but support the authors'structural racism hypothesis, suggesting that socioeconomic status associated with race has stronger explanatory power.

Tybur et al. (2016) surveyed 11,501 participants from 30 countries and obtained historical archival data on pandemic incidence for each country. They found that at the country level, pandemic stress was significantly positively correlated with traditionalism but not with social dominance orientation or disgust sensitivity.

At the individual level, the relationship between pathogen avoidance motivation and tradition was stronger than its relationship with social dominance orientation.

The results of these two studies are not entirely consistent with previous research. Ross and Winterhalder controlled for more variables and used Bayesian models—rarely used in previous research—yielding results inconsistent with prior studies. Tybur et al.' s study supported an ingroup explanation for the relationship between pandemics and political conservatism (people tend to comply with ingroup cultural norms to cope with pandemic stress) but did not support an outgroup perspective (avoiding contact with outgroup members to reduce infection risk). These findings suggest that simultaneously considering group and individual levels can exclude or control factors that previous studies could not, potentially leading to different results.

3.3 Summary, Problems, and Reflection

From the above review, we can see that research at both levels covers many domains and topics, including perception, mate selection, interpersonal attraction, group attitudes, sexual psychology, cultural psychology, political ideology, and religious beliefs. To clarify findings on each topic at both levels, we have reorganized these studies by topic and level in a table (see Table 1).

Table 1 clearly shows that some findings are supported at both levels. For example, both group- and individual-level studies find that pandemics or pandemic threats increase outgroup rejection, manifested as distrust, prejudice, and stigma toward outgroup members and certain special groups (e.g., obese, elderly, homosexual individuals), while strengthening bonds among ingroup members. However, some findings come only from one level. For instance, research on pandemics' impact on interpersonal perception has been obtained almost exclusively through individual-level laboratory studies, with no group-level research identified. Conversely, research on religious beliefs has been conducted only at the group level, lacking individual-level investigation.

Overall, behavioral immune system theory has received support from many studies. However, we find that, except for perception, almost all other research topics show findings inconsistent with or contradictory to behavioral immune system theory. For example, some studies find that disease threat does not necessarily affect facial preferences or mate preferences (Brown & Sacco, 2016; Walter et al., 2020). Pandemic stress does not necessarily lead to stronger xenophobic reactions (Cashdan & Steele, 2013), does not necessarily lead women to adopt more open sexual strategies (Hill et al., 2015), and is not necessarily related to mate preferences (Walter, et al., 2020). Pandemic stress does not necessarily enhance collectivism and reduce individualism, promote conservative political attitudes and religious beliefs, or reduce democratization. Instead, it may reduce collectivism, increase individualism, decrease religiosity, and promote democratization (Cashdan & Steele, 2013; Grossmann & Varnum, 2015; Ross &

Winterhalder, 2016).

Thus, almost all classic predictions of behavioral immune system theory have inconsistent or contradictory findings. Why do these inconsistencies arise? Through careful analysis of existing research, we identify three possible reasons related to research methods, theoretical assumptions, and applicability in modern society.

Methodological Issues

Both levels of research suffer from methodological problems (Kuppens & Pollet, 2014; Pollet, 2014; Pollet et al., 2014; Tybur et al., 2014). At the group level, almost all studies are based on historical archival data and conduct correlational analyses between pandemic stress and other cultural-psychological variables. These studies have three main problems. First, there are issues with the validity of pandemic stress indicators. Many previous studies have simply combined various different pandemics—for example, integrating indirect indicators such as infant mortality and overall life expectancy to mark pandemic stress. The reliability of such indicators is problematic. For instance, life expectancy is closely related to economic development and modernization. While it may have been a valid indicator of pandemic threat under conditions of low productivity and backward science and technology in history, in modern society it may more likely reflect modernization and technological development levels.

Second, this approach ignores differences in transmission routes of various pandemics and the ecological and population characteristics of affected regions, likely confounding results with other variables such as race, regional ecological conditions (temperate vs. frigid zones), and modes of production (nomadic vs. agricultural). This may lead to spurious correlations (Hackman & Hruschka, 2013). For example, high pandemic incidence regions are mostly in temperate zones with abundant rainfall and widespread rice cultivation. Recent research shows that rice cultivation promotes collectivism (Talhem et al., 2014). Thus, the prevalence of collectivism in these regions may result from either pandemic stress or rice cultivation, making unique interpretation difficult.

Third, many studies have problematic data analysis methods. Because many potential influencing factors exist and different researchers control for different variables in their analyses, inconsistent results emerge (Cashdan & Steele, 2013; Currie & Mace, 2012; Pollet, 2014). Most existing studies also assume that different regions or countries are independent. However, this assumption often does not hold because many countries or regions have spatial associations or spatial autocorrelation due to geographical, ecological, and historical proximity. Ignoring correlations between different regions or countries substantially increases the probability of obtaining false significant results (Horita & Takezawa, 2018). Temporal autocorrelation is also a frequently overlooked factor. For example, when researchers reanalyzed Beall et al.' s (2016) data and controlled for temporal autocorrelation, they found that the effect of the Ebola outbreak on political

voting preferences was no longer significant (Tiokhin & Hruschka, 2017).

Individual-level research also has methodological problems. The most commonly used method in experimental research is behavioral priming. When different pandemic cues are used for priming, disease cues from different sensory modalities may lead to different consequences (e.g., visual, olfactory, gustatory), and different individuals may have different sensitivities to different sensory modalities. Existing research rarely considers the potential moderating effects of cue characteristics and individual differences, leading to inconsistent results (e.g., Ackerman et al., 2009; Mortensen et al., 2010; Tybur, Bryan, Lieberman et al., 2011). In correlational research, a common problem is the reliability and validity of individual difference measures. For example, disgust sensitivity does not necessarily reflect pathogen avoidance tendency (Tybur et al., 2014), creating uncertainty in interpreting results. Additionally, correlational research reveals only correlational relationships, which may be entirely caused by unrelated third factors and thus may be spurious.

Overall, inconsistencies between findings at the two levels may be theoretically reasonable because research at the two levels does not necessarily generalize to each other.

Theoretical Issues

Behavioral immune system theory focuses on behavioral strategies individuals adopt when facing pandemic threats, including various psychological mechanisms for identifying pathogens and behavioral responses for avoiding them. An important foundation of this theory is that outgroup members may carry pathogens to which ingroup members are not immune, and contact with outgroup members carries higher risk of contracting novel pathogens. Therefore, outgroup members should be rejected and contact avoided, while strict behavioral norms should be implemented for ingroup members to ensure unified action. However, this assumption may not be scientifically or realistically valid (De Barra & Curtis, 2012).

From a physiological and pathological perspective, pathogens carried by outgroup members are not necessarily more dangerous than those jointly carried by ingroup members (De Barra & Curtis, 2012). In ancient times, limited by transportation conditions, humans rarely traveled far enough to encounter outgroups carrying different pathogens (Van Leeuwen & Petersen, 2018). Moreover, ingroup members could contract novel pathogens through contact with outgroup members, and interactions with ingroup members also carried risks. Avoiding contact with outgroups is detrimental to economic cooperation and technological innovation (Robinson & Barker, 2017). Therefore, recent researchers have proposed that it is unreasonable for behavioral immune system theory to assume xenophobic reactions as a basic immune behavioral response (Tybur et al., 2016; Petersen, 2017).

Existing psychological research also shows that xenophobia, as a highly social be-

havior, is influenced not only by disease threat but also by many other personal and social factors. Current behavioral immune system theory almost completely ignores the influence of other factors, which is unreasonable (Kusche & Barker, 2019). The theory also overlooks the role of genetic selection resulting from evolution (Shakhar, 2019): behavioral immune responses may have evolved to enhance the entire group' s resistance to pandemics and better preserve genes or ensure group continuation. Therefore, these behavioral responses may also be caused by genes, not entirely by external stimuli.

Furthermore, pandemic threats also trigger many positive psychological and behavioral responses such as compassion, concern, gratitude, mutual assistance, and altruism. Theoretically and objectively, these behaviors can help threatened individuals and groups receive more support, thereby better resisting disease, surviving, and reproducing, thus serving an immune function. However, current theory does not address this.

Modern Applicability

Behavioral immune system theory may have specific applicable conditions. Under conditions of backward science and technology and limited human understanding of pandemic causes and patterns, pandemic threats were enormous, and people had to rely on primitive behavioral immune responses to protect themselves and their groups. However, in today' s highly technologically advanced society, human understanding of disease and anti-epidemic methods have advanced by leaps and bounds. Modern medical and health conditions are highly developed, and many former potential threats (such as malaria) no longer pose contagion risks (Kusche & Barker, 2019). Additionally, behavioral immune responses themselves carry huge costs and are very disadvantageous for innovation-oriented modern society (Davtyan et al., 2014; Murray, 2014; Smith & Hughes, 2014). Therefore, many researchers propose that behavioral immune theory is more applicable to the past but may not be fully applicable to modern society (Hruschka et al., 2014). Thus, tremendous changes in social conditions may also lead to inconsistent research findings.

In summary, existing behavioral immune system research methods may be unreliable, theoretical assumptions may be unreasonable, and the theory may not be applicable in modern society. Therefore, many inconsistent findings may result from methodological issues or may be inherently reasonable, and existing behavioral immune system theory requires revision.

4. Future Research Directions

Behavioral immune theory has not been proposed for long. Although it has received support from numerous studies across different perspectives and levels, many questions remain unresolved in both breadth and depth. Meanwhile, existing research has many methodological and theoretical problems. Future research should first improve methods by adopting more effective pandemic stress indica-

tors, more effective disease susceptibility measurement tools, and simultaneously considering potential ecological autocorrelation (or regional non-independence) and other potential confounding variables to reduce the possibility of false or erroneous discoveries. Additionally, several directions require special attention.

4.1 Conduct Cross-Level Research Considering Both Macro and Micro Levels

Through our literature review from macro and micro perspectives, we find that existing research is overwhelmingly conducted at a single level—either macro or micro. Cross-level research is extremely rare. These single-level studies cannot explore how macro pandemic ecology and micro individual psychology and behavior influence each other, leaving us with little knowledge about these questions: How does pandemic ecology affect individual psychology and behavior? How do individual-level psychology and behavior evolve into macro-level culture? What are the processes and mechanisms? How do factors at one level moderate and influence patterns at another level? Future research needs a more systematic perspective (such as ecocultural theory, Berry, 2018) that simultaneously considers macro pandemic ecology and micro individual psychology and behavior to conduct cross-level research (e.g., Jing & Cai, 2020).

4.2 Explore Boundaries of Behavioral Immune Research and Theory

As previously noted, many behaviors involved in behavioral immune system theory are influenced not only by disease factors but also by many other methodological, individual, group, and environmental factors. Existing findings may vary with changes in these factors or be moderated by them. Therefore, the boundaries of existing research and theory are a particularly important issue for future research. Specifically, future research can explore whether specific findings vary with changes in personal and environmental characteristics or are moderated by these variables, particularly whether they are moderated by factors such as modernization. Whether the large number of findings from laboratory settings can be generalized to real pandemic situations and whether they have ecological validity are also important questions.

4.3 Expand the Scope of Behavioral Immune Theory Research

Although existing behavioral immune system research spans a wide range of psychological and behavioral domains from attention, perception, and emotion to intergroup attitudes and culture, many areas remain untouched. For example, regarding emotional responses triggered by pandemics, current research has mainly focused on disgust, with few studies examining emotions such as anxiety, fear, and anger (Murray & Schaller, 2016). Regarding pandemics' impact on cultural psychology, existing research has focused more on individualism-collectivism and obedience, but almost no research has examined pandemics' impact on other cultural psychological phenomena, including self-construal, cul-

tural cognition, and tightness-looseness. Future research needs to investigate these related psychological phenomena.

Particularly, behavioral immune system theory has ignored pandemics' impact on positive psychology, such as compassion, sympathy, concern, cooperation, altruism, friendship, and even sacrifice. We can speculate that pandemics not only make people feel disgust, fear, and anxiety but may also make people feel love and compassion toward each other, prompting them to re-examine the value and meaning of life and relationships between people and between humans and nature. Preliminary research shows that during SARS, people who could simultaneously recognize both positive and negative impacts of the pandemic showed better psychological adaptation (Cheng et al., 2006). Positive psychological changes brought by pandemics undoubtedly also help humans cope with disease and long-term survival and reproduction and should become an important topic for future research.

4.4 Deeply Explore the Neurophysiological Mechanisms of the Behavioral Immune System

Although numerous studies have examined the behavioral immune system at the behavioral level, understanding of its physiological mechanisms remains very limited (Murray et al., 2019). Emerging psychobehavioral immunology has begun some beneficial explorations in this area (Murray et al., 2019), with preliminary findings: At the sensory level, olfactory sensitivity is significantly correlated with avoidance motivation strength (Fay & Bovier, 2018), and visual disease stimuli can enhance tactile sensitivity and accent sensitivity in hearing (Hunt et al., 2017). At the cellular level, visual stimuli of infectious diseases cause increases in oral and blood immune-inflammatory biomarkers (Schaller et al., 2010; Stevenson et al., 2012), increased blood levels of inflammation-related interleukin-6 (Schaller et al., 2010), and increased salivary tumor necrosis factor and albumin (Stevenson et al., 2012). Individuals with high physiological immune responses may show weaker behavioral immune responses (Kandrik et al., 2017). At the genetic level, individuals carrying genes related to infectious disease susceptibility (IFNG +874 gene) reported lower levels of extraversion and higher levels of harm avoidance (Macmurray et al., 2014), and women with low-level immune capacity biomarkers reported more positive attitudes toward short-term mating and more casual sexual histories (Murray et al., 2017).

These preliminary explorations suggest that the human behavioral immune system may have extensive biological and physiological foundations and that complex interactions may exist between human physiological and behavioral immune systems. Undoubtedly, future research needs to deeply explore these complex relationships, which will not only promote understanding of human physiological and behavioral immune mechanisms but may even give rise to new, integrated, and more explanatory immune theories.

References

吴宝沛, 张雷. (2011). 疾病的心理防御：人类如何应对病菌威胁. 心理科学进展, 19(3), 410-419.

Aarøe, L., Petersen, M. B. & Arceneaux, K. (2017). The behavioral immune system shapes political intuitions: Why and how individual differences in disgust sensitivity underlie opposition to immigration. *American Political Science Review*, 111(02), 277-294.

Ackerman, J. M., Becker, D. V., Mortensen, C. R., Sasaki, T., Neuberg, S. L., & Kenrick, D. T. (2009). A pox on the mind: Disjunction of attention and memory in the processing of physical disfigurement. *Journal of Experimental Social Psychology*, 45(3), 478-485.

Ackerman, J. M., Hill, S. E., & Murray, D. R. (2018). The behavioral immune system: Current concerns and future directions. *Social and Personality Psychology Compass*, 12, e12371.

Al-Shawaf, L., Lewis, D. M. G., Alley, T. R., & Buss, D. M. (2015). Mating strategy, disgust, and food neophobia. *Appetite*, 85, 30-35.

Al-Shawaf, L., Lewis, D. M. G., Ghossainy, M. E., & Buss, D. M. (2018). Experimentally inducing disgust reduces desire for short-term mating. *Evolutionary Psychological Science*, 5, 267-275.

Beall, A. T., Hofer, M. K., & Schaller, M. (2016). Infections and elections: Did an Ebola outbreak influence the 2014 U.S. federal elections (and if so, How)? *Psychological Science*, 27(5), 595-605.

Berry, J. W. (2018). Ecocultural perspective on human behavior. In A. K. Uskul & S. Oishi (Eds.), *Socioeconomic Environment and Human Psychology: Social, Ecological, and Cultural Perspectives* (pp. 3-32). Oxford University Press.

Brenner, C. J., & Inbar, Y. (2015). Disgust sensitivity predicts political ideology and policy attitudes in the Netherlands. *European Journal of Social Psychology*, 45, 27-38.

Brown, G. D. A., Fincher, C. L., & Walasek, L. (2016). Personality, parasites, political attitudes, and cooperation: A model of how infection prevalence influences openness and social group formation. *Topics in Cognitive Science*, 8, 98-117.

Brown, M., & Sacco, D. F. (2016). Avoiding extraverts: pathogen concern downregulates preferences for extraverted faces. *Evolutionary Psychological Science*, 2(4), 278-286.

Buckels, E. E., & Trapnell, P. D. (2013). Disgust facilitates outgroup dehumanization. *Group Processes & Intergroup Relations*, 16, 771-780.

Cashdan, E., & Steele, M. (2013). Pathogen prevalence, group bias, and collectivism in the standard cross-cultural sample. *Human Nature*, 24(1), 59-75.

Cheng, C., Wong, W., & Tsang, K. W. (2006). Perception of benefits and costs during SARS outbreak: An 18-month prospective study. *Journal of Consulting and Clinical Psychology*, 74(5), 870–879.

Currie, T. E., & Mace, R. (2012). Analyses do not support the parasite-stress theory of human sociality. *Behavioral and Brain Sciences*, 35(2), 83–85.

Davtyan, M., Brown, B., & Folayan, M. O. (2014). Addressing Ebola-related stigma: Lessons learned from HIV/AIDS. *Global Health Action*, 7(1), 26058.

De Barra, M., & Curtis, V. (2012). Are the pathogens of out-groups really more dangerous? *Behavior and Brain Sciences*, 35, 85–86.

De Barra, M., DeBruine, L. M., Jones, B. C., Mahmud, Z. H., & Curtis, V. A. (2013). Illness in childhood predicts face preferences in adulthood. *Evolution and Human Behavior*, 34(6), 384–389.

DeBruine, L. M., Jones, B. C., Crawford, J. R., Welling, L. L., & Little, A. C. (2010). The health of a nation predicts their mate preferences: Cross cultural variation in women' s preferences for masculinized male faces. *Proceedings of the Royal Society of London: Series B: Biological Sciences*, 277, 2405–2410.

DeBruine, L. M., Jones, B. C., Tybur, J. M., Lieberman, D., & Griskevicius, V. (2010). Women' s preference for masculinity in male faces are predicted by pathogen disgust, but not by moral or sexual disgust. *Evolution and Human Behavior*, 31, 69–74.

Duncan, L. A., & Schaller, M. (2009). Prejudicial attitudes toward older adults may be exaggerated when people feel vulnerable to infectious disease: Evidence and implications. *Analyses of Social Issues and Public Policy*, 9(1), 97–115.

Duncan, L. A., Schaller, M., & Park, J. H. (2009). Perceived vulnerability to disease: Development and validation of a 15-item self-report instrument. *Personality and Individual Differences*, 47(6), 541–546.

Eckersley, R. (2010). Commentary on Trzesniewski and Donnellan (2010): A transdisciplinary perspective on young people' s well-being. *Perspectives on Psychological Science*, 5, 76–80.

Eckersley, R., & Dear, K. (2002). Cultural correlates of youth suicide. *Social Science & Medicine*, 55, 1891–1904.

Elad-Strenger, J., Proch, J., & Kessler, T .(2020). Is disgust a "conservative" emotion? *Personality and Social Psychology Bulletin*, 46(6), 896–912.

Erskine, K. J., Kacinik, N. A., & Prinz, J. J. (2011). A bad taste in the mouth: Gustatory disgust influences moral judgment. *Psychological Science*, 22(3), 295–299.

Faulkner, J., Schaller, M., Park, J. H., & Duncan, L. A. (2004). Evolved disease-avoidance mechanisms and contemporary xenophobic attitudes. *Group Processes & Intergroup Relations*, 7, 333–353.

Fay, A. J., & Bovier, E. R. (2018). Testing a curvilinear relationship between chemosensory responsivity and avoidance motivation. *Adaptive Human Behavior and Physiology*, 4, 207–222.

Fincher, C. L., & Thornhill, R. (2008). Assortative sociality, limited dispersal, infectious disease and the genesis of the global pattern of religion diversity. *Proceedings of the Royal Society of London:Series B: Biological Sciences*, 275, 2587–2594.

Fincher, C. L., & Thornhill, R. (2012). Parasite-stress promotes in-group assortative sociality: The cases of strong family ties and heightened religiosity. *Behavioral & Brain Sciences*, 35(2), 85–86.

Fincher, C. L., Thornhill, R., Murray, D. R., & Schaller, M. (2008). Pathogen prevalence predicts human cross-cultural variability in individualism/collectivism. *Proceedings of the Royal Society B*, 275(1640), 1279–1285.

Ganesan, A., & Dar-Nimrod, I. (2019). Experimental examination of social transmission of health information using an online platform. *Health Communication*, 21, 1–9.

Ganesan, A., Kashima, Y., Kiat, J. E., & Dar-Nimrod, I. (2019). Transmission of disorder and etiological information: Effects on health knowledge recollection and health-related cognition. *PloS One*, 14(6), e0218703.

Gangestad, S. W., & Buss, D. M. (1993). Pathogen prevalence and human mate preferences. *Ethology and sociobiology*, 14(2), 89–96.

Gretz, M. R., & Huff, M. J. (2019). Did you wash your hands? Evaluating memory for objects touched by healthy individuals and individuals with contagious and noncontagious diseases. *Applied Cognitive Psychology*, 33(6), 1271–1278.

Grossmann, I., & Varnum, M. E. W. (2015). Social structure, infectious diseases, disasters, secularism, and cultural change in America. *Psychological Science*, 26(3), 311–324.

Hackman, J., & Hruschka, D. (2013). Fast life histories, not pathogens, account for state-level variation in homicide, child maltreatment, and family ties in the U.S. *Evolution and Human Behavior*, 34(2), 118–124.

Hadley, C., & Hruschka, D. (2017). Stability and change in in-group mate preferences among young people in Ethiopia are predicted by food security and gender attitudes, but not by expected pathogen exposures. *Human Nature*, 28(4), 395–406.

Haselton, M. G., & Nettle, D. (2006). The paranoid optimist: An integrative evolutionary model of cognitive biases. *Personality and Social Psychology Review*, 10(1), 47–66.

Hill, S. E., Prokosch, M. L., & DelPriore, D. J. (2015). The impact of perceived disease threat on women' s desire for novel dating and sexual partners: Is variety the best medicine? *Journal of Personality and Social Psychology*, 109(2), 244-261.

Horberg, E. J., Oveis, C., Keltner, D., & Cohen, A. B. (2009). Disgust and the moralization of purity. *Journal of Personality and Social Psychology*, 97(6), 963-976.

Horita, Y., & Takezawa, M. (2018). Cultural differences in strength of conformity explained through pathogen stress: A statistical test using hierarchical bayesian estimation. *Frontiers in Psychology*, 9, e1921.

Hruschka, D., Efferson, C., Jiang, T., Falletta-Cowden, A., Sigurdsson, S., McNamara, R., ···Henrich, J. (2014). Impartial institutions, pathogen stress and the expanding social network. *Human Nature*, 25(4), 567-579.

Huang, J. Y., Ackerman, J. M., & Sedlovskaya, A. (2017). (De)contaminating product preferences: A multi-method investigation into pathogen threat' s influence on used product preferences. *Journal of Experimental Social Psychology*, 70, 143-152.

Huang, J. Y., Sedlovskaya, A., Ackerman, J. M., & Bargh, J. A. (2011). Immunizing against prejudice: Effects of disease protection on attitudes toward out-groups. *Psychological Science*, 22(12), 1550-1556.

Hunt, D. F., Cannell, G., Davenhill, N. A., Horsford, S. A., Fleischman, D. S., & Park, J. H. (2017). Making your skin crawl: The role of tactile sensitivity in disease avoidance. *Biological Psychology*, 127, 40-45.

Inbar, Y., Pizarro, D. A., & Bloom, P. (2012). Disgusting smells cause decreased liking of gay men. *Emotion*, 12(1), 23-27.

Inbar, Y., Westgate, E. C., Pizarro, D. A., & Nosek, B. A. (2016). Can a naturally occurring pathogen threat change social attitudes? Evaluations of gay men and lesbians during the 2014 Ebola epidemic. *Social Psychological and Personality Science*, 7, 420-427.

Jing, Y., & Cai, H. (2020). Understanding Chinese morality from a cultural diversity perspective. (unpublished manuscript).

Jones, B. C., Feinberg, D. R., Watkins, C. D., Fincher, C. L., Little, A. C., & DeBruine, L. M. (2013). Pathogen disgust predicts women' s preferences for masculinity in men' s voices, faces, and bodies. *Behavioral Ecology*, 24, 373-379.

Jones, K. E., Patel, N. G., Levy, M. A., Storeygard, A., Balk, D., Gittleman, J. L., & Daszak, P. (2008). Global trends in emerging infectious diseases. *Nature*, 451(7181), 990-993.

Kandrik, M., Hahn, A. C. Fisher, C. I. Wincenciak, J. & Jones, B. C. (2017). Are physiological and behavioral immune responses negatively correlated? Ev-

idence from hormone-linked differences in men' s face preferences. *Hormones and Behavior*, 87, 57–61.

Kim, H. S., Sherman, D. K., & Updegraff, J. A. (2016). Fear of Ebola: the influence of collectivism on xenophobic threat responses. *Psychological Science*, 27(7), 935–944.

Kuppens, T., & Pollet, T. V. (2014). Mind the level: Problems with two recent nation-level analyses in psychology. *Frontiers in Psychology*, 5, e1110.

Kusche, I., & Barker, J. L. (2019). Pathogens and immigrants: A critical appraisal of the behavioral immune system as an explanation of prejudice against ethnic outgroups. *Frontiers in Psychology*, 10, e2412.

Lee, A. J., Brooks, R. C., Potter, K. J., & Zietsch, B. P. (2015). Pathogen disgust sensitivity and resource scarcity is associated with mate preference for different waist-to-hip ratios, shoulder-to-hip ratios, and body mass index. *Evolution & Human Behavior*, 36(6), 480–488.

Lee, A. J., Dubbs, S. L., Kelly, A. J., von Hippel, W., Brooks, R. C., & Zietsch, B. P. (2013). Human facial attributes, but not perceived intelligence, are used as cues of health and resource provision potential. *Behavioral Ecology*, 24(3), 779–787.

Little, A. C., DeBruine, L. M., & Jones, B. C. (2011). Exposure to visual cues of pathogen contagion changes preferences for masculinity and symmetry in opposite-sex faces. *Proceedings of the Royal Society of London: Series B: Biological Sciences*, 278, 2032–2039.

Lund, E. M., & Miller, S. L. (2014). Is obesity un-American? Disease concerns bias implicit perceptions of national identity. *Evolution and Human Behavior*, 35(4), 336–340.

Macmurray, J., Comings, D. E., & Napolioni, V. (2014). The gene-immune-behavioral pathway: Gamma-interferon (IFN-γ) simultaneously coordinates susceptibility to infectious disease and harm avoidance behaviors. *Brain Behavior and Immunity*, 35, 169–175.

Miller, S. L., & Maner, J. K. (2011). Sick body, vigilant mind: The biological immune system activates the behavioral immune system. *Psychological Science*, 22(12), 1467–1471.

Miller, S. L., & Maner, J. K. (2012). Overperceiving disease cues: The basic cognition of the behavioral immune system. *Journal of Personality and Social Psychology*, 102(6), 1198–1213.

Mortensen, C. R., Becker, D. V., Ackerman, J. M., Neuberg, S. L., & Kenrick, D. T. (2010). Infection breeds reticence the effects of disease salience on self-perceptions of personality and behavioral avoidance tendencies. *Psychological Science*, 21(3), 440–447.

Mullett, T. L., Brown, G. D. A., Fincher, C. L., Kosinski, M., & Stillwell, D. (2019). Individual-level analyses of the impact of parasite stress on personality: Reduced openness only for older individuals. *Personality and Social Psychology Bulletin*, 46(1), 79–93.

Murray, D. R. (2014). Direct and indirect implications of pathogen prevalence for scientific and technological innovation. *Journal of Cross-Cultural Psychology*, 45(6), 971–985.

Murray, D. R., Gildersleeve, K. A., Fales, M. R., & Haselton, M. G. (2017). MHC homozygosity is associated with fast sexual strategies in women. *Adaptive Human Behavior and Physiology*, 3, 101–117.

Murray, D. R., Jones, D. N., & Schaller, M. (2013). Perceived threat of infectious disease and its implications for sexual attitudes. *Personality and Individual Differences*, 54(1), 103–108.

Murray, D. R., Prokosch, M. L., & Airington, Z. (2019). PsyhoBehavioroimmunology: Connecting the behavioral immune system to its physiological foundations. *Frontiers in Psychology*, 10, e200.

Murray, D. R., & Schaller, M. (2012). Threat (s) and conformity deconstructed: Perceived threat of infectious disease and its implications for conformist attitudes and behavior. *European Journal of Social Psychology*, 42(2), 180–188.

Murray, D. R., & Schaller, M. (2016). The behavioral immune system: Implications for social cognition, social interaction, and social influence. In J. M. Olson & M. P. Zanna (Eds.), *Advances in experimental social psychology: Vol. 53. Advances in experimental social psychology* (pp. 75–129). Elsevier Academic Press.

Murray, D. R., Schaller, M., & Suedfeld, P. (2013). Pathogens and politics: Further evidence that parasite prevalence predicts authoritarianism. *PLoS One*, 8(5), e62275.

Murray, D. R., Trudeau, R., & Schaller, M. (2011). On the origins of cultural differences in conformity: Four tests of the pathogen prevalence hypothesis. *Personality and Social Psychology Bulletin*, 37(3), 318–329.

Na, J., Grossmann, I., Varnum, M. E., Kitayama, S.,Gonzalez, R., & Nisbett, R. E. (2010). Cultural differences are not always reducible to individual differences. *Proceedings of the National Academy of Sciences of the United States of America*, 107(14), 6192–6197.

Navarrete, C. D., & Fessler, D. M. T. (2006). Disease avoidance and ethnocentrism: The effects of disease vulnerability and disgust sensitivity on intergroup attitudes. *Evolution and Human Behavior*, 27, 270–282.

Nesse, R. M. (2005). Natural selection and the regulation of defenses: A signal detection analysis of the smoke detector principle. *Evolution and Human Behavior*, 26(1), 88–105.

Nussinson, R., Mentser, S., & Rosenberg, N. (2018). Sensitivity to deviance and to dissimilarity: Basic cognitive processes under activation of the behavioral immune system. *Evolutionary Psychology*, 16(4), 1-13.

Olatunji, B. O., Adams, T., Ciesielski, B., David, B., Sarawgi, S., & Broman-Fulks, J. (2012). The three domains of disgust scale: Factor structure, psychometric properties, and conceptual limitations. *Assessment*, 19(2),

Olatunji, B. O., & Puncochar, B. D. (2016). Effects of disgust priming and disgust sensitivity on moral judgement. *International Journal of Psychology*, 51(2), 102-108.

Oosterhoff, B., Shook, N. J., & Ford, C. (2018). Is that disgust I see? Political ideology and biased visual attention. *Behavioural brain research*, 336, 227-235.

Oosterhoff, B., Shook, N. J., & Iyer, R. (2018). Disease avoidance and personality: A meta-analysis. *Journal of Research in Personality*, 77, 47-56.

O' Shea, B., Watson, D., Brown, G., & Fincher, C. (2020). Infectious disease prevalence, not race exposure, predicts both implicit and explicit racial prejudice across the United States. *Social Psychological and Personality Science*, 11(3), 345-355.

Park, J. H., Faulkner, J., & Schaller, M. (2003). Evolved disease-avoidance processes and contemporary anti-social behavior: Prejudicial attitudes and avoidance of people with physical disabilities. *Journal of Nonverbal Behavior*, 27(2), 65-87.

Park, J. H., Schaller, M., & Crandall, C. S. (2007). Pathogen-avoidance mechanisms and the stigmatization of obese people. *Evolution and Human Behavior*, 28(6), 410-414.

Petersen, M. B. (2017). Healthy out-group members are represented psychologically as infected in-group members. *Psychological Science*, 28(12), 1857-1863.

Pollet, T. V. (2014). A re-analysis of the relationship between "parasite stress" and authoritarianism. *Frontiers in Psychology*, 5(3), e638.

Pollet, T. V., Tybur, J. M., Frankenhuis, W. E., & Rickard, I. J. (2014). What can cross-cultural correlations teach us about human nature? *Human Nature*, 25(3), 410-429.

Prokosch, M. L., Gassen, J., Ackerman, J. M., & Hill, S. E. (2019). Caution in the time of cholera: Pathogen threats decrease risk tolerance. *Evolutionary Behavioral Sciences*,13(4), 311-334.

Puterman, E., Delongis, A., Lee-Baggley, D., & Greenglass, E. (2009). Coping and health behaviours in times of global health crises: Lessons from SARS and West Nile. *Global Public Health*,4(1), 69-81.

Robinson, E. J. H., & Barker, J. L. (2017). Inter-group cooperation in humans and other animals. *Biology Letters*,13(3), 20160793.

Robinson, W. S. (1950). Ecological correlations and the behavior of individuals. *International Journal of Epidemiology*, 38, 337–341.

Ross, C. T., & Winterhalder, B. (2016). A hierarchical Bayesian analysis of parasite prevalence and sociocultural outcomes: The role of structural racism and sanitation infrastructure. *American Journal of Human Biology*, 28(1), 74–89.

Schaller, M. (2006). Parasites, behavioral defenses, and the social psychological mechanisms through which cultures are evoked. *Psychological Inquiry*, 17, 96–101.

Schaller, M. (2015). The behavioral immune system. In D. M. Buss (Eds.), *Handbook of evolutionary psychology* (2nd ed). New York: Wiley.

Schaller, M., Miller, G. E., Gervais, W. M., Yager, S., & Chen, E. (2010). Mere visual perception of other people's disease symptoms facilitates a more aggressive immune response. *Psychological Science*, 21(5), 649–652.

Schaller, M., & Murray, D. R. (2008). Pathogens, personality, and culture: disease prevalence predicts worldwide variability in sociosexuality, extraversion, and openness to experience. *Journal of Personality and Social Psychology*, 95(1), 212–221.

Schaller, M., & Neuberg, S. L. (2012). Danger, disease, and the nature of prejudice(s). In M. P. Zanna, & J. M. Olson (eds.), *Advances in Experimental Social Psychology*, Volume 46. USA: Academic Press.

Schaller, M., & Park, J. H. (2011). The behavioral immune system (and why it matters). *Current Directions in Psychological Science*, 20(2), 99–103.

Shakhar, K. (2019). The inclusive behavioral immune system. *Frontiers in Psychology*, 10, e1004.

Shook, N.J., Oosterhoff, B., Terrizzi, J., & Clay, R. (2017). Disease avoidance: An evolutionary perspective on personality and individual differences. In Shackelford & Ziger-Hill (eds.), *The SAGE handbook of personality and individual differences*. New York, NY: Sage.

Smith, R. A., & Hughes, D. (2014). Infectious disease stigmas: Maladaptive in modern society. *Communication studies*, 65(2), 132–138.

Smith, K. B., Oxley, D., Hibbing, M. V., Alford, J. R., & Hibbing, J. R. (2011). Disgust sensitivity and the neurophysiology of left-right political orientations. *PloS ONE*, 6, e25552.

Stevenson, R. J., Hodgson, D., Oaten, M. J., Moussavi, M., Langberg, R., Case, T. I., & Barouei, J. (2012). Disgust elevates core body temperature and up-

regulates certain oral immune markers. *Brain Behavior and Immunity*, 26(7), 1160–1168.

Stone, A., & Potton, A. (2017). Emotional responses to disfigured faces and disgust sensitivity: An eye-tracking study. *Journal of Health Psychology*, 24(9), 1191–1200.

Talhelm, T., Zhang, X., Oishi, S., Shimin, C., Duan, D., Lan, X., & Kitayama, S. (2014). Large-scale psychological differences within china explained by rice versus wheat agriculture. *Science*, 344(6184), 603–608.

Terrizzi, J. A., Clay, R., & Shook, N. J. (2014). Does the behavioral immune system prepare females to be religiously conservative and collectivistic? *Personality and Social Psychology Bulletin*, 40(2), 189–202.

Terrizzi, J. A., Shook, N. J., & McDaniel, M. A. (2013). The behavioral immune system and social conservatism: A meta-analysis. *Evolution and Human Behavior*, 34, 99–108.

Terrizzi, J. A., Shook, N. J., & Ventis, W. L. (2010). Disgust: A predictor of social conservatism and prejudicial attitudes towards homosexuals. *Personality and Individual Differences*, 49, 587–592.

Terrizzi, J., Shook, N., & Ventis, L. (2012). Religious conservatism: An evolutionarily evoked disease-avoidance strategy. *Religion, Brain & Behavior*, 2, 105–120.

Thornhill, R., Fincher, C. L., Murray, D. R., & Schaller, M. (2010). Zoonotic and non-zoonotic diseases in relation to human personality and societal values: Support for the parasite-stress model. *Evolutionary Psychology*, 8(2), 151–169.

Tiokhin, L., & Hruschka, D. (2017). No evidence that an Ebola outbreak influenced voting preferences in the 2014 elections after controlling for time-series autocorrelation: A Commentary on Beall, Hofer, and Schaller (2016). *Psychological science*, 28(9), 1358–1360.

Tskhay, K. O., Wilson, J. P., & Rule, N. O. (2016). People use psychological cues to detect physical disease from faces. *Personality and Social Psychology Bulletin*, 42(10), 1309–1320.

Tybur, J. M., Bryan, A. D., Lieberman, D., Hooper, A. E. C., & Merriman, L. A. (2011). Sex differences and sex similarities in disgust sensitivity. *Personality and Individual Differences*, 51(3), 343–348.

Tybur, J. M., Bryan, A. D., Magnan, R. E., & Hooper, A. E. C. (2011). Smells like safe sex: Olfactory pathogen primes increase intentions to use condoms. *Psychological Science*, 22(4), 478–480.

Tybur, J. M., & de Vries, R. E. (2013). Disgust sensitivity and the HEXACO model of personality. *Personality and Individual Differences*, 55, 660–665.

Tybur, J. M., Frankenhuis, W. E., & Pollet, T. V. (2014). Behavioral immune system methods: Surveying the present to shape the future. *Evolutionary Behavioral Sciences*, 8(4), 274–283.

Tybur, J. M., & Gangestad, S. W. (2011). Mate preferences and infectious disease: Theoretical considerations and evidence in humans. *Philosophical Transactions of the Royal Society of London: Series B: Biological Sciences*, 366, 3375–3388.

Tybur, J., Inbar, Y., Aarøe, L., Barclay, P., Barlow, F. K., de Barra, M., ···Žezelj., I. (2016). Parasite stress and pathogen avoidance relate to distinct dimensions of political ideology across 30 nations. *Proceedings of the National Academy of Sciences*, 113(44), 12408–12413.

Tybur, J. M., & Lieberman, D. (2016). Human pathogen avoidance adaptations. *Current Opinion in Psychology*, 7,

Tybur, J. M., Lieberman, D., & Griskevicius, V. (2009). Microbes, mating, and morality: Individual differences in three functional domains of disgust. *Journal of Personality and Social Psychology*, 97(1), 103–122.

Van Leeuwen, F., & Petersen, M. B. (2018). The behavioral immune system is designed to avoid infected individuals, not outgroups. *Evolution and Human Behavior*, 39, 226–234.

Walter, K. V., Conroy-Beam, D., Buss, D. M., Asao, K., Sorokowska, A., Sorokowski, P., ···Zupančič, M. (2020). Sex differences in mate preferences across 45 countries: A large-scale replication. *Psychological Science*, 31(4), 408–423.

Wheaton, M. G., Abramowitz, J. S., Berman, N. C., Fabricant, L. E., & Olatunji, B. O. (2012). Psychological predictors of anxiety in response to the H1N1 (swine flu) pandemic. *Cognitive Therapy & Research*, 36(3),

White, A. E., Kenrick, D. T., & Neuberg, S. L. (2013). Beauty at the ballot box: Disease threats predict preferences for physically attractive leaders. *Psychological Science*, 24(12), 2429-2436.

World Health Organization. (2015). *World health in 2015: From MDGs, millennium development goals to SDGs, sustainable development goals*. Geneva, Switzerland.

Wu, B. P., & Chang, L. (2012). The social impact of pathogen threat: How disease salience influences conformity. *Personality and Individual Differences*, 53(1), 50–54.

Young, S. G., Sacco, D. F., & Hugenberg, K. (2011). Vulnerability to disease is associated with a domain-specific preference for symmetrical faces relative to symmetrical non-face stimuli. *European Journal of Social Psychology*, 41, 558–563.

Zhang, J. (2018). Contemporary parasite stress curvilinearly correlates with outgroup trust: Cross-country evidence from 2005 to 2014. *Evolution and Human Behavior*, 39(5), 556–565.

The Behavioral Immune System: A Multi-Level Reconsideration

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Abstract: The theory of Behavioral Immune System (BIS) posits that to cope with pandemic stress, human beings have evolved a series of behavioral responses, including vigilance to and disgust of disease cues, preference for healthy mate and collectivism, prejudice against out-groups and so on. For the first time, the existing studies were reviewed according to research level (individual vs. group). A large body of supportive evidence for BIS at both levels was identified, though many inconsistent and/or conflicting findings exist. Reasons leading to such inconsistencies include inadequacies of research methods, theory basis, and applicability in modern society. Future research should examine the boundary conditions of existing findings and theory; extend the scope of the current research; explore the underlying biological and physiological mechanism of BIS.

Keywords: pathogen; Behavioral Immune System; infectious disease

Note: Figure translations are in progress. See original paper for figures.