BEHAVIORAL IMMUNE SYSTEM: ITS PSYCHOLOGICAL BASES AND FUNCTIONS

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BEHAVIORAL IMMUNE SYSTEM: ITS PSYCHOLOGICAL BASES AND FUNCTIONS

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EDITORIAL
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Editorial: Behavioral Immune System: Its Psychological Bases and Functions

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Editorial on the Research Topic

Behavioral Immune System: Its Psychological Bases and Functions

Currently, the world is in the midst of the COVID-19 pandemic. This has reminded us of the threat posed by infectious diseases. In some countries, cities were temporarily locked down and people were restricted from traveling. This severely affected our economy and culture, and mental health problems associated with this situation have arisen. This infectious disease has significantly impacted societies and people. Moreover, the threat has significantly altered individual behavior. People have become socially distant and have had to frequently sterilize their hands. In some areas, wearing masks has become mandatory, and there have even been legal penalties for those who violated local rules. The pandemic has changed our behavior dramatically.

These behavioral changes, both at the individual and community levels, appear to have been driven by the goal of disease avoidance. From the standpoint of this Research Topic, it can also be said that the threat of infectious diseases has resulted in a collective activation of the behavioral immune system (BIS). When we started this Research Topic, we did not anticipate this situation. Now, however, it has become highly relevant. While not welcome, it has provided a basis for understanding human behaviors under pandemics.

BIS is a motivational system with the goal of disease avoidance. It estimates the presence of pathogens from perceptual cues in the environment and elicits relevant emotional and cognitive responses. Such responses induce avoidance behavior in a pathogenic environment (Schaller and Park, 2011). This sequence of psychological responses, by preventing contact with and penetration into the body of these infectious sources, compensates for the physiological immune system which can sometimes be physically high cost (Murray and Schaller, 2016). The theory of BIS has an evolutionary psychological basis, and it has been used to explain and predict a wide range of human behaviors (Ackerman et al., 2018). Additionally, the description of detailed mechanisms for disease avoidance redefined the adaptive value of disgust, which is a key emotion in BIS.

BIS has been revealed to be associated with diverse human behaviors. However, it remains unclear what components it consists of and how it is derived from our biological foundations. In this regard, Murray et al. provided a comprehensive discussion of the psychophysiological basis of BIS, which included sensory, cellular, and genetic perspectives. They offered an in-depth description of the current state of PsychoBehavioroimmunology regarding BIS, including an extensive review. The work of Cañas-Gonzaléz et al. demonstrated that physiological immunity affects the state of depression. A study by Iwasa et al., which provided a psychophysical analysis of

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visual pathogen detection, can be understood as a practical example of a specific study for the general remarks made by Murray et al.. Additionally, Shakhar provided a conceptual analysis of a more inclusive view of BIS based on its genetic origins. While referring to Hamilton (1964) inclusive selection theory, Shakhar stated that BIS works to protect not only an individual itself but also the kin around the person. In this regard, BIS protects others through the individual's disease behaviors and social immunity behaviors, favoring the whole "kin selection." This is an attempt to conceptually extend BIS and provide a fresh perspective in this field.

The study of the relationship between BIS and various human behaviors elucidates its functional characteristics. One of the human behaviors affected by BIS is sexual conduct. Sexual behavior is inevitably associated with the risk of sexually transmitted infections (STIs). Sexual arousal and physical attractiveness influence male sexual decision making; considering the risk of STI, the disgust emotion may also be associated with it. Oaten et al., using a survey to detect substantial sexual arousal, indicated that arousal decreases state disgust and STI risk judgments, and increases willingness to have sex. Furthermore, they identified that low trait disgust predicted a strong willingness to have sex. This study is a good example of the functional characteristics of BIS, describing how the sexual motivation system and BIS work against each other to control sexual decision-making.

Considering the functional aspects of BIS, we cannot ignore its pervasive influence on our attitudes. Liuzza et al. revealed that moral judgments about purity are influenced by disgust sensitivity to body odor; Tsegmed et al. observed that negative implicit attitudes toward agricultural and aquatic products from Fukushima were related to thoughts about nuclear contamination. These studies reiterate how the BIS functions to avoid disease through attitude change. The work of Stewart et al., revealing the impact of disgust on people's religiosity, is another example depicting the influence of BIS on people's attitudes. In contrast, some articles presented new research agendas in this area. Horita and Takezawa reexamined the impact of pathogen stress on collectivism and conformity using Bayesian statistics and revealed that the impact may be more limited than originally thought. Wu et al. revealed that the degree of acceptance of ingroup members tended to decrease compared to outgroup members in the context of disease (e.g., ingroup derogation). Concerning the association between BIS and outgroup prejudice, Kusche and Barker's article, which proposed a model including social contexts such as family environment and mass media, provided us with substantial inspiration.

Research on BIS has come to encompass a wide range of human behavior. Ito et al. discussed the role of BIS in social anxiety in terms of the behavioral inhibition system and behavioral activation system; the impact of BIS on mental and physical health is one of the areas that is expected to grow, especially in today's world, under the influence of serious infectious diseases. In conclusion, based on the psychophysiological foundation of BIS, it is necessary to further clarify the relationship between perception, cognition, personality, social relationships, and psychiatric disorders, and individual behavior and attitudes, thus developing a conceptual, mathematical, and psychological model that comprehensively explains their functioning. Only then will we be able to understand the practical applicability of BIS to psychotherapies and policymaking.

AUTHOR CONTRIBUTIONS

The editorial was drafted by KI and YY and approved by the topic co-editors. All authors listed have made a substantial contribution to this Research Topic and have approved this editorial for publication.

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ORIGINAL RESEARCH
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Cultural Differences in Strength of Conformity Explained Through Pathogen Stress: A Statistical Test Using Hierarchical Bayesian Estimation

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The severity of the environment has been found to have played a selective pressure in the development of human behavior and psychology, and the historical prevalence of pathogens relate to cultural differences in group-oriented psychological mechanisms, such as collectivism and conformity to the in-group. However, previous studies have also proposed that the effectiveness of institutions, rather than pathogen stress, can account for regional variation in group-oriented psychological mechanisms. Moreover, previous studies using nations as units of analysis may have suffered from a problem of statistical non-independence, namely, Galton's problem. The present study tested whether or not regional variation in pathogen stress, rather than government effectiveness, affected collectivism and conformity to social norms by adjusting the effect of global regions using hierarchical Bayesian estimation. We found that the overall effect of pathogen stress remained significant in only one out of the four indices of the regional variability of conformity, and the effects of the government effectiveness also disappeared. Instead, we found that significant effects of both pathogen stress and government effectiveness in specific regions of the world, but these effects were not stable across the measurements. These results indicate that both the effects of pathogen stress and government effectiveness need further reevaluation.

Keywords: collectivism, conformity, pathogen stress, institution, Galton's problem, hierarchical model, Bayesian estimation

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INTRODUCTION

Humans live in large-scale groups, and each group forms different cultural values. Studies in cross-cultural psychology have reported cultural differences in psychological mechanisms (Triandis, 1995; Hofstede, 2001; Gelfand et al., 2004). Recently, the reasons for these cross-cultural differences in values have been explained as adaptation to ecological threats.

A group of cultural and evolutionary psychologists have argued that ecological threats such as pathogen stress have played a significant role in adapting human psychology to local ecology. A series of studies based on the "behavioral immune system hypothesis" (Schaller, 2011; Murray and Schaller, 2016) has argued that the prevalence of infectious diseases was one of the important ecological variables to explain the cultural differences in human collectivistic psychology and behaviors (Fincher et al., 2008; Schaller and Murray, 2008; Thornhill et al., 2009, 2010; Murray and Schaller, 2010, 2012; Murray et al., 2011, 2013; Schaller, 2011; Fincher and Thornhill, 2012; Van Leeuwen et al., 2012; Cashdan and Steele, 2013; Varnum, 2013; Murray, 2014; Tybur et al., 2016). Infectious diseases historically served as significant ecological hazards and imposed strong selection pressure on humans. Humans, along with other animals, are thought to have acquired functionally adaptive psychological or behavioral responses to the dangers posed by infectious diseases. In contexts characterized by a higher prevalence of infectious diseases, avoiding interactions with unknown out-group members might have been an adaptive response, since extroversion brings a greater risk of exposure to infections. In addition, conformity to social norms has also been argued to be beneficial in such contexts, because the traditional norms or rituals incorporate methods of avoiding infection, and individuals gain significantly more social support from in-group members by adhering to these norms (Schaller, 2011; Murray and Schaller, 2016).

Cross-cultural studies have provided evidence supporting this hypothesis. Previous studies that conducted group-level analysis with countries as units of analysis have shown that the regional variation in the historical prevalence of pathogens was positively associated with regional variation in collectivism (Fincher et al., 2008; Murray and Schaller, 2010; Thornhill et al., 2010; Cashdan and Steele, 2013). Although collectivism is a broad and multifaceted concept, researchers have further found positive relationships with other, more concrete variables, including the diversity of extraversion personality (Schaller and Murray, 2008), tightness of social norms (Gelfand et al., 2011), strength of family ties (Fincher and Thornhill, 2012), group-oriented moral concerns (Van Leeuwen et al., 2012), individuals' authoritarian personality (Murray et al., 2013), adherence to traditional norms (Tybur et al., 2016), and conformity (Murray et al., 2011; Murray and Schaller, 2012; Varnum, 2013). Thus, these studies suggested that harsh natural environments functioned as selection pressure to enhance the psychology supporting in-group cooperation.

Other researchers have argued that the effect of pathogen stress has been confounded with the other social factors such as effectiveness of institutions (Hruschka and Henrich, 2013; Hruschka et al., 2014). Hruschka and Henrich (2013) found that the relationships between pathogen stress and the regional level of collectivism and in-group favoritism disappeared when regional differences in the effectiveness of modern institutions were controlled. These differences represent how effectively regions provide civil or public services, which were significantly (and negatively) associated with regional levels of collectivism and in-group favoritism (Hruschka and Henrich, 2013). Thus, such recent studies have raised doubts about the effects of pathogen stress on the development of group-oriented psychological mechanisms.

Nation-unit analyses always suffer from Galton's problem (Mace and Pagel, 1994), in which units of analysis fail to ensure statistical independence. These previous studies employed regression analysis using countries (or regions) as units of analysis (Fincher et al., 2008; Thornhill et al., 2010; Murray et al., 2011; Hruschka and Henrich, 2013). However, countries are not statistically independent units; neighboring countries often share a common historical ancestry and thus tend to share similar cultural traits, not as a result of adaptation to a similar local ecology but simply as a result of shared historical backgrounds. Therefore, results of simple country-level analysis are not reliable, since they incorrectly assume the statistical independence of their units, which raises the risk of spurious associations. Currie and Mace (2012) found no consistent associations between pathogen prevalence and one form of human social behavior (religious participation) within each global region (i.e., Africa, Europe, East Eurasia, and so on).

Previous studies have accounted for this problem in several different ways. Some grouped countries into global regions related to shared historical and geographical backgrounds, computing correlations with these as units of analysis (Fincher et al., 2008; Murray et al., 2011; Fincher and Thornhill, 2012; Murray, 2014). However, this solution greatly reduces the number of data points to 6–10. Correlation coefficients calculated using such small samples are known to be unreliable and often exhibit inflated effect sizes (Yarkoni, 2009; Schönbrodt and Perugini, 2013). A common solution that is often employed in anthropology is to use the Standard Cross-Cultural Sample (SCCS; Murdock and White, 1969). This is a database that mainly consists of traditional smaller-scale societies sampled so that the cultural and historical relationships among the data points are minimized. Certain scholars have analyzed the SCCS to test the influence of pathogen prevalence on group-oriented psychology (Cashdan and Steele, 2013; Murray et al., 2013) and ritualized behavior (Murray et al., 2017). However, this solution is not feasible for the analysis of different types of data, in which nation states are a primary unit. More importantly, it has been recently shown that significant autocorrelations exist in the SCCS (Dow and Eff, 2008), which raises the question of the validity of the SCCS as a dataset for solving Galton's problem (for other problems of the SCCS, see Mace and Holden, 2005; Nettle, 2009). Researchers seem to have agreed that the best approach to take is the phylogenetic one (Mace and Pagel, 1994; Mace and Holden, 2005; Beheim and Bell, 2011; Botero et al., 2014; Mathew and Perreault, 2015), in which the influences of shared cultural and historical ancestry are statistically controlled using phylogenetic information estimated from other sources, such as language family, historical records, and spatial proximity. However, the information necessary for applying the phylogenetic approach is not always available.

In this study, we propose another method for handling Galton's problem for nation-level analysis: hierarchical Bayesian models, with global regions as random effects. Nettle (2009) reviewed anthropological studies on the influence of pathogen prevalence on human social systems, explicitly discussing the advantages of this approach. Galton's problem can be rephrased to state that countries sharing a common historical and cultural ancestry should be correlated with each other and cannot be assumed to be statistically independent data points. This non-independence is often exhibited as spatial autocorrelation. With the use of global regions as random effects, autocorrelation can be appropriately controlled, even without knowing the exact processes that produce the correlations among neighboring countries (Nettle, 2009). The benefits of this approach have recently been demonstrated in the context of language evolution. Using cross-cultural, correlational analyses, Kashima and Kashima (1998) found that the presence of a linguistic phenomenon called the "pronoun-drop effect" is significantly correlated with the level of collectivism of the given culture. Lee (2017) conducted hierarchical Bayesian modeling to test the robustness of the finding, showing that the relationship between the phenomenon and individualism was not universal but observed only in a particular language family (the Indo-European language family).

We conducted hierarchical Bayesian modeling to estimate the effects of both regional pathogen stress and government effectiveness on variables related to group-oriented psychology. In our models, each country was nested within one of the six global regions, and the global regions were included as random effects. Under this framework, countries belonging to the same global region was assumed to share a common effect of the global region.

We conducted the analyses with two dependent variables: collectivism and conformity. Although collectivism is a broad and multifaceted concept, it appears to be a core dependent variable in the literature and its relationship with pathogen prevalence has been replicated in multiple studies. Collectivism includes both intergroup-oriented (e.g., xenophobic attitudes or barriers between social groups) and intragroup-oriented (e.g., conformity to social norms or in-group members) psychological constructs. Past studies have suggested that the regional strength of pathogen stress is more strongly related to the latter than to the former (Cashdan and Steele, 2013; Tybur et al., 2016). Thus, to rigorously examine the association of environmental severity with in-group oriented psychological constructs, we particularly focused on a concept of conformity, testing the hypothesis that pathogen stress affects conformity, even when the effect of institutions is controlled for.

MATERIALS AND METHODS

Measures and Analysis

The basic unit in our analysis is geographical regions. In most cases, the unit is a country (e.g., France), but in some exceptional cases, culturally distinct regions within a country were used as basic units of analysis (e.g., Hong Kong). These treatments follow the previous studies (Fincher et al., 2008; Murray and Schaller, 2010; Thornhill et al., 2010; Murray et al., 2011; Hruschka and Henrich, 2013). We used standardized scores for all variables of analysis (except for categorical variables such as global regions).

Independent Variables

Pathogen Stress

We used numerical estimates of the historical prevalence of pathogens provided by Murray and Schaller (2010), which reported the index of the historical prevalence of nine different infectious diseases (leishmania, schistosoma, trypanosome, leprosy, malaria, typhus, filarial, dengue, and tuberculosis) in the early 1900s within 230 geopolitical regions.

Government Effectiveness and GDP Per Capita

We used the World Bank's measure of government effectiveness, which measures "*perceptions of the quality of public services, the quality of the civil service and the degree of its independence from political pressures, the quality of policy formulation and implementation, and the credibility of the government's commitment to such policies* (World Bank, 2018)." The index includes the quality of bureaucracy, infrastructures such as roads and public transportation system, the quality of education system, and so on. The score was estimated ranging from −2.5 to 2.5 for each nation or region. Higher values mean better the quality of public services. We calculated the mean score from 1981 to 2008 and used this for analysis.

We also used GDP per capita as a factor representing the economic or institutional qualities of each region. We assessed GDP per capita from the World Bank's data. We then averaged the scores of GDP per capita from 1981 to 2008. We also reported the results of an analysis using GDP per capita rather than government effectiveness as the independent variable.

Dependent Variables

Individualism

We used Hofstede's (2001) measures of individualism, which assess individualism and collectivism values, from more than 100,000 individuals worldwide. Higher scores indicate greater individualism, and lower scores indicate greater collectivism. This index is commonly used in studies that examine the relationship between pathogen stress and collectivism (Fincher et al., 2008; Murray and Schaller, 2010; Hruschka and Henrich, 2013). We retrieved updated scores for each country or region[1]. Other well-known measures exist that represent individualistic and collectivistic values in cross-cultural psychology (Suh et al., 1998; Gelfand et al., 2004). We also conducted that same analysis, only using each of them as a dependent variable, and report it in the **Supplementary Material** (see **Supplementary Analysis**). The results were nearly consistent with those done using Hofstede's (2001) measure.

Regional Level of Conformity

We used cross-cultural survey data from the World Values Survey [WVS] (1981–2008), which are available electronically. This survey included questions about perceptions of human relationships. We used the following items, which represent sensitivity to being monitored by community members and positive views of obedience: *Conformity 1*: "One of my main goals in life has been to make my parents proud," *Conformity 2*: "I make a lot of effort to live up to what friends expect," *Conformity 3*: "Children should be encouraged to learn obedience at home," and *Conformity 4*: "I seek to be myself rather than to follow others." For *Conformity 1, 2,* and *4*, respondents answered degree of agreement (1: agree strongly, 2: agree, 3: disagree, 4: strongly disagree). For each region, we computed the percentage

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[1] https://www.hofstede-insights.com

of respondents who had agreed with each statement (i.e., the percentage of respondents who had chosen 1: agree strongly or 2: agree). For *Conformity 3*, respondents were presented a list of qualities that children should learn at home (including obedience, unselfishness, religious faith, and so on), and were asked to choose qualities that they consider important. For each region, we computed the percentage of respondents who had chosen "obedience." Previous studies have used other indicators to judge the strength of conformity. For example, Murray et al. (2011) used effect sizes for behavioral-conformity experiments, dispositional variability, and the proportion of the population who are left-handed. However, these sample sizes are too small ($n = 17$, 33, 20, respectively) to obtain converged results for complex models as in our hierarchical model. In order to keep as large sample sizes as possible, we used the above four items, which were asked from 1981 to 2009 in the WVS, and we could retrieve data from at least 50 regions. Previous studies also used two of the above four items (*Conformity 1* and *Conformity 3*), and reported that the percentage of the population who prioritize obedience and strength of family ties was strongly correlated with regional pathogen stress (Murray et al., 2011; Fincher and Thornhill, 2012). Fincher and Thornhill (2012) used an index of "strength of family ties" including the item *Conformity 1*. However, Hruschka and Henrich (2013) reported that government effectiveness, rather than pathogen stress, explained regional differences in the strength of family ties. In the present study, we investigated whether pathogen stress still had an effect on these items, which were expected to reflect conformity to community, even after controlling for both institutional factors and global regions.

Global Region

To adjust for the effects of shared historical and cultural factors, we used six global regions defined by the World Bank based on geographic regions or income levels. We coded each country as follows: 1 = Sub-Saharan Africa, 2 = East Asia and Pacific, 3 = Europe and Central Asia, 4 = Latin America and Caribbean, 5 = Middle East and North Africa, and 6 = South Asia. Adopting a strategy from Hruschka and Henrich (2013), we classified some higher-income countries according to shared cultural backgrounds. For example, although the United States, Canada, New Zealand, and Australia are geographically distant from Europe, we grouped them with Europe and Central Asia. The number of countries or regions of each global region used for each analysis is shown in **Supplementary Table S1**.

Models

We conducted three linear regression models to predict the level of conformity in each region from the regional prevalence of pathogens and government effectiveness. We did not assume a unique effect of global region in Model 1, while we did consider this in Models 2 and 3. To ensure the convergence of each model and avoid the problem of multicollinearity, we examined regression models including only two independent variables. In the following three models, we assumed that the dependent variable (standardized score), y_i, obeys normal distribution [i.e., $y_i \sim \text{Normal}(\hat{y}_i, \sigma_y)$]. We implemented a normality assumption to keep the results comparable with those of previous studies, which used a standard linear model.

Model 1

First, we assumed Model 1 as follows:

$$\begin{aligned} \hat{y}_i &= a_0 + \text{GE}x_{1,i} + \text{PS}x_{2,i}, \\ y_i &\sim \text{Normal}(\hat{y}_i, \sigma_y), \end{aligned} \tag{1}$$

where i represents the index of countries or regions, $x_{1,i}$ and $x_{2,i}$ represent the independent variables (government effectiveness and pathogen stress, respectively). y_i represents the dependent variable. a_0, GE, and PS are parameters. a_0 represents an intercept. GE and PS represent the coefficient of the fixed effect of each independent variable. $\hat{y}_i$, the expected value of the dependent variable, is predicted by government effectiveness and pathogen stress. We assumed that the value of the dependent variable, y_i, obeys a normal distribution in which the mean equals $\hat{y}_i$ and the standard deviation equals σ_y. We estimated the values of a_0, GE, PS, and σ_y. We set the uninformed priors (Box and Tiao, 1973) of σ_y to the uniform distribution $[0, \infty]$. This model serves as a benchmark for replicating analyses from past studies in which countries were assumed to be statistically independent units and the effect of shared cultural backgrounds were not controlled for.

Model 2

We conducted two types of hierarchical linear regression analysis to adjust for the effects of global regions. Each country was nested within one of the six global regions, which served as a random effect in the model (i.e., unique effect by global regions) as well as a fixed effect (i.e., common effect across global regions). Model 2 is the random intercept model in which the global regions were used as a random effect affecting the intercept:

$$\begin{aligned} \hat{y}_i &= a_j + \text{GE}x_{1,i} + \text{PS}x_{2,i}, \\ a_j &\sim \text{Normal}(\mu_a, \sigma_a), \\ y_i &\sim \text{Normal}(\hat{y}_i, \sigma_y), \end{aligned} \tag{2}$$

where j represents the global region ($j \in [1, 6]$), and a_j represents a random effect specific to the global region affecting the intercept. It is assumed that a_j obeys the normal distribution [i.e., $a_j \sim \text{Normal}(\mu_a, \sigma_a)$]. a_j is sampled from the normal distribution in which the mean equals μ_a and standard deviation equals σ_a. The values of a_j, GE, PS, μ_a, σ_a, and σ_y were estimated as parameters. We set the uninformed priors of μ_a to the uniform distribution $[-\infty, \infty]$, and those of σ_a and σ_y to the uniform distribution $[0, \infty]$.

Model 3

We also conducted Model 3 using global region as a random effect affecting both the intercept and the slopes as follows:

$$\begin{aligned} \hat{y}_i &= a_j + \text{GE}_j x_{1,i} + \text{PS}_j x_{2,i}, \\ a_j &\sim \text{Normal}(\mu_a, \sigma_a), \\ \text{GE}_j &\sim \text{Normal}(\mu_{\text{GE}}, \sigma_{\text{GE}}), \\ \text{PS}_j &\sim \text{Normal}(\mu_{\text{PS}}, \sigma_{\text{PS}}), \\ y_i &\sim \text{Normal}(\hat{y}_i, \sigma_y). \end{aligned} \tag{3}$$

In this model, we assume that not only intercepts but also each effect of GE and PS differs according to the global region. GE_j was also sampled from the normal distribution in which the mean equals μ_{GE} and standard deviation equals σ_{GE}. PS_j was also sampled in similar manner. μ_{GE} and μ_{PS} represent slopes globally affecting government effectiveness and pathogen stress, respectively. The values of a_j, GE_j, PS_j, μ_a, σ_a, μ_{GE}, σ_{GE}, μ_{PS}, σ_{PS}, and σ_y were estimated as parameters. We set the uninformed priors of μ_a, μ_{GE}, and μ_{PS} to uniform distribution $[-\infty, \infty]$, and those of σ_a, σ_{GE}, σ_{PS}, and σ_y to the uniform distribution $[0, \infty]$.

In our reporting of results using GDP per capita as an independent variable instead of government effectiveness, we changed the names of parameters, representing the effects of institution (i.e., "GE") for "GDP" in each model.

Bayesian Estimation

We estimated the values of parameters in each model using Bayesian estimation. We conducted MCMC simulations with four independent chains in each model. A total of 5,000 iterations per chain were conducted, and first 1,000 were discarded as burn-in steps. We checked the convergence of the MCMC simulations using the Gelman–Rubin statistic ($\hat{R}$ values) (Gelman and Rubin, 1992). $\hat{R}$ values were less than 1.10 for all parameters in each model, which means that the MCMC simulations converged. In addition, we also checked effective sample sizes (ESSs) of parameters, that is, the number of independent MCMC samples related to autocorrelation (the total number of MCMC samples was 16,000 samples). Greater ESSs are related to lower autocorrelation. In the **Supplementary Material**, we reported trace plots of MCMC simulations and the density plots of the posterior distributions of each parameter to understand visually whether or not the parameter values had converged. We estimated a 95% Bayesian credible interval for each parameter. If the interval did not contain zero, we interpreted the effect as significant. The MCMC simulations were conducted using the Stan and rstan package (Stan Development Team, 2017) with R v. 3.5.0 (R Core Team, 2018). Stan uses Hamiltonian Monte Carlo sampling for estimating parameters.

Model Selection

We also evaluated the models by comparing the "Widely Applicable Information Criterion" (WAIC; Watanabe, 2010). WAIC values were calculated using the following definition, proposed in Gelman et al. (2013):

$$\mathrm{WAIC} = -2(lppd - p_{\mathrm{WAIC}}). \tag{4}$$

lppd means log pointwise posterior predictive density, and p_{WAIC} means effective number of parameters. The models with the smallest WAIC were selected as the best models. We calculated WAIC values using loo package with R.

RESULTS

Zero-Order Correlations

We calculated the correlation coefficients (ρ) between dependent variables and independent variables (pathogen stress or government effectiveness) using Bayesian estimation (see the **Supplementary Method**). **Table 1** shows the zero-order correlation coefficients and their 95% Bayesian credible intervals. Like previous studies (Fincher et al., 2008; Murray and Schaller, 2010; Hruschka and Henrich, 2013), we also found that the regional historical pathogen stress was negatively and significantly correlated with the score for individualism. The regional scores for government effectiveness were positively and significantly correlated with it. The regional historical pathogen stress was significantly associated with all four indices of regional strength of conformity, and regional scores of government effectiveness were also significantly associated with indices of strengths of conformity. Note that *Conformity 4* was negatively correlated with pathogen stress and positively correlated with government effectiveness, since a higher score of *Conformity 4* indicates a willingness to be independent of others ("I seek to be myself rather than to follow others"). We also calculated the correlation coefficients between GDP per capita and conformity, and confirmed that it is strongly correlated with the individualism score and all four indices of conformity. We also confirmed that pathogen stress, government effectiveness, and GDP per capita were strongly correlated with each other. Pathogen stress was correlated strongly with government effectiveness (ρ : *Mean* $= -0.68$, *SD* $= 0.04$, $n = 156$, 95% CI $[-0.76, -0.59]$, *ESS* $= 10896$) and GDP per capita (ρ : *Mean* $= -0.60$, *SD* $= 0.05$, $n = 154$, 95% CI $[-0.70, -0.49]$, *ESS* $= 12150$). Government effectiveness was also strongly correlated with GDP per capita (ρ : *Mean* $= 0.76$, *SD* $= 0.03$, $n = 197$, 95% CI $[0.70, 0.82]$, *ESS* $= 9916$). Hence, we decided not to enter all the three independent variables

TABLE 1 | Posterior distribution of zero-order correlation coefficients between independent variables and dependent variables.

			Quantiles			Sample	
	Mean	***SD***	**2.5%**	**50%**	**97.5%**	**Size**	***ESS***
Correlation coefficient of pathogen stress with							
Individualism	−0.66	0.06	−0.76	−0.67	−0.54	100	11656
Conformity 1	0.71	0.06	0.59	0.71	0.81	83	10760
Conformity 2	0.54	0.08	0.37	0.55	0.68	81	13663
Conformity 3	0.49	0.08	0.33	0.50	0.63	94	14535
Conformity 4	−0.52	0.10	−0.70	−0.53	−0.30	51	12945
Correlation coefficient of government effectiveness with							
Individualism	0.68	0.05	0.57	0.69	0.78	103	10671
Conformity 1	−0.62	0.07	−0.74	−0.62	−0.47	85	12599
Conformity 2	−0.46	0.09	−0.62	−0.47	−0.28	83	16000
Conformity 3	−0.47	0.08	−0.62	−0.48	−0.30	95	16000
Conformity 4	0.43	0.11	0.19	0.44	0.64	51	14371
Correlation coefficient of GDP per capita with							
Individualism	0.63	0.06	0.50	0.63	0.74	102	12100
Conformity 1	−0.64	0.07	−0.75	−0.64	−0.50	84	11311
Conformity 2	−0.45	0.09	−0.61	−0.46	−0.27	82	14207
Conformity 3	−0.43	0.08	−0.58	−0.43	−0.25	94	14347
Conformity 4	0.46	0.11	0.22	0.47	0.66	50	14514

ESS represents effective sample sizes of MCMC simulations.

simultaneously to avoid the problem of multicollinearity. (We found that parameter estimation did not converge when the three independent variables were included in each multilevel model.)

We also reported correlation coefficients between dependent variables in **Supplementary Table S2**. We confirmed that the individualism score was correlated negatively and significantly with the following three indices: *Conformity 1*, *Conformity 2*, and *Conformity 3*. *Conformity 4* was positively correlated with individualism, although the 95% Bayesian credible intervals included zero. The four indices of conformity were also correlated with each other, with the exception of the correlation between *Conformity 2* and *Conformity 3*, and that between *Conformity 3* and *Conformity 4.*

Results of Bayesian Estimation

Figure 1A shows the inferred parameter values and the 95% Bayesian credible intervals in Model 1, which did not take the effect of shared cultural background into account (see **Supplementary Table S3** for numerical values). For the individualism score, it was confirmed that both pathogen stress (i.e., PS) and government effectiveness (i.e., GE) had a significant effect on it: that is, the 95% Bayesian credible intervals of both of two coefficients did not include zero. None of the indices of strength of conformity, the 95% Bayesian credible intervals of coefficients of pathogen stress included zero, which indicated that pathogen stress had significant positive effects on the regional strength of conformity. The coefficients of government effectiveness also had significant negative effects on *Conformity 1* and *Conformity 3*, but not on *Conformity 2* or *Conformity 4*.

Figure 2A illustrated the results of Model 2, a random intercept model in which global regions were used as random intercepts. This model assumes that the effects of pathogen stress and government effectiveness are common to all global regions (see **Supplementary Table S4** for numerical values). Pathogen stress was not significantly related to the individualism score, whereas government effectiveness had still a significant effect on it. As noted in the introduction, Hruschka and Henrich (2013) found that government effectiveness could explain regional variations in individualism when they controlled for both pathogen stress and global regions using a standard regression model. However, for indices of conformity, pathogen stress still had significant positive effects on two indices. *Conformity 1* and *Conformity 2*, after both government effectiveness and global regions were controlled for, although the effects on the indices, *Conformity 3* and *Conformity 4*, disappeared. Also, government effectiveness still had a significant negative effect on *Conformity 1*. However, its effect on *Conformity 3*, which was significant in Model 1, disappeared in Model 2.

Figure 3A shows the results of Model 3, in which global regions were treated as both random slopes and intercepts. **Figure 3** shows means and 95% Bayesian credible intervals of parameters estimated for each global region (see **Supplementary Table S5** for numerical values). For the individualism score, the global effect of government effectiveness (i.e., μ_{GE}) remained significant. Significant region-specific effects of government effectiveness on slopes were also found in three global regions (Europe and Central Asia, Latin America and Caribbean, and South Asia). Both global and region-specific effects of pathogen stress were insignificant. For the index of *Conformity 1*, we found that the global effects of both pathogen stress and government effectiveness across global regions were no longer significant (i.e., the 95% Bayesian credible intervals of μ_{PS} and μ_{GE} included zero). However, a significant region-specific effect of pathogen stress on slope was observed in Europe and Central Asia. A significant region-specific effect of government effectiveness was also observed in this region. For the index of *Conformity 2*, the global effect of pathogen stress (i.e., μ_{PS}) remained significant. As with Model 2, the global effect of government effectiveness (i.e., μ_{GE}) was not significant. Significant region-specific effects of pathogen stress on slopes were also found in three global regions (Sub-Saharan Africa, Europe and Central Asia, and Latin America and Caribbean). On the other hand, no significant region-specific slope effects of government effectiveness were found in any of the global regions. For the index of *Conformity 3*, we found that neither the global slope effects of pathogen stress nor government effectiveness were significant. None of the region-specific effects of pathogen stress on slopes were significant in any global region, while the negative region-specific effects of government effectiveness were significant in Middle East and North Africa. For the index of *Conformity 4*, neither the global and region-specific effects of pathogen stress nor government effectiveness were significant. **Supplementary Figures S1–S10** illustrates the relationship between government effectiveness or pathogen stress and each index by global region.

We summarize the results of above analysis here (see also **Supplementary Table S6** for additional details of the following summary). For the individualism score, the global effects of pathogen stress, which was significant in Model 1, disappeared in both Model 2 and Model 3, whereas the significant global effects of government effectiveness remained in all models. For the indices of conformity, the global effects of pathogen stress, which were significant for all four conformity indices in Model 1, remained significant for two indices in Model 2, and for only one index in Model 3. The global effects of government effectiveness that were significant for two conformity indices in Model 1 remained significant for only one index in Model 2, and for none in Model 3. These results suggest that the previous studies may have suffered from Galton's problem, and the relationship between the collectivism, conformity, pathogen prevalence, and government effectiveness may not be universal phenomena. On the other hand, in Model 3, several region-specific effects were found to be significant. The region-specific effects of pathogen stress were significant in Europe and Central Asia for *Conformity 1* and *2*, and in Sub-Saharan Africa, Latin America, and Caribbean, for *Conformity 2.* For the Individualism, the region-specific effect of government effectiveness was significant in Europe and Central Asia, Latin America and Caribbean, and South Asia. The same region-specific effects were also significant in the Europe and Central Asia for the *Conformity 1*, and in the Middle East and North Africa for the *Conformity 3*.

Here, we reported additional tests using GDP per capita as the independent variable instead of government effectiveness

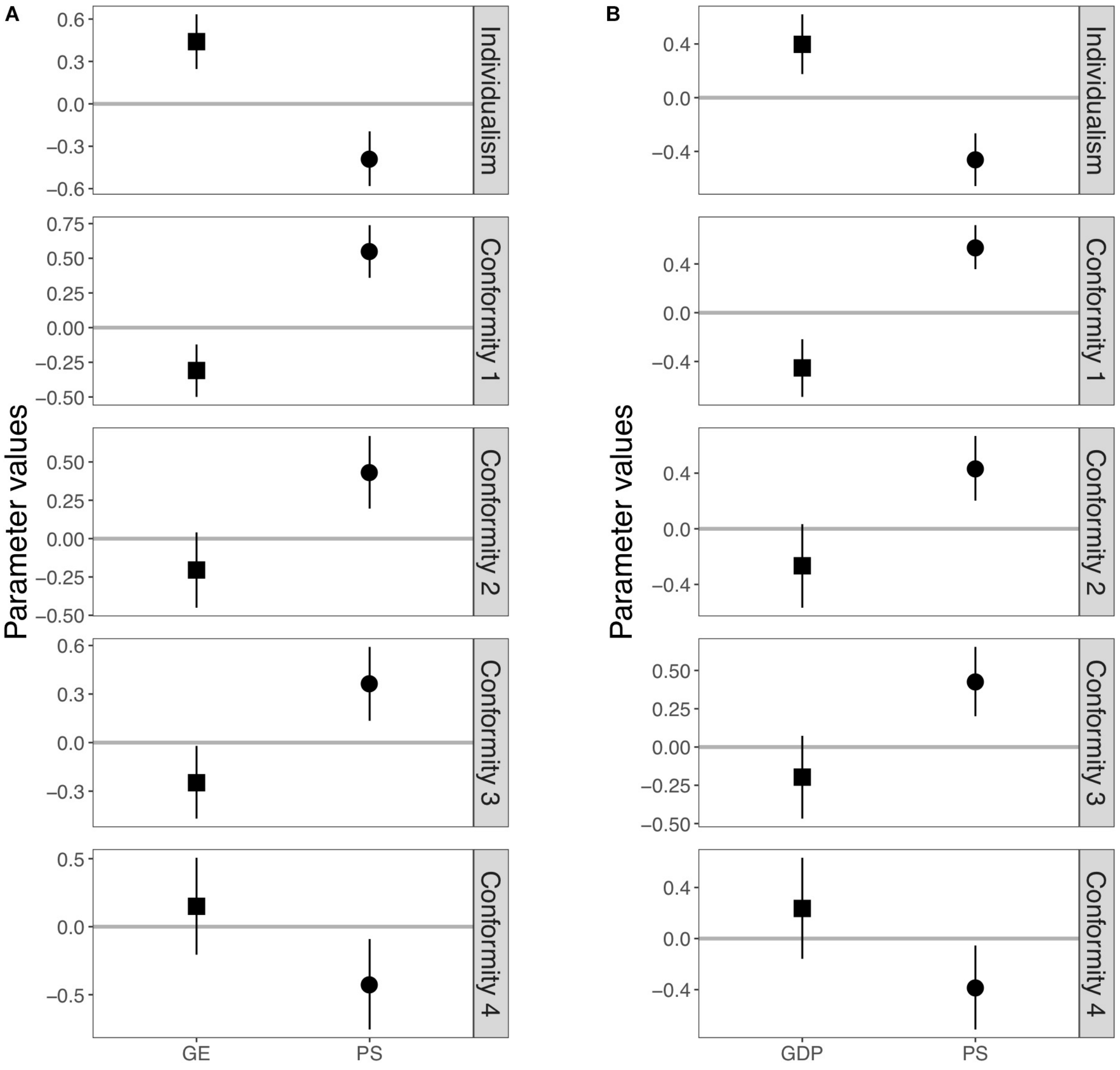

FIGURE 1 | Posterior distributions of the estimated values of slopes in Model 1. **(A)** Results using government effectiveness as an independent variable. **(B)** Results using GDP per capita as an independent variable instead of government effectiveness. Squares and circles represent posterior mean of slope affecting government effectiveness (or GDP per capita) and pathogen stress, respectively. Each error bar represents a 95% Bayesian credible interval.

(see **Figures 1B**, **2B**, **3B**, **Supplementary Figures S11–S15**, and **Supplementary Tables S7–S9**). See also **Supplementary Table S10** for further details on the following summary. We confirmed that the overall results using GDP as the independent variable were similar to the previous results. First, the global effects of pathogen stress, which were significant for individualism and all four conformity indices in Model 1, remained significant for individualism and two indices (*Conformity 1* and *2*) in Model 2. The global effects of GDP, which were significant for individualism and *Conformity 1* in Model 1, remained significant in Model 2. In Model 3, the global effects of pathogen stress remained significant for only *Conformity 2*, whereas that of GDP was not significant for any indices. These results are consistent with previous analyses and imply that the effects of pathogen stress and government effectiveness are not universal.

Most region-specific effects of pathogen stress were also replicated. As with the previous analyses, the region-specific effect of pathogen stress was again found significant in Europe and Central Asia for *Conformity 1* and *2*, and in Sub-Saharan Africa, Latin America and Caribbean, for *Conformity 2*. In addition, we found region-specific effects of pathogen stress in Europe and Central Asia for individualism, whereas this was not found in previous analyses. Patterns of region-specific effects of GDP differed from those for government effectiveness. Region-specific effects of GDP were found significant in Europe and Central Asia for Individualism and *Conformity 1*. We were unable to find significant region-specific effects for GDP in Latin America and Caribbean or South Asia for individualism, whereas effects were found for government effectiveness. Moreover, region-specific effects of GDP, which were not significant in

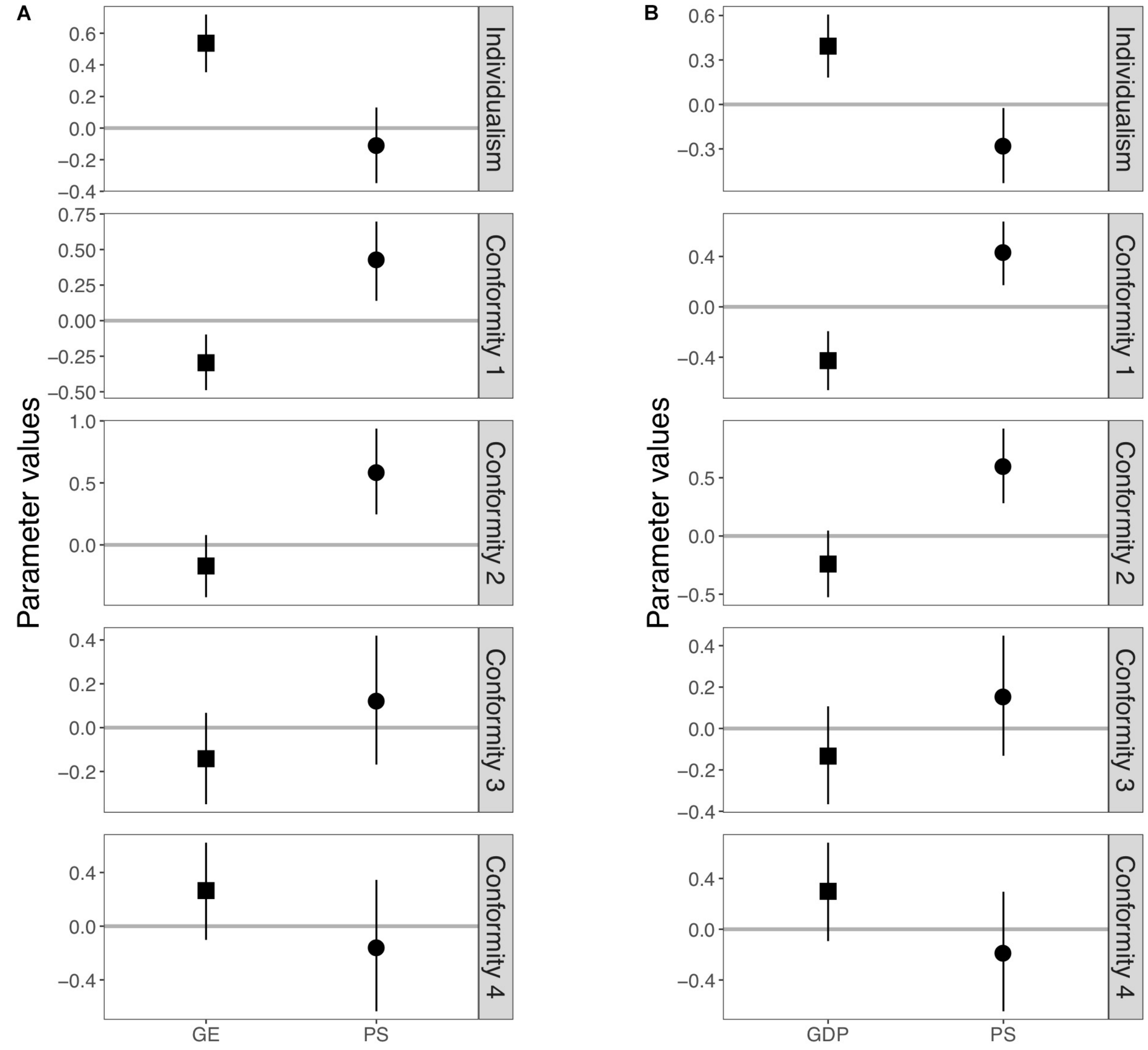

FIGURE 2 | Posterior distributions of the estimated values of slopes in Model 2. **(A)** Results using government effectiveness as an independent variable. **(B)** Results using GDP per capita as an independent variable instead of government effectiveness. Squares and circles represent posterior mean of slope affecting government effectiveness (or GDP per capita) and pathogen stress, respectively. Each error bar represents a 95% Bayesian credible interval.

previous analyses, were also found to be significant in East Asia and Pacific for *Conformity 1* and *Conformity 3*.

Model Selection

Table 2 shows the WAIC values for each model. For all combinations of dependent and independent variables, the WAIC for hierarchical models (i.e., Model 2 or Model 3) was consistently lower than a non-hierarchical model (i.e., Model 1). For *Conformity 4*, even though the WAIC value for Model 3 was higher than Model 1, the WAIC value for Model 2 was the lowest of all three models. These results indicate that hierarchical models considering region-specific effects are better and more appropriate than those of a standard non-hierarchical linear model, as was employed in the previous studies. The results of comparisons between Model 2 and Model 3 are mixed. Regardless of the type of independent variables, Model 3 fit better for the individualism score and *Conformity 3*; otherwise, Model 2 was better than Model 3. The results of the best fit models suggest that, when government effectiveness was controlled for, the global effects of pathogen stress (i.e., PS) remained significant only for two out of four indices of conformity (*Conformity 1* and *Conformity 2*). Similar results were obtained when GDP per capita was controlled; the global effect of pathogen prevalence remained significant for the same two conformity indices (*Conformity 1* and *Conformity 2*).

DISCUSSION

Previous studies have consistently suggested that the historical prevalence of pathogens played an important role in explaining the cultural differences in group-oriented psychology. However,

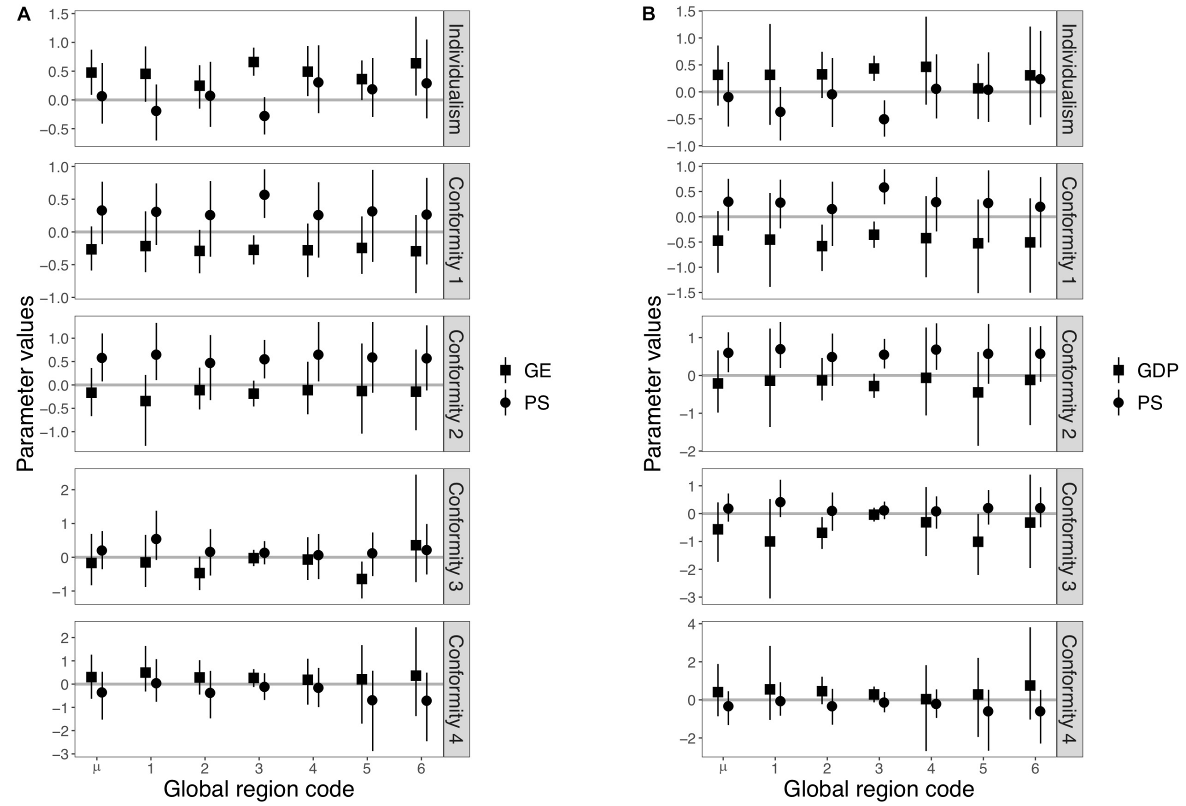

FIGURE 3 | Posterior distributions of the estimated values of slopes in Model 3. **(A)** Results using government effectiveness as an independent variable. **(B)** Results using GDP per capita as an independent variable instead of government effectiveness. Squares and circles represent posterior means of slopes affecting government effectiveness (or GDP per capita) and pathogen stress, respectively. Each number on the horizontal axis represents a global region (1 = Sub-Saharan Africa, 2 = East Asia and Pacific, 3 = Europe and Central Asia, 4 = Latin America and Caribbean, 5 = Middle East and North Africa, and 6 = South Asia). μ in horizontal axis represents global slopes across global regions (i.e., μ_{GE}, μ_{GDP}, or μ_{PS}). Each error bar represents a 95% Bayesian credible interval.

TABLE 2 | WAIC values of each model (IND: *Individualism*, C1: *Conformity 1*, C2: *Conformity 2*, C3, *Conformity 3*, C4: *Conformity 4*).

Results in which government effectiveness was used as an independent variable

	IND	*C1*	*C2*	*C3*	*C4*
Model 1	212.53	174.28	203.56	238.08	133.62
Model 2	189.86	170.35	197.42	213.25	133.41
Model 3	181.86	172.88	200.15	211.90	137.57

Results in which GDP per capita was used as an independent variable

	IND	*C1*	*C2*	*C3*	*C4*
Model 1	218.11	168.63	201.78	237.46	131.04
Model 2	208.89	164.37	194.30	212.01	130.45
Model 3	202.40	167.66	197.23	210.05	133.99

the correlation between pathogen stress and human collectivistic psychology found in previous studies may suffer from the problem of statistical non-independence, called Galton's problem. We checked the robustness of the effect of pathogen stress on collectivism and conformity using a hierarchical linear model with MCMC simulations. First, we successfully reproduced the significant effects of regional pathogen stress on collectivism and all the four indicators of conformity without adjusting the effect of global regions. When adjusting the global regions to the random intercept model, significant global effects of pathogen stress remained on only two of the four indicators of conformity. Moreover, in the models including both random slopes and intercepts, the global effects of pathogen stress remained significant for only one indicator. Significant effects of pathogen stress were limited only in some global regions. However, these effects did not seem to be robust. For instance, the most robust local effect was found in Europe and Central Asia, but it was limited to only two out of four indicators of conformity. Model selection revealed that hierarchical models that took into account region-specific effects (Models 2 or 3) improved predictive accuracy more than a non-hierarchical model (Model 1). These results suggested the existence of spatial autocorrelations between countries that share a global region, and such correlations must be statistically controlled. For some indices of conformity, Model 2 fit to the data better than Model 3 did. For *Conformity 4*, predictive accuracy of Model 3 was worst in three models. This indicated that random slopes may be redundant parameters for the prediction of the variances of the regional level of conformity. However, even when only the best models are considered, we can conclude that either global or region-specific effects of pathogen stress are limited to only two indices of conformity.

Group-level analyses, which are often conducted in cross-cultural research, inevitably suffer from Galton's problem (Mace and Pagel, 1994; Nettle, 2009) as neighboring groups or countries occasionally share a common descent and cannot be assumed to be statistically independent units. Two other approaches that do not use Bayesian multilevel modeling may be effective for handling this problem. One is the use of standard regression models using the effect of global regions as intercepts, an approach employed by Hruschka and Henrich (2013). The other is a standard regression model with interaction terms between the global region and independent variables. However, the Bayesian multilevel model approach has several advantages over these approaches. The Bayesian multilevel analysis with MCMC simulation can simultaneously estimate the region-specific effect (as the random effects of both slopes and intercepts) and the global effects. This is achieved by assuming that each effect of global region (e.g., PS_j in our Model 3) is produced by a common variable (e.g., μ_{PS} in our Model 3). Under this assumption, we can avoid the problem of overfitting (i.e., the results of analysis fit to existing data well, but could not be generalized to unseen new data) even when the number of samples is small. Furthermore, the results of Bayesian multilevel models are in general intuitively interpretable.

Our analyses can be improved in the future. In our approach, selection of the global regions plays an important role and should influence model results. We followed Hruschka and Henrich (2013) in categorizing the countries into six global regions. However, not all the countries belonging to a global region necessarily share identical historical or cultural roots. The best method for adjusting the effects of shared ancestry is a phylogenetic approach (Mace and Pagel, 1994; Mathew and Perreault, 2015). Since it is usually difficult to reconstruct cultural phylogenetic trees of modern countries, the multilevel model is an effective candidate for partly overcoming Galton's problem (Nettle, 2009). Further analyses, using different categorizations of global regions with variables other than conformity and collectivism that were found to be correlated with the prevalence of pathogens, are required to rigorously test the robustness of the effects of pathogen stress on the collectivistic psychological mechanisms.

Recent studies have raised doubts about the effect of pathogen stress on the development of collectivistic psychological mechanisms. As noted in the introduction, Hruschka and Henrich (2013) indicated that modern institutions rather than pathogen stress impact collectivism and in-group favoritism. In addition, Talhelm et al. (2014) indicated that forms of subsistence (e.g., rice-growing) rather than pathogen stress affected collectivistic styles of thinking. In contrast to these studies, recent studies suggested that regional levels of pathogen stress might be related to adherence to social norms, but not to negativity toward outgroups (Cashdan and Steele, 2013; Tybur et al., 2016). In the current study, we found that pathogen stress, if it exists, is related to only some group-oriented psychological mechanisms, such as concerns about evaluation by community members. Because the concept of collectivism includes many different group-oriented psychological mechanisms, scholars must divide it into its core aspects and test the effect of environmental severity on each of these.

A problem regarding the restricted samples from WEIRD (Western, Educated, Industrial, Rich, and Democratic) societies has been recently noted in cross-cultural studies (Henrich et al., 2010). Our analysis seems to illuminate the related possibility that pathogen stress has a significant effect on collectivism or conformity only in restricted global regions, such as European and Asian societies. However, the dataset still did not seem to be sufficient for making bold conclusions about region-specific effects. In general, Bayesian credible intervals (i.e., variance of posterior distributions) become larger as a sample size gets smaller. Significant region-specific effects of Europe and Central Asia might have been statistical artifacts stemming from a larger sample size in this region (for instance, relative to a few countries in the South Asia region). If mean values of significant region-specific effects are close to those of non-significant effects while standard deviations of the significant region-specific effects are much smaller, differences in sample size might cause such artifacts. Close inspection of means of the posterior distributions (**Figure 3** and **Supplementary Tables S5, S9**) suggests that this problem might have arisen on *Conformity 2* in Model 3 but not in the other cases. Although one advantage of using Bayesian estimation with MCMC simulation is that it can estimate parameter values even with small samples, Bayesian credible intervals need to be carefully interpreted. Additional data need to be included in future analyses to identify the robustness of region-specific effects of pathogen prevalence on collectivistic psychological mechanisms.

AUTHOR CONTRIBUTIONS

YH and MT contributed equally to the research design, data analysis, and writing of the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpsyg.2018.01921/full#supplementary-material

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The Role of Disgust in Male Sexual Decision-Making

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Sexual arousal is known to increase risky behaviors, such as having unprotected sex. This may in part relate to the emotion of disgust, which normally serves a disease avoidant function, and is suppressed by sexual arousal. In this report we examine disgust's role in sexual decision-making. Male participants received two study packets that were to be completed at home across two different time-points. Participants were asked to complete one packet in a sexually aroused state and the other in a non-aroused state. Participants were asked to rate: (1) arousal, (2) disgust, (3) willingness for sex, and (4) disease risk toward a range of female targets, which varied in level of potential disease risk (sex-worker vs. non sex-worker) and attractiveness. A measure of trait disgust was also included along with other related scales. Sexual arousal was associated with reduced disgust and reduced judgments of disease risk for all targets—these latter two variables being correlated—and with enhanced willingness to have sex with all of the depicted persons. Willingness to have sex when aroused (in contrast to non-aroused) was predicted by disease risk judgments and trait disgust, suggesting both direct (state) and indirect (trait) effects of disgust on sexual decision-making.

Keywords: disgust, disease, sexual arousal, contamination, decision making

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INTRODUCTION

Sexually transmitted infections (STI) are common, with around 0.5 billion new cases occurring each year (World Health Organization, 2013). These are associated with considerable morbidity and mortality, notably from HIV infection, fetal syphilis and cervical cancer (World Health Organization, 2013). Much of the STI disease burden falls on young people, who while accounting for around a quarter of the sexually active population, contract around half of all diagnosed STIs (Eaton et al., 2008; Centers for Disease Control, 2012). Given these statistics, an important consideration is the process by which young people make sexual decisions as they relate to STI risk. In this report we examine the role of the emotion of disgust in this process. As we describe below, disgust seems to be involved in driving avoidance of disease transmitting objects (e.g., body products; Curtis et al., 2004; Oaten et al., 2009) and people (e.g., Ryan et al., 2012), and it has been suggested that it may perform a similar role in the sexual domain (e.g., Stevenson et al., 2011; Borg and de Jong, 2012). We chose to only include young men because our previous work indicated that disgust toward sex-related cues could be reduced in male participants during heightened sexual arousal, and we were interested to test whether this effect could also be observed in sex-related disease avoidance behavior (e.g., Stevenson et al., 2011).

Two important variables have been identified that affect sexual decision-making as they pertain to STI risk perception. The first, and most potent, is sexual arousal. Blanton and Gerrard (1997), appear to have been the first to demonstrate in male participants that judgments of STI risk were significantly reduced by sexual arousal. Several subsequent studies have tended to confirm this result, finding first, that sexual and non-sexual risk taking in both men and women is enhanced by sexual arousal (Skakoon-Sparling et al., 2016) and second, that feelings of self-control and sexual-restraint are reduced (Skakoon-Sparling and Cramer, 2016). Although, one study reports that sexual arousal only affects risk taking as it pertains to sexual behavior (Imhoff and Schmidt, 2014), the broad and well-supported finding is that enhanced sexual arousal alters behavioral intentions, such that activities that might be deemed risky and unacceptable when unaroused are deemed more acceptable and less risky when aroused (Ariely and Loewenstein, 2006).

A second and related factor is physical attractiveness. Two studies have explored the impact of this variable on sexual decision-making. In one report HIV+ gay men were asked to make judgments about a series of scenarios when in a sexually aroused and in a non-aroused state (Shuper and Fisher, 2008). Intention to have unprotected sex was independently reduced by the attractiveness of the potential partner, the potential partner's HIV status and sexual arousal. Similar findings have also been obtained in heterosexual men and women, with increased willingness to have unprotected sex with an attractive partner, relative to a less attractive one (Epstein et al., 2007). While these two studies did not directly ask for STI risk judgments, it is apparent that the behavioral intentions carry a heightened risk of disease transmission, and that this heightened risk is very likely to be known to the participant.

If a state of sexual arousal and an attractive potential partner increase the likelihood of making a suboptimal sexual decision—e.g., having unprotected sex—an obvious question is why? One possibility, and the focus of this study, is the emotion of disgust. Apart from the broader observation made earlier that disgust serves a disease avoidance function (e.g., Curtis and Biran, 2001; Marzillier and Davey, 2004; Oaten et al., 2009; Fleischmann and Fessler, 2011), three lines of evidence suggest it may be a significant contributor to STI-related sexual decision-making. First, Stevenson et al. (2011), examined the effects of sexual arousal on male participants' disgust reactions to sex-relevant and sex-non-relevant disgust elicitors, in the visual, auditory and tactile modalities. Sexual arousal selectively reduced disgust for sex-relevant elicitors, but not for sex-non-relevant elicitors. Similar findings were also obtained by Borg and de Jong (2012), but with female participants. A further study examined whether sexual arousal would affect a self-report measure of disgust in men and women, and found evidence of reduced disgust for sex-related questions, but solely in women (Lee et al., 2014). Although there is some uncertainty about the nature of disgust in non-human species, it has been suggested that similar decision processes may also occur here, with sexual arousal suppressing the normal avoidance of diseased, but sexually available, conspecifics (e.g., brief exposure to female odors enhanced the willingness of male mice to approach infected females; Kavaliers and Choleris, 2013).

A second line of evidence that points to disgust's involvement in sexual decision making is the finding that eliciting a state of disgust can inhibit sexual arousal in both men and women. Priming disgust in participants leads to reduced arousal-related judgments of erotica (Andrews et al., 2015), with this effect also obtained in a further study using just female participants (Fleischman et al., 2015). Relatedly, it has also been suggested that elevated trait disgust sensitivity may be a contributory factor to sexual dysfunction in women, by inhibiting sexual arousal (e.g., Van Overveld et al., 2012). A third line of evidence comes from finding that lower trait based measures of disgust, especially that pertinent to sex-related elicitors, are associated with a greater number of short-term sexual partners in heterosexual men and women (Al-Shawaf et al., 2015), and in gay men (Zhang et al., 2017). In sum, the general suggestion here is that disgust normally inhibits disease-related contact and that sexual arousal suppresses this emotionally driven avoidance—presumably to aid the greater goal of procreation (de Jong et al., 2013).

In the current study we aimed to examine the role of disgust—both *in reaction* to the stimuli in the study (i.e., state) and as a trait (i.e., disgust sensitivity)—in sexual decision-making, as it relates to STI risk. To examine this, we asked young men to make four types of judgment about a range of potential female sexual partners: (1) how disgusting they found the potential partner, (2) how likely they were to contract an STI, (3) how arousing they found the potential partner, and (4) their willingness to have sex with them. The disgust rating formed our stated-based judgment of this emotion. STI risk rating allowed us an over-arching assessment of disease related knowledge, irrespective of what factors might contribute to it. Ratings of arousal and willingness to have sex were presumed to assess different aspects of behavioral intention—its more distal (i.e., arousal driving approach) and proximal (i.e., consummatory intent) aspects.

Using a fully within-subject design, these judgments were made under two conditions, either when sexually aroused or when in a neutral non-aroused state. In both states participants were asked to evaluate the same set of images (each with a label) depicting four types of potential female sexual partner; attractive sex-workers, unattractive sex-workers, attractive similarly aged controls, and unattractive similarly aged controls. This aspect of the manipulation allowed us to explore two levels of physical attractiveness—a factor known to influence sexual decision making—and two levels of perceived STI risk. Evidence suggests that the prevalence of STIs are higher among female sex-workers than other women (Scott et al., 1995; Mak et al., 2005; Zermiani et al., 2012). This design also allowed us to test interaction effects. Finally, we also obtained a trait measure of core disgust sensitivity (Olatunji et al., 2008), a trait measure of dispositional concerns about disease (Duncan et al., 2009), and the sociosexuality index (Penke and Asendorpf, 2008) to determine attitudes and behavior to short-term sexual relationships.

We hypothesized, first, that heightened sexual arousal would reduce judgments of disgust and disease risk toward all of the depicted female targets—attractive and unattractive, and sex-workers and age-matched controls. Second, we predicted that disgust and disease risk ratings would be positively correlated. Third, we hypothesized that reduced judgments of disgust and disease risk would predict: (1) increases in willingness to have sex and arousal ratings toward all of the images, when contrasting the aroused and unaroused states, (2) reductions in willingness to have sex and arousal ratings toward images of sex-workers, compared to similarly aged controls, and (3) increases in willingness to have sex and arousal ratings toward images of attractive female images vs. unattractive images. Fourth, we hypothesized that state disgust (i.e., measured in the moment) and trait disgust, would exert different effects, reflecting a high or low baseline (i.e., trait), and its exacerbation (i.e., state). However, while we predicted different effects, we were uncertain as to their specific direction, as this was an exploratory and auxiliary hypothesis.

METHOD

Participants

Participants were required to be male and aged 18 years and over. Study packets were initially distributed to 94 eligible participants, with 51 returning data for both the neutral and self-arousal sessions. Community participants were given $20 cash for taking part, with 60-min course credit provided for first-year psychology students. Informed consent was provided by each participant, and the study was approved by Griffith University Human Research Ethics Committee (GU Ref No: 2014/577).

Design and Study Overview

We used a wholly within-subject design. Participants each completed two sessions at home. In one session they were asked to masturbate to a sub-orgasmic level of arousal and in the other to complete the session in a non-aroused state. On each session they made judgments of arousal, willingness for sex, disgust, and disease risk for a set of images depicting female targets. Two features of the images were manipulated: (1) Whether the female target was attractive or unattractive, and (2) Whether the target was a sex-worker or an age matched control woman.

Materials

Participants were asked to judge the images of 16 different female targets, with the same images being used in both sessions. These 16 female targets were arranged into four cells: Attractive Sex-worker (ASW), Unattractive Sex-worker (USW), Attractive Age-matched controls (AC), and Unattractive Age-matched controls (UC), resulting in four images per cell. Each image depicts a rear-view of female target—e.g., face not visible to protect the privacy of individual depicted; and each image cues condition (Sex worker vs. Age-matched control) via the clothing and physical stance of the female target depicted. The image dimensions were 8 × 6 cm, and were sourced from Google images (with permissions to use; Image set available via request to author). To definitively categorize the sex-worker or control images, each was paired with one of the following labels: prostitute, escort, sex-worker, hooker, or office worker, secretary, clerical assistant, or book-keeper, and one of the following "attractiveness" vignettes: beautiful, sexy, desirable, attractive, or plain-featured, homely, undesirable, or unattractive, to categorize the attractive or unattractive targets. The images and vignettes had been individually pilot tested on a separate group of participants ($n = 20$) to confirm that the sex-worker and control-related stimuli were classified as such by naïve participants, and that the vignettes corresponded to the attractiveness categories assigned to them. The images were not piloted on attractiveness because female targets were depicted in a rear-view only.

Participants in the current study were required to provide a single rating per image and vignette set, which asked: "How sexually arousing do you find this woman?" (1 = Not at all sexually arousing, 7 = Very sexually arousing); or "Would you be willing to have sex with this woman?" (1 = Not at all willing, 7 = Very willing); or "How disgusting do you find this woman?" (1 = Not at all disgusting, 7 = Very disgusting), or "Are you likely to contract a disease from this woman?" (1 = Not at all likely, 7 = Very likely). The image and vignette combinations were both counterbalanced and randomly allocated (one from each cell) to blocks of four organized by rating category to control for order effects.

Each participant received two experimental packets: a neutral study packet, and an arousal study packet. The neutral study packet contained a participant instruction sheet, demographic questions asking each participant to nominate in an open-ended question format their sex, age, and sexual orientation, and a pre-picture viewing manipulation check which asked participants to rate on a seven-point category scale, "How sexually aroused do you feel right now?" (1 = Not at all aroused, 7 = Very aroused). This was followed by 16 experimental rating sheets each featuring a single female image and vignette (4 from each category—ASW, USW, AC, UC), along with a single rating of either arousal, willingness for sex, disgust, or risk of disease. The final page consisted of a post-picture viewing manipulation check, which asked participants to rate on a seven-point category scale "How sexually aroused do you feel right now?" (1 = Not at all aroused, 7 = Very aroused).

The arousal study packet contained the same materials, albeit with different instructions as detailed further below. In addition, it also contained a small sealable plastic bag and gauze pad to obtain a sweat sample, under the guise that this would be used later to determine the participants objective state of sexual arousal during the session. This deception item was included to ensure participants completed the task as instructed (all aspects of the study were approved by Griffith University Human Research Ethics Committee; GU Ref No: 2014/577).

Participants were also asked to complete three short (i.e., to minimize inconvenience and maximize survey return) questionnaires at the end of their second session—these being included in the relevant study packet. These were: (1) The core disgust questions from the Disgust Sensitivity Questionnaire (Revised; Olatunji et al., 2008), (2) The Perceived Vulnerability to Disease questionnaire (PVD; Duncan et al., 2009), and (3) The Sociosexuality index (SOSI; Penke and Asendorpf, 2008).

Procedure

Face-to-face contact between experimenter and participant was kept to a minimum to reduce embarrassment. Participants learned of the study via advertisements posted on social media, across the Griffith University campus, and on an undergraduate psychology research participation website. Each advertisement directed interested individuals to a website where more information regarding the study and its requirements were presented. This page provided straightforward information regarding the purpose of the experiment, the tasks to be performed by participants, as well as information regarding the compensation individuals would receive in return for their participation. Individuals who remained interested were directed to contact the study email address. Email correspondence between the participants and experimenters was standardized. A final information sheet was provided to individuals who emailed the researcher, and upon indicating their continued interest in the study, the participant could elect to collect the study materials from the Griffith University, School of Applied Psychology—Gold Coast reception or have the materials posted to their address.

Participants received two separate study packets to complete at home. Participants were instructed in the information sheet to abide by a minimum 24-h period between the completion of the first and second packet, with approximately half of them instructed to follow a neutral-arousal study packet order and vice versa. In the neutral study packet, participants were directed to complete the entirety of the study packet whilst in a "unaroused/neutral state." In the self-arousal study packet, participants were instructed to "self-stimulate (masturbate) to a point of high but sub-orgasmic level of arousal (i.e., not to the point of ejaculation), and to then complete the rating tasks whilst remaining in this aroused state." During the self-arousal session, participants were directed to take a sample of their forehead sweat using the provided gauze pad and were asked to place this sample in the bag provided. Participants were informed on the information sheet that perspiration can provide a reliable measure of sexual arousal and the collection of the sweat sample was to ensure that participants were completing the experimental task as instructed. This was the only form of deception used in the study and was employed to encourage participants to complete the task as instructed (i.e., in a high state of sexual arousal). Upon completion of both study packets, participants could elect to return them to the school reception or via mail. When participants presented to collect their payment for participation, they were provided with a debrief form which contained information regarding the use of deception in the study and were also given the choice to withdraw from participation without penalty.

Analysis

Participants completed a manipulation check at the start and end of each session, so that we could ensure that their level of self-reported sexual arousal was: (1) higher at the start of the self-arousal session than at the start of the control session, and (2) that in the sexual arousal session all ratings exceeded 1 (i.e., above a report of "no sexual arousal"). Two participants reported being as aroused at the start of the non-arousal session as they were on the self-arousal session, so their data were excluded from the analysis. A further participant reported no sexual arousal at the end of the self-arousal session and was thus also excluded.

Participants were also asked about their sexual orientation, with one participant reporting being exclusively homosexual. This participant was also excluded from the study.

All of the data were suitable for parametric analysis (i.e., data were normally distributed [evaluated using skewness and kurtosis values], there was homogeneity of variance [established using Levene's test for between variables] and there were no violations of sphericity [established using Mauchly's test]). Due to the nature of the study several participants had missing data, which meant their exclusion from certain ANOVAs. For the regression analyses, we were able to impute some of the missing data based on averaging the remaining responses (e.g., for comparisons of the self-aroused vs. unaroused sessions "Willingness to have sex" ratings, at an individual level this was computed by subtracting the mean of the four "Willingness to have sex" ratings for each cell of the design [attractive vs. unattractive by sex-worker by non-sex worker] in the unaroused state, from the mean of those same four ratings in the self-aroused state. If one rating were missing, say the attractive sex-worker in the unaroused state, then the three remaining data points were averaged and this formed the score to subtract from the corresponding mean score in the self-aroused state; such imputation was conducted for 8 cases). We note that utilizing the extant data with no imputation yields similar, albeit less powerful, results.

We started by examining the manipulation check arousal ratings using a three-way mixed design ANOVA, with Arousal (self-arousal session vs. non-arousal session) and Time (rating at the start vs. end of the session) as within-factors and Session order (arousal-non arousal vs. non-arousal-arousal) as the between factor. The ratings of the images obtained on each session were analyzed using four-way mixed design ANOVAs, with Arousal (self-arousal session vs. non-arousal session), Attractiveness (attractive vs. unattractive) and Sex-worker status (Sex-worker vs. Control) as within-factors and Session order (arousal-non arousal vs. non-arousal-arousal) as the between factor. The final set of analyses examined predictors of the observed alterations in arousal and willingness for sex, that were identified in the analysis of the image ratings. Here we used a two-stage regression procedure, first entering state disgust and STI risk ratings of the images, and then, second, entering the more trait-based predictors, namely Core disgust sensitivity, Perceived vulnerability to disease and the Sociosexuality index. A data summary is available in **Supplementary Material**.

RESULTS

Participants

The final sample consisted of 47 men, aged between 18 and 45 (M age = 23.9, *SD* = 6.1). Forty-two of these men reported being heterosexual and five bisexual. Core disgust sensitivity (DS) scores ranged from 0.5 to 9.5 (M DS = 5.4, *SD* = 2.1), PVD total scores ranged from 1.9 to 5.3 (M PVD = 3.2, *SD* = 0.8), and Sociosexuality Index (SOI) scores ranged from 1.9 to 8.9 (M SOI = 5.3, *SD* = 1.6)—thus in all cases providing a good degree of variability. There were no differences between these variables by the order in which the sessions were completed.

Manipulation Check

Participants rated their degree of sexual arousal at the start and end of each session. The ANOVA revealed a main effect of

TABLE 1 | Means (and standard deviations) for each dependent variable organized by the experimental manipulations.

Independent variables	**Dependent variables**			
	Disgust	**STI risk**	**Arousal**	**Willingness for sex**
	***M* (*SD*)**	***M* (*SD*)**	***M* (*SD*)**	***M* (*SD*)**
UNAROUSED STATE				
Attractive control	1.7 (1.3)	2.5 (1.1)	3.2 (1.4)	4.0 (1.7)
Attractive sex-worker	3.9 (2.0)	5.2 (1.4)	2.7 (1.6)	2.5 (1.4)
Unattractive control	2.2 (1.4)	2.5 (1.2)	3.0 (1.4)	3.6 (1.4)
Unattractive sex-worker	4.2 (2.0)	5.2 (1.4)	2.4 (1.4)	2.6 (1.8)
AROUSED STATE				
Attractive control	1.5 (1.1)	2.3 (1.2)	4.8 (1.3)	5.2 (1.3)
Attractive sex-worker	3.7 (1.9)	4.7 (1.7)	4.2 (1.8)	4.4 (1.9)
Unattractive control	1.8 (1.3)	2.1 (1.1)	4.1 (1.5)	5.0 (1.3)
Unattractive sex-worker	3.6 (2.1)	4.8 (1.6)	3.5 (1.8)	4.0 (2.2)

Arousal, $F_{(1,44)} = 433.73$, $p = 0.0000152$, $\eta^2 = 0.91$, with this being qualified by an Arousal by Time interaction, $F_{(1,\,44)} = 18.63$, $p = 0.0000887$, $\eta^2 = 0.30$. On the control non-arousal session, sexual arousal increased from a starting mean of 1.4/7 ($SD = 0.5$) to 1.9/7 ($SD = 1.0$), while in the self-arousal session it waned from a starting mean of 5.8/7 ($SD = 1.1$) to 5.5/7 at the end of the session. Session order also exerted an effect. Sexual arousal was reportedly higher in participants who received the non-arousal session first ($M = 3.9/7$; $SD = 0.7$), relative to those who received the arousal session first ($M = 3.5/7$; $SD = 0.8$). In addition, there was a Session order by Time interaction, $F_{(1,\,44)} = 4.32$, $p = 0.04$, $\eta^2 = 0.09$, with a small reduction in arousal across Time in participants who received the self-arousal session first (*M diff* $= 0.1$; $SD = 1.0$), relative to those who received it second (*M diff* $= 0.3$; $SD = 1.1$). Irrespective of these differences, it is readily apparent that participants reported considerably greater sexual arousal in the self-arousal session than in the control non-arousal session, both at its start and finish.

Analysis of the Image Ratings

Table 1 presents the mean values (and standard deviations) for all of the dependent and independent variables used in the study. **Table 2** details the ANOVA results from the analyses.

For disgust ratings, all three main effects were significant, but with no interactions or session order effects (see **Table 2**). Consistent with our first hypothesis, greater sexual arousal was associated with a mean reduction in disgust of 4.7%. Unattractive images were judged a mean of 5.0% more disgusting than attractive images. Images of sex-workers were judged a mean of 30.1% more disgusting than controls. Notably, all of these effects were independent, such that when disgust fell following sexual arousal, this reduction was evident irrespective of whether the image being rated was attractive or unattractive, and of a sex-worker or a control.

Disease risk ratings mirrored disgust ratings for the main effects of Arousal and Sex-worker status, but Attractiveness had no impact on this type of evaluation (see **Table 2**). Sex-worker status exhibited the largest effect on risk ratings, with sex-workers judged a higher disease risk than controls by a mean of 36.8%. Consistent with our first hypothesis, sexual arousal was associated with a mean fall of 5.6% in disease risk ratings. However, the order in which the sessions were completed significantly affected this. Participants, who completed the self-arousal session first, reported the same level of disease risk on both sessions (M self-arousal session = 3.9/7, $SD = 1.1$; M non-aroused session = 3.9/7, $SD = 1.3$), while participants who completed the non-arousal session first reported reduced disease risk on their arousal session (M self-arousal session = 3.0/7, $SD = 1.4$; M non-aroused session = 3.8/7, $SD = 1.2$). This would suggest that sexual-arousal only reduces risk assessment when there is non-arousing pre-exposure to the stimuli—an unexpected outcome. There was also a main effect of Session order, but this was of lesser interest due to the interaction.

Participants also evaluated their willingness to have sex with the people depicted in the images (see **Table 2**). Participants reported a mean 20.7% greater willingness to have sex following the arousal manipulation. Sex-worker status affected willingness to have sex, with a mean reduction of 15.1% when the depicted person was a sex-worker. There was an interaction between the Arousal manipulation and Sex-worker status. There was a greater mean increase in willingness to have sex with a sex-worker ($M = 23.6\%$), relative to a control ($M = 17.7\%$), when contrasting the self-arousal session to the control session. There were also two effects involving order. First, participants who completed the self-arousal session first, reported a smaller increase in willingness to have sex across sessions (*M diff* $= 1.1$, $SD = 1.6$), than participants who completed the non-arousal session (*M diff* $= 1.9$, $SD = 1.8$). Second, participants who had completed the self-arousal session first, reported a smaller difference in willingness to have sex between appealing control and sex-workers (*M diff* $= 0.9$, $SD = 2.0$), when contrasted to unappealing control and sex workers (*M diff* $= 1.3$). This relationship was reversed for participants who completed the self-arousal condition second (corresponding values; *M diff* $= 1.4$, $SD = 2.3$; *M diff* $= 0.7$, $SD = 1.9$).

Finally, participants judged how sexually arousing they found each type of image. Four effects were evident here (see **Table 2**). All three main effects were significant, and in addition Attractiveness interacted with Arousal. In the self-arousal session, participants judged all of the images a mean of 19.1% more arousing than when they viewed them in the control session. However, this effect interacted with Session order. Participants who completed the self-arousal session first, demonstrated a smaller difference in arousal between the two sessions (*M diff* $= 0.9$, $SD = 1.3$), than participants who completed the control session first (*M diff* $= 1.8$, $SD = 1.4$). Images of sex-workers were judged a mean 7.5% less sexually arousing than images of controls and this too interacted with Stimulus order. Here, participants who completed the arousal session first reported a much larger drop in arousal between the images of the control and sex-worker pictures (*M diff* $= -1.1$, $SD = 1.0$), than participants who completed the control condition first (*M diff* $= 0.0$, $SD = 1.6$). Attractive images were rated

TABLE 2 | Analysis of variance results for each dependent variable organized by main effects and interactions.

Effects	**Dependent variables**			
	Disgust $F_{(1, 41)} =$	**STI risk $F_{(1, 42)} =$**	**Arousal $F_{(1, 42)} =$**	**Willingness for sex $F_{(1, 40)} =$**
Arousal (AR)	$4.94, p = 0.03, \eta^2 = 0.11$	$8.21, p = 0.006, \eta^2 = 0.16$	$110.46, p = 1.26 \times 10^{-5}, \eta^2 = 0.73$	$70.32, p = 1.26 \times 10^{-5}, \eta^2 = 0.64$
Attractive (AT)	$6.26, p = 0.02, \eta^2 = 0.13$	<1	$9.51, p = 0.004, \eta^2 = 0.19$	<1
Sex-work status (SW)	$83.04, p = 1.26 \times 10^{-5}, \eta^2 = 0.67$	$141.68, p = 1.26 \times 10^{-5}, \eta^2 = 0.77$	$4.86, p = 0.03, \eta^2 = 0.10$	$17.78, p = 0.0001, \eta^2 = 0.31$
Session order (SO)	<1	$4.60, p = 0.04, \eta^2 = 0.10$	<3.9	<1
AR × AT	<1.5	<1	$7.44, p = 0.09, \eta^2 = 0.15$	<1
AR × SW	<1.5	<1	<1	$5.08, p = 0.03, \eta^2 = 0.11$
AR × SO	<1	$8.21, p = 0.006, \eta^2 = 0.16$	$11.98, p = 0.001, \eta^2 = 0.22$	$4.40, p = 0.04, \eta^2 = 0.10$
AT × SW	<1	<1	<1	<1
AT × SO	<1	<1	<1	<1
SW × SO	<1	<3.5	$6.91, p = 0.01, \eta^2 = 0.14$	<1
AR × SW × SO	<1	<1	<2.1	<2.7
AT × AR × SO	<1	<1	<1	<1
AT × AR × SW	<1	<1	<1	<2.1
AT × SW × SO	<1	<1	<1	$4.27, p = 0.05, \eta^2 = 0.10$
AT × AR × SW × SO	<1.5	<1	<1.3	<1

a mean 7.0% more sexually arousing than unattractive images. Attractiveness and Arousal interacted, with attractive images demonstrating a much larger change in their capacity to arouse across the self-arousal and control sessions ($M = 22.1\%$), than unattractive images ($M = 16.2\%$).

Predictors of Change

Judgments of how sexually arousing the images were and how willing the participant was to have sex them, were both significantly affected by the self-arousal manipulation and by whether the image was of a sex-worker or control. Here we examined whether individual variation in these effects could be predicted by disgust and disease risk measures obtained in the study, and by trait measures of core disgust sensitivity, perceived vulnerability to disease and attitudes to short-term relationships. We note that none of the effects examined here, differed by Session order, even when tested (Williams test) without correction for multiple comparisons.

As we predicted in our second hypothesis, reductions in disease risk judgments were positively associated with reductions in disgust (see **Table 3**). Across arousal state, judgments of both willingness to have sex and of how arousing the images were, increased in unison (see **Table 3**). Consistent with hypothesis 3(1), both of these increases were correlated with decreases in risk judgments. However, these increases were not related to changes in disgust, refuting the other part of hypothesis 3(1). For the trait measures, greater core disgust sensitivity was associated with larger changes in arousal, with a similar trend for willingness. These findings were largely borne out by the regression analyses detailed in **Table 4**. Larger changes in ratings of willingness for sex and of arousal, were most reliably predicted by reductions in STI risk rating, higher trait disgust and lower perceived vulnerability to disease. The differing outcomes for state and trait disgust were consistent with hypothesis 4.

We also examined changes in reported willingness to have sex, and how arousing the images were, when contrasting controls with sex-workers. The correlations, reported in **Table 5**, indicate that changes in arousal and willingness ratings were again related, with a trend for both of these variables to be associated with trait core disgust—nothing else was evident, refuting hypothesis 3(2). The regression analyses again reflected these findings (see **Table 4**). For willingness to sex, the final model was significant, with core disgust sensitivity and perceived vulnerability to disease the only significant predictors. Lower disgust sensitivity and lower perceived vulnerability to disease was associated with a larger difference in reported willingness to have sex between a control and a sex-worker. For the sexual arousal rating regression, the models were not significant. The differing outcomes for state and trait disgust were consistent with hypothesis 4.

We then conducted a second set of regression analyses on the remaining significant effects for the willingness to have sex and arousal ratings reported in **Table 2** (i.e., Attractiveness, Arousal by Attractiveness for arousal ratings; Arousal by Sex-worker status for willingness ratings). There were no significant effects (refuting hypothesis 3(3)), when using the same set of predictor variables as detailed in the preceding analyses.

DISCUSSION

This study examined the role of disgust in STI-related sexual decision-making in young men. Consistent with prior findings

TABLE 3 | Pearson correlations between rating difference scores for change in arousal state and trait scores.

Variable	Change in arousal state (self-arousal session—control)				Trait scores	
	Δ Willingness	**Δ Arousal**	**Δ Risk**	**Δ Disgust**	**Core DSQ***	**PVD total***
ΔArousal	0.69†					
ΔRisk	−0.50†	−0.43†				
ΔDisgust	−0.18	−0.18	0.50†			
Core DSQ*	0.27	0.33†	−0.03	−0.13		
PVD total*	−0.06	−0.17	−0.17	0.04	0.27	
SOSI*	0.15	0.13	−0.13	−0.24	0.01	0.06

*Core DSQ, Disgust Sensitivity Questionnaire Revised; PVD total, Perceived vulnerability to disease; SOSI, Socio-sexuality index. $^{\dagger}p < 0.05$.

TABLE 4 | Regression analyses.

Model and predictors	Change in arousal state (self-arousal session-control)		Change in sex-worker status (control—sex-worker)	
	Willingness for sex rating	**Sexual arousal rating**	**Willingness for sex rating**	**Sexual arousal rating**
Model 1	$F_{(2, 41)} = 7.89, R^2 = 0.24^{*}$	$F_{(2, 39)} = 4.29, R^2 = 0.14^{*}$	$F_{(2, 44)} = 1.86$, NS	$F_{(2, 44)} = 0.20$, NS
STI risk	$\beta = -0.57, p = 0.001$	$\beta = -0.45, p = 0.011$	$\beta = 0.27$, NS	$\beta = 0.08$, NS
Disgust	$\beta = 0.10$, NS	$\beta = 0.05$, NS	$\beta = -0.13$, NS	$\beta = 0.05$, NS
Model 2	$F_{(5, 38)} = 5.34, R^2 = 0.34^{*}$	$F_{(5, 36)} = 5.92, R^2 = 0.38^{*}$	$F_{(5, 41)} = 2.59, R^2 = 0.15^{*}$	$F_{(5, 41)} = 0.75$, NS
Fit improvement	$F_{(3, 38)} = 2.90, p = 0.048$	$F_{(3, 36)} = 5.93, p = 0.002$	$F_{(3, 41)} = 2.91, p = 0.046$	$F_{(3, 41)} = 1.11$, NS
STI risk	$\beta = -0.63, p = 0.0001$	$\beta = -0.57, p = 0.001$	$\beta = 0.23$, NS	$\beta = 0.04$, NS
Disgust	$\beta = 0.21$, NS	$\beta = 0.23$, NS	$\beta = -0.18$, NS	$\beta = 0.00$, NS
Core DS**	$\beta = 0.33, p = 0.02$	$\beta = 0.43, p = 0.002$	$\beta = -0.36, p = 0.016$	$\beta = -0.26$, NS
PVD**	$\beta = -0.27, p = 0.056$	$\beta = -0.44, p = 0.002$	$\beta = 0.30, p = 0.041$	$\beta = -0.05$, NS
SOSI**	$\beta = 0.12$, NS	$\beta = 0.14$, NS	$\beta = 0.05$, NS	$\beta = 0.00$, NS

$^{*}p < 0.05$, R values are adjusted. **Core DS, Disgust Sensitivity Questionnaire Revised; PVD, Perceived vulnerability to disease total; SOSI, Socio-sexuality index total.

TABLE 5 | Pearson correlations between rating difference scores for change in sex-worker status and trait scores.

Variable	Change in Sex-worker status (control—sex-worker)				Trait scores	
	Δ Willingness	**Δ Arousal**	**Δ Risk**	**Δ Disgust**	**Core DSQ***	**PVD total***
Δ Arousal	0.38†					
Δ Risk	0.25	0.08				
Δ Disgust	−0.10	0.06	0.14			
Core DSQ*	−0.28††	−0.28††	−0.16	−0.19		
PVD total*	0.21	−0.12	−0.04	−0.07	0.27	
SOSI*	0.03	0.00	−0.01	0.15	0.01	0.06

*Core DSQ, Disgust Sensitivity Questionnaire Revised; PVD total, Perceived vulnerability to disease; SOSI, Socio-sexuality index. $^{\dagger}p < 0.05$, $^{\dagger\dagger}p = 0.055$.

of reduced object-related disgust with higher sexual arousal (Stevenson et al., 2011; Borg and de Jong, 2012), and with our first hypothesis, we found that disgust judgments of potential sexual partners were reduced when participants were sexually aroused. Similarly, and consistent with previous studies (Blanton and Gerrard, 1997; Shuper and Fisher, 2008; Imhoff and Schmidt, 2014; Skakoon-Sparling et al., 2016) and with our first hypothesis, judgments of STI risk were also reduced, and as predicted in our second hypothesis, this reduction in risk was significantly associated with the fall in disgust. Participants also judged how sexually arousing the target images were and how willing they were to have sex with the person depicted in them. These ratings increased when participants were aroused and when they depicted images of control women. Attractiveness had little effect on willingness for sex, but a greater effect on arousal ratings. Overall, there were few interaction effects. We also explored whether disgust and STI risk ratings, along with trait-related measures, could predict participants arousal and willingness for sex ratings. In partial support of our third hypothesis (first part), when participants were sexually aroused, in contrast to when they were unaroused, disease risk ratings but not disgust ratings, were significantly predictive of changes in willingness for sex with, and arousal for, all of the depicted images. Trait disgust and perceived vulnerability to disease were also found to be significant predictors, but these effects, as we suspected (hypothesis four) did not parallel trait disgust measures. Finally, for judgments most directly connected with STI risk perception—between images depicting sex-workers vs. controls, only trait disgust and perceived vulnerability to disease were found to be predictive—contrary to the second part of hypothesis three.

Before turning to the implications of these findings, it is important to reflect upon their validity. First, while we could not take any physiological measures of arousal due to the way that we designed the study (i.e., conduct at home), we note that self-report measures of sexual arousal in men have been found to closely correspond to objective measures of arousal in several studies (see Chivers et al., 2010). Second, as we noted above, our findings follow expectations derived from prior laboratory studies, including reductions in disgust and STI risk perception under conditions of sexual arousal, suggesting convergent validity. Third, participants—as many did—could opt out of the study simply by failing to return the study packets. This can be taken to imply that those who did return the study packets, did so having followed the study instructions, and in the knowledge that their sweat sample would be tested for evidence of sexual arousal. While we cannot be sure that participants reported sexual intentions would actually translate into behavior—an issue for all studies in this area—it would seem likely that our participants did as they were asked to do. Fourth, participants self-selected for inclusion in this study, and so it is possible that as with all other studies in this area, they may be unrepresentative of the broader young male population. Nonetheless, their scores on the self-report individual differences measures did not suggest that the sample were particularly unusual. Finally, we also note that these findings may not generalize to the entire male population, although some of our results replicate effects observed in different samples of men and women.

As predicted sexual arousal (in comparison to a non-aroused state), increased ratings of willingness to have sex, and judgments of how arousing the target images were. This change in willingness and image arousal ratings was significantly predicted by the change in risk perception, but not by change in disgust ratings (i.e., state). In addition, we also found that trait disgust and perceived vulnerability to disease explained additional variance here. Ideally, these relationships need to be examined using structural equation modeling—something precluded here because of our sample size and due to the exploratory nature of this study—nonetheless our data suggest a plausible model for future testing. We suggest that state disgust, namely that felt at a particular moment, contributes to a risk decision, presumably alongside other inputs such as a person's knowledge of STI transmission. This combined risk measure then informs both arousal and willingness judgments. In addition, there is a second and seemingly independent influence of disgust, through trait core disgust sensitivity. Here, greater trait core disgust sensitivity is associated with a greater propensity for sexual arousal to drive changes in willingness to have sex and image arousal ratings. What this may mean is that individuals who are generally highly disgust sensitive, are those who most strongly change behavioral intentions under conditions of sexual arousal. We note here the interesting parallel with Grauvogl et al. (2015), who found that high levels of trait disgust were linked to greater genital and self-reported sexual arousal. Thus, we suggest that state disgust has an indirect effect on risk perception, which in turn affects willingness and arousal ratings, while trait core disgust has a direct effect on both.

We also examined the predictors of differences in willingness for sex and arousal ratings for images depicting sex-workers and age-matched controls. While there was a close yoking between state disgust and willingness (and arousal ratings)-−88% of participants reported greater disgust for sex-workers *and* a reduced willingness for sex, these two variables were not significantly associated. However, trait disgust, and perceived vulnerability to disease, were both correlated with these difference scores. Individuals who were high in core disgust sensitivity reported a much smaller difference in willingness for sex (with a similar albeit non-significant trend for arousal) between images of sex-workers and controls. In this case, we suggest that trait core disgust reflects a high baseline level of responding to the possibility of sex with all of the images, thereby reducing the magnitude of the difference between willingness and arousal ratings for sex-workers and controls. Perceived vulnerability disease (PVD) had a different relationship. A greater PVD score was linked to a greater difference in response between willingness ratings for sex-workers and controls. That is being germ averse and wary of disease reduced willingness for sex, both here, and similarly so, for changes in sexual arousal.

We did not find an effect of attractiveness on willingness for sex, although it was apparent for the image arousal ratings. What we did find though, was that unattractive images were judged as significantly more disgusting, independent of other effects. This is an interesting observation, because it points again to the possible evolutionary basis of disgust as a disease avoidance system. Attractiveness, in all of its facets, is generally thought to reflect various aspects of health, and thus a key aspect of potential mate value (Buss, 2015). To the extent that disgust is driven by cues that are indicative of disease—directly and indirectly (i.e., indicators of poor health)—unattractiveness might then be regarded as one such indirect cue.

We also found unexpected effects of order. Specifically, participants that first viewed and rated the study stimuli in an unaroused state, and then in an aroused state, reported a greater reduction in perceptions of disease risk (about the target) and a greater willingness for sex (with the target), relative to participants that viewed and rated the study stimuli in the opposite arousal order. Whilst these findings were not predicted, they are not surprising. Prior research on sexual risk taking has shown that increased familiarity with a potential sexual target encourages appraisals that the target is low in disease risk (Swann et al., 1995). Swann et al. (1995) reported that receiving 1 min of video-taped information about a potential sexual target, even though the information was irrelevant to the target's sexual health status, increased participants' feelings of familiarity and liking, and decreased appraisals of disease risk. Potential sexual partners who are familiar may be perceived as safe due to person perception biases and the reliance on incorrect heuristics to estimate a potential sexual partner's disease risk. For example, familiarity may influence disease risk perceptions via social projection bias, which is the tendency to expect similarities between ourselves and others, especially those who are familiar to us (Robbins and Krueger, 2005). Most young adults consider themselves at low risk of STIs (Fromme et al., 1999), and may project this perception of self to familiar others. Our findings are tentative, but suggest that familiarity with a potential sexual partner can operate as a situational cue that the potential partner is low in sexual disease risk and therefore condom use, for example, is not warranted.

In conclusion, we have suggested that disgust may play multiple roles in STI-related sexual decision making, both at a state and trait level. Two important issues emerge for further study. First, we did not assess other potential domains of trait disgust, partly because there is some disagreement over exactly what these other domains might be—noting however that core disgust is widely agreed to exist (i.e., Olatunji et al., 2008; Rozin et al., 2016)—and also because we were restricted in how many questions we could ask participants to complete. Second, we were unable to complete structural equation modeling, as we did not have sufficient number of cases nor a clear enough *a priori* model from which to work. We suggest that the data reported here provides an empirical framework for such an approach. Finally, we note more broadly that these findings implicate disgust as a component of sexual decision-making in the context of STI risk.

AUTHOR CONTRIBUTIONS

MO, RS, and TC conceived of the study. MO and RS designed the study. MO, CT, and AC coordinated and administered the study. MO, RS, and CT participated in data and statistical analysis. All authors helped draft the manuscript, and gave final approval for publication.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpsyg.2018.02602/full#supplementary-material

Supplementary Data Sheet 1 | Data Summary: The role of disgust in male sexual decision-making; Oaten et al. (2009).

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PsychoBehavioroimmunology: Connecting the Behavioral Immune System to Its Physiological Foundations

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Although infectious disease has posed a significant and persistent threat to human survival and welfare throughout history, only recently have the psychological and behavioral implications of disease threat become a topic of research within the behavioral sciences. This growing body of work has revealed a suite of affective and cognitive processes that motivate the avoidance of disease-causing objects and situations—a cascade of processes loosely conceptualized as a "behavioral immune system (BIS)." Recent BIS research has linked disease threat to a surprisingly broad set of psychological and behavioral phenomena. However, research examining how the BIS is nested within our broader physiology is only beginning to emerge. Here, we review research that has begun to elucidate the physiological foundations of the BIS—at the levels of sensory modalities, cells, and genes. We also discuss the future of this work.

Keywords: behavioral immune system, psychoneuroimmunology, health, immune system regulation, social cognition

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PSYCHOBEHAVIOROIMMUNOLOGY: CONNECTING THE BEHAVIORAL IMMUNE SYSTEM TO ITS PHYSIOLOGICAL FOUNDATIONS

The threat posed by infectious disease throughout human evolution has likely caused more deaths than all other causes of mortality combined (e.g., Inhorn and Brown, 1990). This threat is not unique to humans; many biologists characterize the evolution of all animal species as having been driven substantially by a billion-year evolutionary arms race between parasites and their hosts (Zuk, 1992, 2007; Knoll and Carroll, 1999; Zimmer, 2001), with viruses alone estimated to be responsible for one third of mammalian genetic adaptations (Enard et al., 2016). One product of this arms race in humans (and other vertebrates) is the immune system, which is comprised of an astonishingly complex set of mechanisms which reactively vanquish infections when they occur (a system that has the capacity to generate billions of unique antibodies; Fanning et al., 1996; Janeway, 2001). Given the fitness costs of immune system activation, however, humans also proactively respond to disease-connoting cues with a cascade of affective and cognitive responses which, in turn, motivate behavior that minimizes the probability of infection—a psychobehavioral agglomerate now popularly referred to as the *behavioral* immune system (BIS) (see Schaller and Park, 2011; Murray and Schaller, 2016; Ackerman et al., 2018a). But until recently, little work investigated the ways in which the "behavioral" and physiological immune systems interact. Here, we provide an overview of burgeoning research linking the BIS to its physiological foundations.

Recent Behavioral Immune System Research

Behavioral immune system research suggests that the social and behavioral implications of perceived disease threat range from basic perceptual processes (e.g., facial perception), to judgment and decision-making processes, to culture-wide norms and social systems (for reviews see Murray and Schaller, 2014, 2016, 2017). Each of these related lines of research are theoretically underpinned by a distinct conceptual hypothesis which considers the cost/benefit ratio of a given trait or behavior, and how this ratio is variable dependent upon the threat of disease (or perceived threat of disease) within one's environment. For example, whereas gregarious social behavior, risk taking, and promiscuous sexuality all have distinct, unique benefits, they are similar in that high levels of each are associated with disease-specific costs. This costs/benefit logic implies the hypotheses that greater infection threat will be associated with lower gregariousness, lower risk tolerance, and less promiscuous sexuality. Several studies now provide evidence for these hypotheses, using both trait measures of perceived disease threat and laboratory manipulations of disease threat (Mortensen et al., 2010; Murray et al., 2013; Sparks et al., 2018; Prokosch et al., in press), as well as ecological variation in actual disease threat (Schaller and Murray, 2008; Murray and Schaller, 2010; Van Leeuwen et al., 2012; Murray, 2014a,b). Similar implicit cost/benefit logic has also been employed to experimentally link disease threat to outgroup stereotyping and prejudice (Faulkner et al., 2004; Park et al., 2007; Huang et al., 2011), conformity (Murray and Schaller, 2012; Wu and Chang, 2012; Murray et al., 2019c), anticipated future sexual behavior (Hill et al., 2015), and self-image concern (Ackerman et al., 2018b).

Integrating Behavioral and Physiological Immunity

Until relatively recently, BIS research proceeded without much theoretical regard to what the physiological underpinnings of this "system" might be. This is unsurprising given that this research was conducted predominantly in social psychology labs. Therefore, the majority of this work ignored the foundational question of how psychological and behavioral disease avoidance strategies are intrinsically embedded within the immune system proper. In doing so, this work paid little homage to the vast literature comprising the field of psychoneuroimmunology (PNI), which for decades has studied the interactions between the immune system, the brain, and behavior (e.g., see Clark and Fessler, 2014).

This isolated state of affairs is shifting. A growing body of work in the psychological sciences is beginning to elucidate how the BIS is influenced by—and influences—the physiological immune system. We believe that is work is both conceptually related to, but currently distinct from, that which characterizes PNI research for at least two reasons. The first reason is a matter of scale: whereas PNI research frequently concerns questions regarding mechanistic pathways connecting the immune system to the brain (e.g., the immune-brain loop or cell-signaling networks, see Daruna, 2012), physiological BIS research to date is primarily concerned with the relationships between immune processes and overt social cognition and behavior. A second reason is that whereas PNI is more primarily focused on *reactive* psychological responses to already-existing infection (such as sickness behavior, e.g., see Dantzer and Kelley, 2007) or the dysregulation of otherwise adaptive systems (such as cytokine-induced depression, e.g., see Loftis et al., 2010), research investigating the physiological correlates of the BIS is more primarily concerned with how *proactive* (and sometimes ostensibly unrelated) behaviors that minimize infection risk are associated with the immune system. Here, we provide an overview of this emerging subfield.

PHYSIOLOGICAL FOUNDATIONS OF THE BEHAVIORAL IMMUNE SYSTEM

Recent work expanding our understanding of the physiological foundations of the BIS can be parsed into three levels of analysis: Sensory, cellular, and genetic. We review each of these below.

Sensory Components

Early and current work investigating the implications of experimentally "activating" the BIS has predominantly used visual cues of pathogenic risk. However, recent work is elucidating the importance of other sensory modalities in disease detection and its coordinated BIS responses as well.

Some work suggests that olfactory cues of disease not only elicit disgust but also predict prophylactic behaviors. In non-human animal populations, body odorants from conspecifics can convey infection status (mice; Kavaliers et al., 2005; bullfrog tadpoles; Kiesecker et al., 1999). In humans, body odors may convey similar information. Body odors from sick targets are rated less desirable and likeable (Regenbogen et al., 2017), and are also evaluated as unhealthier, more intense, and less pleasant (Olsson et al., 2014). Disgust ratings of body odors are also dependent upon the odor source, with odors of closer family members rated as less disgusting than strangers' body odors (Stevenson and Repacholi, 2005; Case et al., 2006). The strong association between body odor and disgust has even recently inspired a unique psychometric measure, the Body Odor Disgust Scale (BODS; Liuzza et al., 2017).

Interestingly, body odorants may also communicate someone's state disgust. Individuals who smelled body odors from participants primed with disgust had disgust-related reactions (e.g., nose wrinkling, reduced visual scanning; de Groot et al., 2012). Other work suggests that, in addition to activation of the neural structures associated with disgust (Wicker et al., 2003), experimentally inducing aversive odors also leads to patently prophylactic cognitions (greater intentions to use condoms; Tybur et al., 2011) and even less-directly prophylactic cognitions (condemnation of moral violations; Schnall et al., 2008). These results speak to the associations between olfactory detection, disease avoidance, and specific affective and behavioral reactions.

Emerging work is also beginning to link olfactory *acuity* to disgust and associated BIS responses. Given that olfactory cues are often subtle and their meanings ambiguous, a greater ability to detect such cues may be associated with more affective vigilance toward disease cues more generally. Recent work suggests that higher olfactory acuity may be associated with higher avoidance motivation (Fay and Bovier, 2018). Similarly, Murray et al. (unpublished) found that greater olfactory acuity—operationalized as a greater ability to detect, discriminate between, and identify odors—predicted greater sexual disgust and more restricted sociosexuality. However, olfactory acuity was not meaningfully associated with Perceived Vulnerability to Disease (Duncan et al., 2009). Such investigations remain a work in progress.

While work examining olfactory and visual processes in disease detection abounds in comparison with other sensory modalities, there is emerging evidence that the disease avoidance toolkit employs our full complement of senses. Gustatory stimuli, particularly perishable food sources, evoke feelings of disgust and avoidance when paired with disease primes (Tybur et al., 2016). Higher disgust sensitivity also positively predicts aversion to novel or foreign foods (Al-Shawaf et al., 2015). Auditory and tactile senses are also impacted by behavioral immune responses: Visual disease primes increase tactile sensitivity, and lead to perceptions of individuals with foreign accents as more distant, especially for participants scoring higher in disgust sensitivity (Reid et al., 2012; Hunt et al., 2017). Human-specific disgust sensitivity also predicts people's preferred amount of personal space (Park, 2015).

As multi-sensory work grows, increasingly creative examinations of sensory phenomena and their affective reactions are also emerging. For example, Blake et al. (2017) investigated the "heebie-jeebies" as a disease-avoidance response that is distinct from disgust and fear. Taken together, a multi-sensory approach will be increasingly necessary in studying BIS processes.

Cellular Correlates

Broadly, the immune system proper is comprised of dozens of biological components and cellular-level processes of varying specificity that act to detect and neutralize invading pathogens. New research programs are now elucidating how the BIS interacts with these cellular-level processes. Early attempts to study the interplay between the BIS and the body examined how acute environmental disease cues influence immune function. Experimental studies reveal that exposure to visual cues of contagion—in addition to increasing disgust and prejudice responses—upregulate oral and blood immune inflammatory biomarkers (Schaller et al., 2010; Stevenson et al., 2011, 2012, 2015; Makhanova et al., unpublished). For example, men who viewed pathogenic pictures (relative to control images) reported greater disgust, had higher body temperature, and had greater salivary concentrations of TNF-alpha and albumin (Stevenson et al., 2012). Similarly, participants' blood plated *in-vitro* released more IL-6 in response to mitogen stimulation (by LPS) after they viewed pathogenic pictures (Schaller et al., 2010). Such results suggest that visual components of the BIS may proactively induce immunological responses when the threat of infection appears imminent.

However, correlational studies suggest that in the absence of immediate pathogen threat, the relationship between the BIS and physiological immune system may not always be additive. For example, stimulated release of proinflammatory cytokines (IL-6, IL-1β, TNF-alpha) from blood collected from healthy subjects (absent experimental primes) were not related to self-reported germ aversion (Gassen et al., 2018). However, these same participants' spontaneously released (IL-6, IL-1β, TNF-a) and *in-vivo* proinflammatory cytokine (IL-6) levels were *negatively* related to germ aversion and perceived longevity. Taken together, these results suggest that in addition to short-term pathogen management, the BIS may also function to promote long-term health by lowering levels of basal inflammation and cellular oxidation. Relatedly, while IL-6 has traditionally been highlighted for its proinflammatory (i.e., defense) qualities, it also serves downstream anti-inflammatory tissue maintenance functions (Del Giudice and Gangestad, 2018). Future work will unpack the similar or dissimilar functions that defense versus maintenance IL-6 may serve in cueing behavioral defense strategies.

New research also highlights personal control over pathogen exposure as a potential key factor predicting investment in behavioral (e.g., avoidance) versus physiological (e.g., tolerance) immunity. Participants who reported lesser ability to avoid pathogenic threats in their day-to-day lives had a higher white blood cell count and, in turn, slower avoidance of pathogenic stimuli on an approach-avoidance task (Bradshaw et al., unpublished). In an experimental follow-up, ingesting an inflammation-suppressing aspirin led participants to report greater avoidance motivation toward pathogenic stimuli. Non-human research conceptually mirrors these results—social insect species that more effectively behaviorally manage pathogens at the colony level (e.g., by resin-lining their nests) display lower physiological immunity at the individual level (López-Uribe et al., 2016).

Other research has examined how physiological needs impact behavioral immune activity. One study found that men who have a profile indicative of strong physiological immunity (i.e., high testosterone and low cortisol) have weaker behavioral immune responses, as indexed by facial preferences (Kandrik et al., 2017). Conversely, recently ill and frequently ill people show greater BIS activation (e.g., greater disgust, avoidance of others) than healthier peers (Stevenson et al., 2009; Miller and Maner, 2011). Similarly, women experience elevated disgust and ethnocentrism during early pregnancy, when immunosuppression is greatest (Fessler et al., 2005; Navarrete et al., 2007). Preliminary hypotheses posited that progesterone-induced immunosuppression prompts compensatory prophylactic activity (Fleischman and Fessler, 2011), but replication attempts have not found a robust link between progesterone and pathogen-avoidant behaviors. Thus, the roles that progesterone and other pregnancy-related hormones play in evoking BIS responses remain unclear (Jones et al., 2018).

Genetic Correlates

Although the majority of between-person variation in immune function appears to be due to non-heritable factors (see Brodin and Davis, 2017), genetic variation matters for disease vulnerability as well. Other BIS-motivated research is beginning to uncover how genes influence—and are influenced by—overt disease related behaviors and situations. One line of research examines individual differences in the genetic bases of immunocompetence and their relation to individual differences in behavioral tendencies associated with the BIS. One study focused on the IFNG +874 gene, one allele of which is associated with greater susceptibility to infectious diseases such as malaria, tuberculosis, and leprosy. Results revealed that individuals who possessed the disease-risk allele reported generally lower levels of extraversion and higher levels of harm avoidance (MacMurray et al., 2014). Another study focused on a different genetic polymorphism—the ACP1 gene—that also has a specific allele (the C allele) which is associated with poorer immunological function. Individuals who possessed the C allele reported lower levels of both extraversion and openness to experience (Napolioni et al., 2014).

Another recent study investigated genetic variation at the MHC region of the genome—a region in which greater allelic diversity is associated with a greater ability to recognize invading non-self (vs. self) antigens. This study, conceptually underpinned by life history theory, examined whether lower heterozygosity (diversity) at the MHC—a putative marker of lower immunocompetence and thus a marker of greater future uncertainty—was associated with "faster" sexual strategies in women (Murray et al., 2017). Consistent with the predictions implied by life history theory, women who were more homozygous at the MHC region of the genome reported more favorable attitudes toward short-term mating, a more promiscuous sexual history, and perhaps most tellingly, reported being almost a full year younger when they had their sexual debut. Further comparative tests revealed that while more homozygous women reported significantly more sexual relationships, they reported an identical number of *romantic* relationships as did heterozygous women (see **Figure 1**). This comparative test suggests that the interpersonal implications

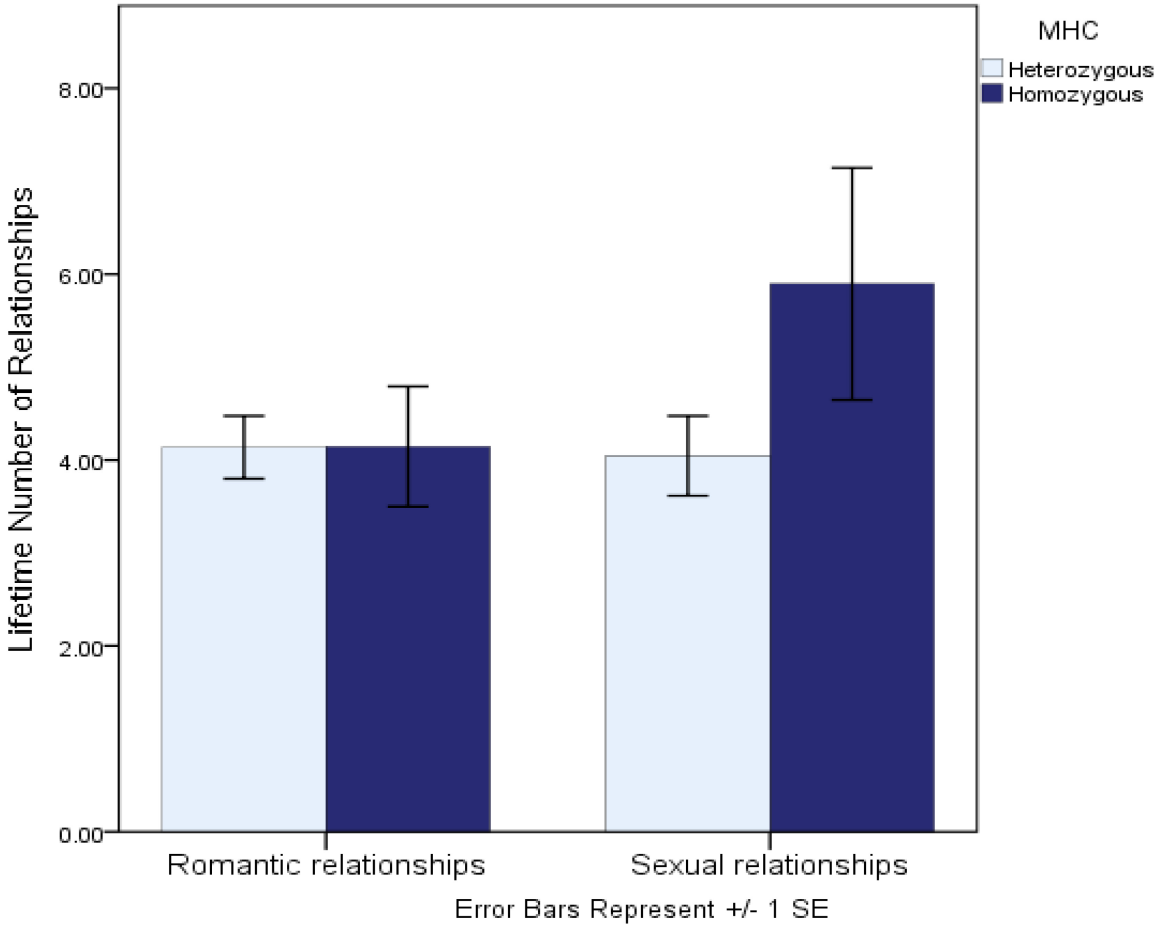

FIGURE 1 | Lifetime number of romantic and sexual relationships reported by MHC-heterozygous and homozygous women (from Murray et al., 2017).

of MHC diversity are specific to sexual strategies, rather than interpersonal dispositions more generally. Taken together, these studies suggest that genetic variants linked to chronically increased immunological vulnerabilities may also be associated with behavioral dispositions that help to either mitigate those vulnerabilities or to calibrate life history strategies accordingly.

Finally, epigenetically inspired work is beginning to investigate whether changes in disease-relevant ecological or social contexts influence disease-related gene expression. Studies from the growing area of social genomics consistently reveal transcriptional consequences of loneliness, such that people who feel lonelier (and are thus less vulnerable to socially transmitted viruses) have a relative downregulation of transcriptional elements associated with antiviral defenses and a reciprocal upregulation of pro-inflammatory transcription factors (e.g., Cole et al., 2007; Cacioppo et al., 2015). Consistent with social-cognitive perspectives on proactive defenses against potential disease threats, these transcriptional profiles are best predicted by subjective assessments (versus objective measures) of one's environment (Cole et al., 2007; Murray et al., 2019b).

The reverse of chronic loneliness—at least physically speaking—is the formation of an intense interpersonal pair-bond. More romantically termed "love" in humans, these experiences of new love and its associated close interpersonal contact also bring with them exposure to a suite of potentially novel viruses. It is thus possible that the subjective experience of new love may be accompanied by a set of epigenetic changes designed to proactively mitigate the threat posed by exposure to new infectious threats. To date, one preliminary study supports this conceptual logic. In a multi-year longitudinal study of young women (who began the study in a new relationship, but who reported *not* yet having fallen in love), falling in love was associated with a transcriptional response consistent with a selective upregulation of antiviral defenses (characterized by upregulation of type-1 interferon response genes and a downregulation of neutrophil-related genes; Murray et al., 2019a). These transcriptional changes were independent of changes in illness, frequency of sexual activity, and self-reported loneliness. No transcriptional changes were observed in inflammation-related transcriptional profiles.

ENVOI

Although BIS and PNI research programs have largely proceeded independently of one another, the above work demonstrates that these programs of research conceptually parallel each other as well. As the lattermost social genomics work shows, logical distinctions between BIS and PNI research are quickly becoming less defensible, consistent with previous perspicacious predictions (e.g., Clark and Fessler, 2014; Gangestad and Grebe, 2014). As this type of socially inspired physiological work on the BIS expands it may, in fact, become indistinguishable from that of more classically focused psychoneuroimmunology, and their distinctions eventually pedantic.

The large rift that remains, however, must first uncover the surely numerous undiscovered pathways between multisensory perception, overt social behavior, immune function, and genes. While PNI has sought to understand how non-specific shifts in immune function impact mental health and behavior (and how non-specific stressors influence immune function), BIS-related research has focused on how pathogen cues impact behavior, as modulated by changes in physiological immunity. Researchers in each field can help to inform the research done in the other. Continued work into the physiological determinants of the BIS can complement PNI research by identifying which specific proinflammatory, anti-inflammatory, and multifunctional components of the immune system impact BIS function and vice versa in both short-term (i.e., flu season) and long-term pathogenic contexts. Further, PNI's study of other functions of the immune system besides avoidance (e.g., defense, tolerance, maintenance) may help inspire BIS research to examine how such components might calibrate BIS function. As this research grows, distinctions between these disciplines will become ever more arbitrary.

AUTHOR CONTRIBUTIONS

DM, MP, and ZA all contributed to the drafting of the manuscript and making critical revisions. All authors approved the manuscript prior to submission.

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Body Odor Disgust Sensitivity Predicts Moral Harshness Toward Moral Violations of Purity

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Detecting pathogen threats and avoiding disease is fundamental to human survival. The behavioral immune system (BIS) framework outlines a set of psychological functions that may have evolved for this purpose. Disgust is a core emotion that plays a pivotal role in the BIS, as it activates the behavioral avoidance motives that prevent people from being in contact with pathogens. To date, there has been little agreement on how disgust sensitivity might underlie moral judgments. Here, we investigated moral violations of "purity" (assumed to elicit disgust) and violations of "harm" (assumed to elicit anger). We hypothesized that individual differences in BIS-related traits would be associated with greater disgust (vs. anger) reactivity to, and greater condemnation of Purity (vs. Harm) violations. The study was pre-registered (https://osf.io/57nm8/). Participants ($N = 632$) rated scenarios concerning moral wrongness or inappropriateness and regarding disgust and anger. To measure individual differences in the activation of the BIS, we used our recently developed Body Odor Disgust Scale (BODS), a BIS-related trait measure that assesses individual differences in feeling disgusted by body odors. In line with our predictions, we found that scores on the BODS relate more strongly to affective reactions to Purity, as compared to Harm, violations. In addition, BODS relates more strongly to Moral condemnation than to perceived Inappropriateness of an action, and to the condemnation of Purity violations as compared to Harm violations. These results suggest that the BIS is involved in moral judgment, although to some extent this role seems to be specific for violations of "moral purity," a response that might be rooted in disease avoidance. Data and scripts to analyze the data are available on the Open Science Framework (OSF) repository: https://osf.io/tk4x5/. Planned analyses are available at https://osf.io/x6g3u/.

Keywords: moral judgment, disgust, purity, behavioral immune system, body odors

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INTRODUCTION

Detecting pathogen threats and avoiding disease is fundamental to human survival. The behavioral immune system (BIS, Schaller and Park, 2011) is a proposed set of psychological functions evolved to detect pathogen threats and avoid disease. Disgust is a core emotion that plays a pivotal role in the BIS, as disgust activates behavioral avoidance reactions which prevent people from being in contact with pathogens. For instance, people display higher levels of disgust when viewing pictures that convey the concept of contagion, as compared to physically similar pictures that do not convey any contagion-related concept (Curtis et al., 2004).

Are such intuitive avoidance reactions also relevant in making moral judgments on other people's' behaviors? Moral judgment was for a long time characterized as a result of "cold," cognitive deliberation (Kohlberg, 1969). However, accumulating evidence supports instead a sentimentalist, or intuitionist, view (Haidt, 2001) that contends that affect may play a causal role in moral judgment. In fact, core – pathogen – disgust and moral disgust seem to be closely intertwined (Chapman et al., 2009; Vicario et al., 2018) and may share a common neurocognitive system (Vicario et al., 2017).

One method for testing this sentimentalist hypothesis is to induce feelings of disgust that, even though irrelevant, may amplify the severity of moral condemnation. Indeed, recent meta-analytical evidence suggests an amplification of the severity of moral condemnation when disgust is induced through taste or olfaction (Landy and Goodwin, 2015). Moreover, support for a causal link between feelings of disgust and moral judgments comes from recent research demonstrating that a chemical inhibition of nausea reduces the perceived severity of judgments toward moral violations (Tracy et al., 2019). These results are consistent with the notion that judgments of morality are associated with mechanisms evolved for detecting pathogen threats, and that the chemical senses (taste/olfaction) may be particularly relevant for this disgust-morality relation.

A pivotal question is whether incidental disgust is confined to the judgment of specific types of moral transgressions or to moral condemnation more generally. Graham et al. (2009) suggested that people's morality rests on five moral foundations: harm/care, fairness/reciprocity, ingroup/loyalty, authority/respect, and purity/sanctity. In particular, purity principle violations (violations of decency norms) evoke disgust reactions (Graham et al., 2011) and high trait disgust is related to an emphasis on this moral foundation (van Leeuwen et al., 2017). Moreover, it was recently found that disgust sensitivity relates more strongly to moral condemnation of purity-based transgressions than to moral condemnation of transgressions in any of the other domains (Wagemans et al., 2018a). However, in their literature review on emotions and morality, Cameron et al. (2015), suggest that people experience as much disgust in response to purity transgressions as in response to harm transgressions. Hence, while some findings indicate that BIS-related emotions play a specific role in transgressions that have some ancestral relation with disease-related behaviors (e.g., sexually promiscuous behavior, Tybur et al., 2009), further evidence is needed to clarify this issue.

Another open issue is whether disgust plays a specific role in the amplification of moral condemnation, or whether negative emotions in general lead to such effects. Chapman and Anderson (2014) showed that disgust sensitivity, but not general emotionality (e.g., measured with STAI and trait aggression), predicts moral reactions, indicating that disgust has a uniquely moral function. Landy and Piazza (2017) in their Study 1 used the scenarios from Chapman and Anderson and, in addition, personal "imprudent actions," namely actions where only the actor is affected by the behavior ("a person running in the rain or eating junk food"). Their results indicated that when reactivity in other emotions is tested with the same specificity as disgust [using the pathogen items from the *Three Domains of Disgust Scale* (TDDS), Tybur et al., 2009], several of these emotions are related to moral judgments as well. Moreover, they showed that more extreme condemnation of moral violations were not uniquely associated with disgust, but to emotional reactivity in general.

In the present study, we address these two open issues by examining reactions to a set of moral violation scenarios developed by Clifford et al. (2015). In their paper, Clifford and colleagues provide a standardized and validated set of moral violation scenarios that span across the five moral domains, with behaviors that violate a particular moral foundation and not others. For the current study, we chose scenarios that either depicted a violation of a care/harm moral principle, or a purity/sanctity moral principle (see section "Materials and Methods"). Participants rated the violations in terms of moral wrongness ("To what extent would you consider that the person's behavior is morally wrong") or inappropriateness ("How likely is it that you would show the person that the behavior is inappropriate?") and in terms of disgust and anger elicited by that action. We hypothesized that purity violations should elicit stronger disgust, while harm violations should elicit stronger anger (Gutierrez and Giner-Sorolla, 2007).

Importantly, as a measure of disgust sensitivity related to the activation of the BIS, we used our recently developed Body Odor Disgust Sensitivity (BODS, Liuzza et al., 2016, 2017), a scale that assesses individual differences in feeling disgusted by body odors (e.g., "You are standing next to a stranger and notice that the t-shirt they are wearing smells strongly from their sweat"). Smells and tastes are arguably the most potent disgust signals, and it has been theorized that moral disgust is intimately linked to chemoreception (see Herz, 2012, for a review). Body-generated odors are considered strong disgust elicitors across cultures (Curtis and Biran, 2001), and are highly stigmatized in contemporary western culture (Soo and Stevenson, 2007). In fact, it has been argued that one of the most prominent functions of our sense of smell is to defend us from microbial hazards (Stevenson, 2009). Body odors can be affected by pathological processes (Shirasu and Touhara, 2011), and it has been shown that humans can detect the presence of an infection by the smell of the infected body (Olsson et al., 2014; Regenbogen et al., 2017). However, in established disgust scales, olfactory disgust in general, and body odor disgust in particular, occupies a very small space. We have previously established that scores on the BODS are strongly predictive of personality traits associated with harsher moral judgments, such as Right-Wing Authoritarianism (RWA), and that it is a better predictor of these traits than more general disgust sensitivity measures such as the TDDS (Liuzza et al., 2018). Informed by the theoretical link between body odor perception and disgust responses, and the evidence that the BODS is strongly predictive of traits related to moral condemnation, the current study explored whether the BODS, tapping into a core pathogen sensitivity, would help delineating the role of disgust in moral judgments.

We expected a moderating effect of the level of BODS on disgust responses. Specifically, we expected that people scoring higher in BODS would show a more pronounced Disgust reactivity (vs. Anger reactivity) to purity violations (vs. Harm violations). Similarly, we expected that people scoring higher in BODS would show harsher moral judgments concerning wrongness (vs. inappropriateness) to Purity violations (vs. Harm violations). Inappropriateness ratings were added in order to rule out that the condemnation of purity transgressions could be driven by the perception of weirdness (Gray and Keeney, 2015).

To rule out that the association between BODS and moral judgment could be fully explained by a general emotional reactivity, we tested whether our effects were retained when controlling for scores in the Emotional Reactivity Scale (ERS, Nock et al., 2008). Importantly, given the supposedly high relevance of the chemical senses in the experience of disgust (Rozin et al., 2009; Stevenson, 2009), and the linkage between incidental disgust and amplification/attenuation of moral condemnation (Landy and Goodwin, 2015; Tracy et al., 2019), we expected the BODS to provide incremental predictive validity when compared to general pathogen-related disgust sensitivity measures such as the pathogen subscale of the TDDS (TDDS-p, Tybur et al., 2009).

The BIS framework implies that psychological mechanisms adapted to detect and avoid pathogen threats may also encourage withdrawal from individuals who pose a threat to the group, such as members of unfamiliar out-groups or people who violate the established social order (e.g., Chapman and Anderson, 2014). As summarized in a recent review on the BIS (Ackerman et al., 2018) disgust leads to an overgeneralization of cues associated with disease (Makhanova et al., 2015) and prejudice toward unfamiliar outgroups (Faulkner et al., 2004; Zakrzewska et al., 2019). This connection between the BIS and avoidance-related social cognitions and behaviors may explain the consistent relation between BIS and social conservative attitudes (Terrizzi et al., 2013; Liuzza et al., 2018). Thus, according to this view, the relation between disgust and harshness in moral judgments should be mediated by individual differences in preference for the maintenance of social order. In support of this notion, recent research has demonstrated a robust association between disgust sensitivity and trait-level preference for orderliness, an association that, in turn, predicts political conservatism (Piazza and Sousa, 2014; Robinson et al., 2019). Considering the evidence suggesting that links from BIS-related traits to moral condemnation may be mediated by orderliness and social conservatism, we were interested in investigating the mediating role of these personality traits. Hence, we included a measure of orderliness, which is one of two aspects of trait conscientiousness (DeYoung et al., 2007), as well as the RWA scale. Therefore, we hypothesized that the moderation effect of the BODS on moral judgments should be mediated by individual differences in these traits.

We preregistered[1] our hypotheses[2], planned sample size, materials and methods and R scripts of the planned analysis on the Open Science Framework repository[3].[4]

Hypotheses

(1) We expected a two-way interaction with harmless moral violations (purity violations) evoking stronger disgust (vs. anger) as compared to harming moral violations. Such an effect, would confirm that disgust is specifically evoked by a subset of moral violations, rather than any type of moral violation.

(2) We expected a three-way interaction, with a moderating effect of the level in Body odor disgust sensitivity, as measured by the BODS scale (Liuzza et al., 2016) on disgust responses. Indeed, we expected that people scoring higher in BODS would show a more pronounced disgust-reactivity (vs. anger reactivity) to purity violations (vs. harm violations). This interaction would point toward a specific role of the individual differences in the BIS activation in reacting with disgust to body-related – but harmless – moral violations.

(3) We expected a three-way interaction, with a moderating effect of the level in BODS on moral wrongness (vs. inappropriateness) ratings. Specifically, we expected that people scoring higher in BODS would show harsher moral judgments in terms of wrongness (vs. inappropriateness) to purity violations (vs. harm violations). An interaction like this would point toward a specific role of the individual differences in the BIS activation in the moral condemnation of body-related – but harmless – moral violations.

(4) We hypothesized that, as compared to the Three Domains of Disgust Scale (Tybur et al., 2009), the BODS would show incremental validity by playing a stronger moderating role as compared to TDDS-p.

(5) We expected a main effect of the level of general emotional reactivity on affective reactions – higher affective ratings regardess of the emotion rated – but no interactions with the type of scenario or type of affective reaction.

(6) We hypothesized that the moderation effect of the BODS would be mediated by Orderliness, as measured by one aspect of trait conscientiousness within the Big Five Aspect Scale (BFAS; DeYoung et al., 2007) and Authoritarianism, as measured by the RWA (Zakrisson, 2005).

(7) We hypothesized that all the above effects would remain significant when controlling for a general measure of Emotional Sensitivity as measured by the ERS (Nock et al., 2008). This effect would militate in favor of the idea that a specific BIS-related emotion (disgust), rather than a general emotional reactivity, that relates to the reaction to and the condemnation of body-related, harmless moral violations.

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[1] Due to a misunderstanding in the pre-registration procedure, our documents were saved as a draft, but not published, on the 28th of November 2017. We realized this mistake and published these documents unedited on the 22nd of March 2018, after data were collected and partly analyzed.

[2] https://osf.io/57nm8/

[3] https://osf.io/2cnrf/

[4] As compared to the pre-registration, we used the terms purity and harm in place of sanctity and care to refer to the same types of moral transgressions. We did so to be more consistent with the terminology used in the literature.

MATERIALS AND METHODS

Ethics Statement

This research was conducted in full in accordance with the ethical principles outlined by the Swedish Research Council, http://www.codex.vr.se/, and with the 1964 Helsinki declaration and its later amendments. The current research did not include factors that require ethical vetting according to Swedish legislation on research ethics, http://www.epn.se/en/start/regulations/. All participants gave written informed consent before participating. Minimal risks studies are exempt from formal approval in the country where the study was conducted (Sweden).

Participants

We had planned a sample of $n = 620$, which has a power of 80% to detect an effect as small as $r = 0.1$ having an alpha level = 0.05 and a planned directional hypothesis. Power analysis was performed in R Core Team (2018) through the "pwr" package (Champely, 2018). We recruited participants on Amazon Mechanical Turk (MTurk), for a compensation of 50¢. We recruited only participants with an approval rate of 85% and who participated in no fewer than 50 surveys and no more than 1,000 surveys. The lower limit served to provide a reliable estimate of participants' reliability, while the upper limit aimed at limiting the participation of too-experienced MTurk workers.

Data were collected on Qualtrics between the 28th of November 2017 and the 3rd of December 2017. We excluded participants who had not completed the survey (i.e., marked as unfinished on MTurk). A final sample of 632 respondents participated in the study (279 Females, mean Age = 38.74, *SD* = 11.88). Of these participants, 0.96% had not graduated from high school, 9.63% were high school graduates, 23.92% had some college, 49.12% were college graduates, and 16.37% had a post-college degree.

Measures

Body Odor Disgust Sensitivity

As a measure of body odor disgust sensitivity, we used the 12-items Body Odor Disgust Scale (BODS, Liuzza et al., 2016). BODS presents participants with a series of descriptions of situations (e.g., "You are standing next to a stranger and notice that the t-shirt they are wearing smells strongly from their sweat."), and they have indicated the degree to which they find the situation disgusting on a five-point Likert-type item (1 = "Not disgusting at all" and 5 = "Extremely disgusting").

Pathogen Disgust Sensitivity

As a measure of pathogen-related disgust sensitivity, we used the seven-items pathogen disgust scale from the Three Domain of Disgust Scale (Tybur et al., 2009). Pathogen disgust "is elicited by objects likely to contain infectious agents, including dead bodies, rotting foods, and bodily fluids such as feces, phlegm, vomit, blood, and semen, and it motivates proximal avoidance of such things" (Tybur et al., 2009, p. 105). To measure individual differences in pathogen disgust sensitivity, the participants rated how disgusting they would find each of the following concepts (e.g., "Accidentally touching a person's bloody cut") on a seven-point Likert-type item (0 = "Not disgusting at all" and 6 = "Extremely disgusting").

Right-Wing Authoritarianism

In order to measure individual differences in RWA (Altemeyer, 1998), we used the Zakrisson's RWA scale (Zakrisson, 2005), consisting of 15 items (e.g., "Our forefathers ought to be honored more for the way they have built our society, at the same time we ought to put an end to those forces destroying it.") that did not refer to specific minority populations, and hence avoided conflating authoritarianism with specific prejudice. Participants reported their reaction to each statement on 15 seven-point Likert-type items (1 = "Very negative" and 7 = "Very positive").

Emotional Reactivity Scale

We used the ERS to measure individual differences in general reactivity. The ERS is a 21-item self-report measure designed to assess individuals' everyday emotional experiences. Participants are asked to state on a five-point scale (0 = not at all like me; 1 = a little like me; 2 = somewhat like me; 3 = a lot like me; 4 = completely like me) to what extent different statements regarding emotional experiences characterizes them. Example items are: "I experience emotions very strongly"; "If I have a disagreement with someone, it takes a long time for me to get over it"; "I am often bothered by things that other people don't react to." The ERS has been found to be related to depressive mood, frustration, aggression, fear, and shyness. Furthermore, the scale is inversely related to attentional control, inhibitory control, and activation control. Thus, the ERS is a broad and general measure of emotional reactivity (see e.g., Nock et al., 2008).

Orderliness

Trait orderliness is one of two aspects of trait conscientiousness (the other is industriousness) identified within the Big Five Aspects Scales (DeYoung et al., 2007). Orderliness is characterized by a general predisposition toward maintaining structure, organization, and neatness. On the 10 items assessing orderliness, participants rate their level of agreement with statements such as "I want every detail taken care of."

Affective Reactions and Evaluative Judgments to Moral Violation Scenarios

We used eight scenarios from the material developed by Clifford et al. (2015), a standardized and validated set of moral transgressions that encompasses the moral domains as proposed by the Moral Foundations Theory. Four scenarios violated moral norms concerning Care/Harm, and four violated norms concerning Purity/Sanctity. The four Care/Harm scenarios were selected to represent different facets of the this principle: (i) emotional harm ("You see a teenage boy chuckling at an amputee he passes by while on the subway"), physical harm directed toward (ii) animals (e.g., "You see a woman throwing her cat across the room for scratching the furniture") (iii) humans ("You see a teacher hitting a student's hand with a ruler for falling asleep in class"). The selected purity scenarios reflected different aspects of this principle (i) sexually deviant acts ("You see a man having sex with a frozen chicken before cooking it for dinner") (ii) contamination concerns ("You see a woman having intimate relations with a recently deceased loved one"), (iii) degrading ("You see a man searching through the trash to find women's discarded underwear"). Participants then rated on seven-point Likert-type (1 = "Not at all" and 7 = "To a very high extent") items:

(a) to what extent they would feel (i) *anger* (Anger Rated Emotion) and (ii) *disgust* (Disgust Rated Emotion).
(b) to what extent they would consider that the person's behavior was (i) morally wrong (Moral Wrongness Moral Rating of condemnation) (ii) how likely they would show the person that the behavior is inappropriate (1 = "Not likely," 7 = "Most likely," Inappropriateness Moral Rating of condemnation).

All the conditions were manipulated within subjects. Hence, each participant read the eight scenarios, and rated them in terms of evoked anger/disgust, and inappropriateness/moral wrongness.

Data Analysis

Prior to computing the scores for our measures, we tested our measures' dimensionality and reliability. Failure to achieve an acceptable level of internal consistency (Cronbach' $\alpha \geq 0.6$), and/or failure to achieve an acceptable goodness of fit for assumptions of uni-dimensionality (RMSEA > 0.1, SRMR > 0.1, CFI < 0.90, TLI < 0.90) led to further inspection in order to exclude the items that impede to reach an acceptable reliability and/or uni-dimensionality. Dimensionality was tested using the *cfa* function from the *lavaan* package in R (Rosseel, 2012), while Cronbach's α was assessed using the *alpha* function from the *psych* package in R (Revelle, 2018).

For each variable, we computed the mean value and standardized it, except for the affective and the moral ratings provided for each scenario, that were only standardized in order to not lose information about the sources of variability, while accounting for the dependence of these observations. We started with a zero-order correlation matrix, then we tested the hypotheses, by conducting a linear multilevel model (LMM or "mixed effects models"; Pinheiro and Bates, 2000), through the package lme4 ver. 1.1–5 (Bates et al., 2015). We used the *Anova* function from the *car* package (Fox and Weisberg, 2011) to compute the χ^2 associated with the Type III Walden test. Contrasts were set through an effect coding strategy (e.g., [1, −1]), in order to better interpret the main effects and interactions. The first model tested our hypotheses on anger and disgust ratings:

(1) If the type of scenario (purity vs. harm) evokes a stronger disgust (vs. anger) reaction to that scenario.
(2) If the BODS interacts with the type of scenario (moral violations of purity vs. harm) to predict disgust (vs. anger).
(3) Then, in a second and third model, we added the TDDS-p and the ERS to the model as moderators along with the BODS.
(4) We used identical models to test ratings of moral wrongness vs. inappropriateness.

RESULTS

Measures of Reliability and Dimensionality

Body Odor Disgust Scale

An initial assessment of the BODS dimensionality as a unidimensional construct showed very poor fit in the present dataset (RMSEA = 0.22, SRMR = 0.09, TLI = 0.68, CFI = 0.74).

We thus tried a two-factor solution (Internal Body Odor Source and External Body Odor source), consistent with a prior validation study (Liuzza et al., 2016), and allowed covariance of the residuals within each odor type. These changes led to an acceptable fit (RMSEA = 0.1, SRMR = 0.04, TLI = 0.93, CFI = 0.95). However, the two latent variables were highly correlated ($r = 0.72$). Therefore, any model using them as separate predictors would have posed issues of collinearity. A CFA assuming a hierarchical structure with the two subscales (Internal, External) as emanating from the same underlying BODS factor showed an acceptable fit (RMSEA = 0.1, SRMR = 0.04, TLI = 0.93, CFI = 0.95) and was consistent with our theoretical assumptions. We therefore continued our analyses by treating the BODS as a unique scale. The internal consistency of the two subscales was excellent (Cronbach's $\alpha > 0.9$) and so it was the internal consistency of the scale when considered as a unique scale (Cronbach's α = 0.94).

Three Domains of Disgust – Pathogen Subscale

The pathogen sub-scale of the TDDS, on the other hand, immediately showed an acceptable fit when using a

TABLE 1 | Descriptive statistics.

	Mean	*SD*	Median	Min	Max	Skewness	Kurtosis
Harm Anger	5.36	1.37	5.50	1	7	−0.87	0.32
Harm Disgust	5.03	1.52	5.25	1	7	−0.74	−0.07
Purity Anger	4.22	1.84	4.25	1	7	−0.20	−1.11
Purity Disgust	6.02	1.28	6.50	1	7	−1.67	2.33
Harm Moral	5.63	1.22	5.75	1	7	−1.05	0.94
Harm Inapp	5.18	1.53	5.50	1	7	−0.80	0.00
Purity Moral	5.45	1.47	5.75	1	7	−0.97	0.19
Purity Inapp	4.81	1.88	5.00	1	7	−0.54	−0.85
BODS	3.57	0.84	3.58	1	5	−0.40	−0.18
Reac	2.63	0.95	2.57	1	5	0.21	−0.78
TDDS	4.81	1.16	4.86	1	7	−0.30	−0.02
RWA	3.25	1.33	3.40	1	6.73	0.11	−0.62
ORD	3.63	0.72	3.70	1.6	5	−0.03	−0.55

Descriptive statistics for the measures and for the ratings on Disgust, Anger, Moral wrongness (Moral) and Inappropriateness (Inapp) evoked by Harm and Purity Scenarios. SD, standard deviation; BODS, Body Odor Disgust Scale score; ERS, Emotional Reactivity; TDDS-p, Three Domains of Disgust – pathogen subscale; RWA, Right Wing Authoritarianism; ORD, orderliness.

TABLE 2 | Zero-order correlations across measures.

Variable	1	2	3	4	5
(1) BODS					
(2) ERS	0.16^{***} [0.09, 0.24]				
(3) TDDS-p	0.69^{***} [0.64, 0.73]	0.21^{***} [0.13, 0.28]			
(4) RWA	0.25^{***} [0.17, 0.32]	0.10^{**} [0.03, 0.18]	0.20^{***} [0.12, 0.27]		
(5) ORD	0.26^{***} [0.18, 0.33]	−0.07 [−0.14, 0.01]	0.28^{***} [0.20, 0.35]	0.18^{**} [0.10, 0.26]	
(6) Age	0.12^{**} [0.04, 0.20]	-0.20^{***} [−0.27, −0.12]	0.03 [−0.05, 0.11]	0.06 [−0.02, 0.14]	0.12^{**} [0.04, 0.20]

BODS, Body Odor Disgust Scale score; ERS, Emotional Reactivity; TDDS-p, Three Domains of Disgust – pathogen subscale; RWA, Right Wing Authoritarianism; ORD, orderliness. M and SD are used to represent mean and standard deviation, respectively. Values in square brackets indicate the 95% confidence interval for each correlation. $^{*}p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$.

unidimensional model (RMSEA = 0.1, SRMR = 0.04, TLI = 0.92, CFI = 0.95). We thus treated TDDS-p as a unidimensional measure and the scale internal consistency was good (Cronbach's α = 0.85).

Emotional Reactivity Scale

CFA on the ERS showed a poor fit for the unidimensional model (RMSEA = 0.13, SRMR = 0.07, TLI = 0.8, CFI = 0.82). An exploration of the modification indices showed a high level of covariation between some items' residuals, possibly because of substantial semantic overlap. After allowing for covariance between some of the items' residuals, the model nearly reached an acceptable fit (RMSEA = 0.1, SRMR = 0.06, TLI = 0.89, CFI = 0.91). We thus treated ERS as a unidimensional measure and the scale showed excellent internal consistency (Cronbach's α = 0.96).

Right-Wing Authoritarianism

The RWA did not show an acceptable fit when using a unidimensional model (RMSEA = 0.15, SRMR = 0.09, TLI = 0.75, CFI = 0.78). After looking at the modification indices, we decided to allow for covariation between the residuals of some items. After this modification, the RWA achieved an acceptable fit (RMSEA = 0.09, SRMR = 0.06, TLI = 0.91, CFI = 0.93), and the scale internal consistency was excellent (Cronbach's α = 0.93).

Orderliness

The Orderliness scale did not show an acceptable fit when using a unidimensional model (RMSEA = 0.14, SRMR = 0.08, TLI = 0.76, CFI = 0.81). After looking at the modification indices, we decided to allow for covariation cross the residuals of some items. In most cases, this covariation was among items that were straight coded items. After this modification, the Orderliness scale achieved an acceptable fit (RMSEA = 0.08, SRMR = 0.05, TLI = 0.91, CFI = 0.94), and the scale internal consistency was good (Cronbach's α = 0.85).

TABLE 3 | Type III Wald χ^2 Analysis of Deviance on affective ratings on moral scenarios.

	χ^2	**Df**	***p***
Age	0.92	1	0.338
Gender	**81.39**	**1**	**<0.001**
Education	0.16	1	0.693
MorCond	**5.29**	**1**	**0.021**
RatEmo	**587.56**	**1**	**<0.001**
BODS	**111.24**	**1**	**<0.001**
MorCond × RatEmo	**1210.44**	**1**	**<0.001**
MorCond × BODS	**9.48**	**1**	**0.002**
RatEmo × BODS	2.47	1	0.116
MorCond × RatEmo × BODS	**4.96**	**1**	**0.026**

MorCond, Moral Condition (Harm vs. Purity); RatEmo, Rated Emotion (Disgust vs. Anger); BODS, Body Odor Disgust Scale score. Bold text indicates a statistically significant correlation with a p-value less than 0.05.

Descriptive Statistics and Zero-Order Correlations

Table 1 provides the descriptive statistics or our measures. Although not planned in advance, we also computed the internal consistency for the affective and moral ratings, and found that, for each type of rating in each condition, the average inter-item correlation ranged between $r = 0.41$ (Moral wrongness in the Harm Condition) to $r = 0.60$ (Disgust in the Purity Condition).

Table 2 shows the zero-order correlations. Replicating previous results (Liuzza et al., 2018), we found a moderate ($r = 0.25$), but statistically significant ($p < 0.001$) correlation between the RWA scores and the BODS. The BODS was positively and significantly associated, to various degrees, to all the other measures. It is worth noticing that the very high level of correlation with the TDDS-p ($r = 0.69$) may undermine the interpretability of the results from models in which both variables are included, due to multicollinearity issues.

Zero-order correlations between the BODS and the ratings ranged between $r = 0.21$ (Inappropriateness in the Purity Condition) to $r = 0.39$ (Disgust, and Moral wrongness in

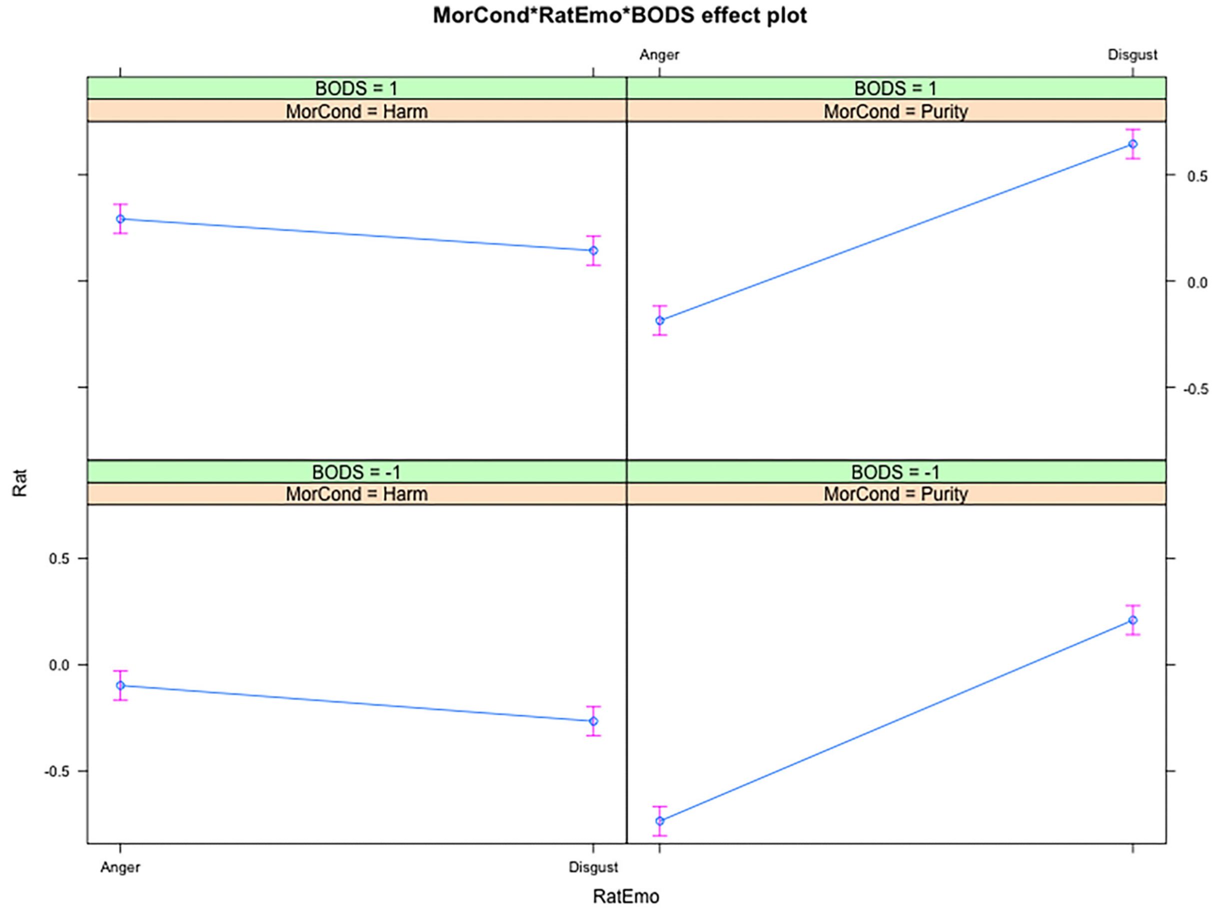

FIGURE 1 | Interaction effects of BODS, Moral Condition and Rated Emotion on affective ratings. Results are displayed for levels of BODS = –1 SD (upper panels) and BODS = +1 SD (lower panels). MorCond, Moral Condition (Harm vs. Purity); RatEmo, Rated Emotion (Disgust vs. Anger); BODS, Body Odor Disgust Scale score.

the Purity Condition). All the correlations were statistically significant ($ps < 0.001$).

Gender Differences

We also checked for gender difference through a series of unpaired *t*-tests. We found that women displayed significantly higher levels of BODS scores, TDDS-p scores, and orderliness scores [$ts(619) > 2.83$, $ps < 0.01$], a finding that replicates previous research (e.g., Mancini et al., 2001; Tybur et al., 2009; Liuzza et al., 2016), although the size of these effects are small (Cohen's Ds < = 0.37). No gender difference was found in RWA scores [$t(619) = 0.19$, $p > 0.05$, Cohen's D = −0.02].

Emotions

In order to test our Hypothesis 1 we fit an LMM with the rating in the affective dimension as our dependent variable and we entered the main effects and all the possible interactions between the rated emotion (disgust vs. anger), the type of moral violation (purity vs. harm), and the scores in the BODS. We added Age, Gender, and Education as covariates to adjust for. Random intercepts for participants were included in the model. However, the random slopes were not included because adding random slopes would have led to convergence issues due to the small number of repetitions per condition (ranging from 4 to 8). This choice is coherent with the pre-registered analysis when we observed convergence issues even in the simulations prior to the launch of the study.

As **Table 3** shows, we found a main effect of participant gender on affective ratings, with women providing higher ratings than men ($\beta = 0.19$, $SE = 0.02$). The main effect of Moral Condition (Purity vs. Harm scenarios) was explained by higher overall affective reactions to the harm violations, as compared to the purity violations ($\beta = 0.02$, $SE = 0.01$), while the effect of the Rated Emotion (anger vs. disgust) was explained by the higher overall ratings in disgust, as compared to anger ($\beta = -0.18$, $SE = 0.01$). Importantly, the two effects were qualified by our predicted two-way interaction (Hypothesis 1) between Moral Condition and Rated Emotion, with Purity transgressions evoking stronger Disgust (vs. Anger) than Harm transgressions. In addition, we found a main effect of BODS in predicting Rated Emotion, such that higher BODS scores were associated with higher ratings of both disgust and anger ($\beta = 0.22$, $SE = 0.02$). This main effect was implicit in our assumptions, although not explicitly stated in our hypotheses where we focused on interactions between the

BODS and other variables. Importantly, we found a significant interaction, anticipated in our Hypothesis 2, with a moderating effect of BODS scores on disgust responses in interaction with the scenario (see **Figure 1**). However, in contrast to our expectations, people scoring higher as compared to low in BODS did not display a more pronounced Disgust reactivity (vs. Anger reactivity) to Purity violations (vs. Harm violations). Follow-up analysis on the two-way interaction in the two different moral scenarios showed that for the Harm violations, the slope for the relation between BODS and Anger ratings was not significantly different from the slope for the relation between BODS and Disgust ratings ($\beta = 0$, $SE = 0.01$, $p > 0.05$). On the other hand, in the Purity condition, the slope for the relation between BODS and Anger ratings was significantly different from the slope for the relation between BODS and Disgust ratings ($\beta = 0.03$, $SE = 0.01$, $p < 0.01$). In other words, in the Purity condition, the difference between participants scoring high vs. low in BODS was higher for the Anger than for the Disgust ratings (see **Figure 1**, right panels).

To test our Hypothesis 4, we added TDDS-p to our model as the main effect and as a moderator. **Table 4** shows that adding the TDDS-p reduces the interaction between BODS, Moral Condition, and the Rated Emotion to non-significance. Instead, the analysis shows an interaction between TDDS-p and Moral scenario that approaches significance ($p = 0.055$), and that mirrors the moderating effects of the BODS. Thus, TDDS-p tended to affect ratings of Anger rather than Disgust in the Purity condition. This result disconfirms the predictions we made in Hypothesis 4 and rather suggests that, when it comes to moral violations, TDDS-p seems to have a better incremental validity than BODS. It should be observed, however, that the correlation between TDDS-p and the BODS found in this study is so high (Pearson's $r = 0.69$) that it undermines the interpretability our results, given the high level of multicollinearity.

Importantly, the main effect of the BODS on the Disgust and Anger ratings is still significant after including TDDS-p ($\beta = 0.09$, $SE = 0.028$, $p = 0.001$). This suggests that, at least for the main effect, there is substantial shared variance between BODS and affective reactions to moral scenarios that is independent of the shared variance between TDDS-p and affective reactions.

In order to test our Hypothesis 5, we entered ERS scores into our model. We found a main effect of ERS on affective ratings, in line with our hypothesis (**Table 5**).

However, the only interaction that included BODS and remained significant when controlling for general Emotional Reactivity was the one between the BODS and Moral Condition, as described earlier (see **Figure 2**).

Thus, when adding the ERS, the association between the BODS and the intensity of the Disgust and Anger was still stronger in the purity scenario than in the harm scenario ($\beta = -0.03$, $SE = 0.008$). However, contrary to our Hypothesis 5, ERS displayed a significant triple interaction with moral scenarios and type of rated emotion. Interestingly, ERS is positively associated with both Anger and Disgust ratings in the Harm condition, and with Anger ratings in the Purity condition ($\beta s \geq 0.1$, $0.02 > SE < 0.04$), but displays a null pattern of association with Disgust ratings in the Purity condition ($\beta = 0$, $SE = 0.03$). Since the Purity scenarios seem to evoke higher disgust ratings even among low ERS participants, this result might be due to ceiling effects (see **Table 1**).

TABLE 4 | Type III Wald χ^2 Analysis of Deviance on affective ratings on moral scenarios.

	χ^2	Df	p
Age	2.34	1	0.126
Gender	**70.73**	**1**	**<0.001**
Education	0.24	1	0.624
MorCond	**5.34**	**1**	**0.021**
RatEmo	**588.45**	**1**	**<0.001**
BODS	**11.30**	**1**	**0.001**
TDDS-p	**45.07**	**1**	**<0.001**
MorCond × RatEmo	**1212.26**	**1**	**<0.001**
MorCond × BODS	0.07	1	0.792
RatEmo × BODS	0.04	1	0.850
MorCond × TDDS-p	**8.13**	**1**	**0.004**
RatEmo × TDDS-p	1.90	1	0.169
MorCond × RatEmo × BODS	0.08	1	0.771
MorCond × RatEmo × TDDS-p	3.67	1	0.055

MorCond, Moral Condition (Harm vs. Purity); RatEmo, Rated Emotion (disgust vs. anger); BODS, Body Odor Disgust Scale score; TDDS-p, Three Domains of Disgust, pathogen scale. Bold text indicates a statistically significant correlation with a p-value less than 0.05.

TABLE 5 | Type III Wald χ^2 Analysis of Deviance on affective ratings on moral scenarios.

	χ^2	Df	p
Age	2.52	1	0.112
Gender	**73.07**	**1**	**<0.001**
Education	0.05	1	0.828
MorCond	**5.37**	**1**	**0.020**
RatEmo	**590.81**	**1**	**<0.001**
BODS	**99.31**	**1**	**<0.001**
ERS	**8.22**	**1**	**0.004**
MorCond × RatEmo	**1217.09**	**1**	**<0.001**
MorCond × BODS	**13.03**	**1**	**<0.001**
RatEmo × BODS	0.81	1	0.368
MorCond × ERS	**11.80**	**1**	**0.001**
RatEmo × ERS	**16.05**	**1**	**<0.001**
MorCond × RatEmo × BODS	1.50	1	0.221
MorCond × RatEmo × ERS	**35.80**	**1**	**0.001**

MorCond, Moral Condition (Harm vs. Purity); RatEmo, Rated Emotion (Disgust vs. Anger); BODS, Body Odor Disgust Scale score; ERS, Emotional Reactivity. Bold text indicates a statistically significant correlation with a p-value less than 0.05.

In partial coherence with what anticipated in our Hypothesis 7, the findings on the BODS are still significant when controlling for ERS. Hypothesis 6 was not further tested because we could not reject the null hypothesis for Hypothesis 2.

Moral Judgment

In order to test our Hypothesis 3, we ran the same analysis as for Hypothesis 2 but on moral ratings (Inappropriateness vs. Moral Wrongness).

Results from moral ratings were similar to those from affective ratings (see **Table 6**), with a main effect of the BODS on both

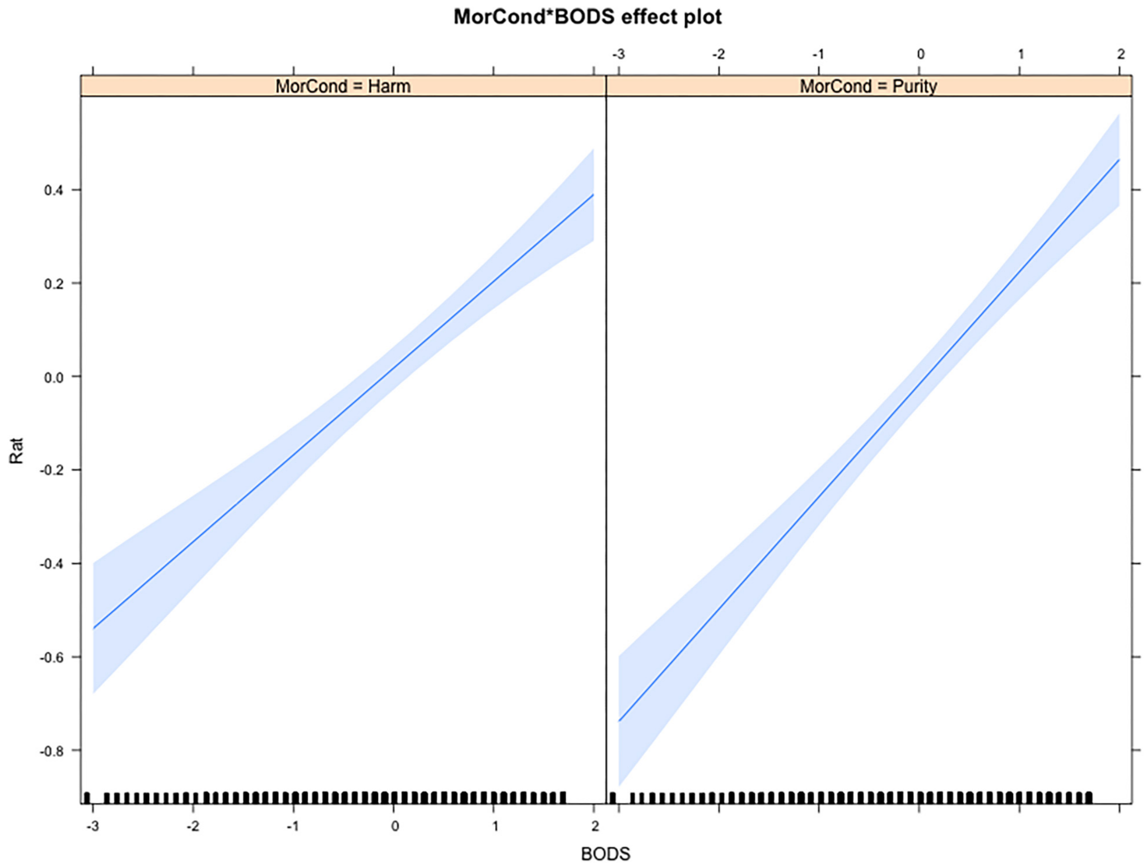

FIGURE 2 | Interaction effect of BODS and Moral Condition on affective ratings, when controlling for overall Emotion Reactivity. MorCond, Moral Condition (Harm vs. Purity); BODS, Body Odor Disgust Scale score.

moral ratings. We found an interaction between the Moral Condition and Moral Rating such that participants reported more willingness to call a behavior as Inappropriate (vs. Wrong) in Harm violation scenarios (vs. Purity, see **Figure 3**).

As was the case for the affective ratings, the BODS holds a stronger association with moral judgments – regardless of the type – in the Purity condition, as opposed to the Harm condition ($\beta = 0.03$, $SE = 0.008$). This interaction remained significant even when controlling for ERS ($\beta = 0.03$, $SE = 0.008$, $p < 0.001$) but not TDDS-p ($\beta = -0.01$, $SE = 0.011$, $p > 0.05$). Furthermore, the BODS holds a stronger association with the Moral Wrongness ratings than the Inappropriateness ratings ($\beta = 0.03$, $SE = 0.008$, **Figure 4**). This interaction remained significant even when controlling for TDDS-p ($\beta = 0.02$, $SE = 0.011$, $p = 0.033$) and ERS ($\beta = 0.03$, $SE = 0.008$, $p < 0.001$). However, the predicted three-way interaction, with a moderating effect of the level in the BODS on Moral Wrongness (vs. Inappropriateness) in the Purity (vs. Harm) condition was not significant ($p > 0.05$).

DISCUSSION

Individual differences in traits that are related to the BIS are also consistently related to moral condemnation (for a review, see Russell and Giner-Sorolla, 2013). Disgust sensitivity, and disgust sensitivity to body odors in particular, plays a central role in the BIS (Liuzza et al., 2016). However, the role of disgust in moral judgment is controversial (Schnall et al., 2008; Chapman et al., 2009; Cameron et al., 2015; Landy and Goodwin, 2015; Wagemans et al., 2018a,b). We hypothesized that a novel

TABLE 6 | Type III Wald χ^2 Analysis of Deviance on Moral judgments.

	χ^2	Df	p
Age	0.00	1	0.957
Gender	**27.83**	**1**	**<0.001**
Education	0.91	1	0.339
MorCond	**71.97**	**1**	**<0.001**
MorRat	**293.05**	**1**	**<0.001**
BODS	**73.03**	**1**	**<0.001**
MorCond × MorRat	**9.32**	**1**	**0.002**
MorCond × BODS	**11.00**	**1**	**0.001**
MorRat × BODS	**15.93**	**1**	**<0.001**
MorCond × MorRat × BODS	2.38	1	0.123

MorCond, Moral Condition (Harm vs. Purity); MorRat, Moral Rating (Wrongness vs. Inappropriateness); BODS, Body Odor Disgust Scale score. Bold text indicates a statistically significant correlation with a p-value less than 0.05.

body odor disgust sensitivity assessment would tap into a core pathogen sensitivity and help explaining moral judgments (BODS, Liuzza et al., 2016, 2017). Specifically we asked whether (a) disgust is evoked by purity violations to a greater extent than anger, (b) individual differences in the BODS moderate this effect, (c) higher scores in BODS predict harsher moral condemnation.

Before specific results are discussed, some possible limitations to the generalizability of the current results should be considered. In this study, we recruited a sample from a Mechanical Turk (M-Turk) pool. Firstly, it is well-known that this kind of sample is not representative of the population. In fact, M-Turk pools are self-selected samples, which may differ from the population in some important demographic and political features (Berinsky et al., 2012; Huff and Tingley, 2015). However, M-Turk samples have been shown to be more diverse and representative than common convenience samples (e.g., college students) typically used in psychological research (Buhrmester et al., 2011; Berinsky et al., 2012). Also important, M-Turk studies have been shown to be psychometrically valid (Buhrmester et al., 2011; Shapiro et al., 2013). Secondly, M-Turk workers may have participated in studies, and therefore they might not be naive to the purpose of the study. This may lead to biases due to participants' expectations. Recent findings suggest that non-naivetè does not affect the performance in cognitive tasks (Zwaan et al., 2017), however, we cannot rule out that this is the case in other domains such as Moral Psychology.

Another limitation that concerns the validity of our measure of disgust sensitivity is the observation that so far we have measured disgust sensitivity using a self-report measure that may not be predictive of the actual behavioral response to disgusting cues. Although we do have some evidence in favor of the criterion validity of our measure (Liuzza et al., 2017), it would be preferable to run a study in which participants are actually exposed to disgusting odors (e.g., Inbar et al., 2012; Cecchetto et al., 2017). In fact, so far we are unsure whether our results reflect genuine differences in the sensitivity to disgusting stimuli, or rather differences, for instance, in seeing disgust sensitivity as an appealing trait.

In the current study, we found support for our hypothesis that Purity transgressions (e.g., "You see an employee at a morgue eating his pepperoni pizza off of a dead body"), as

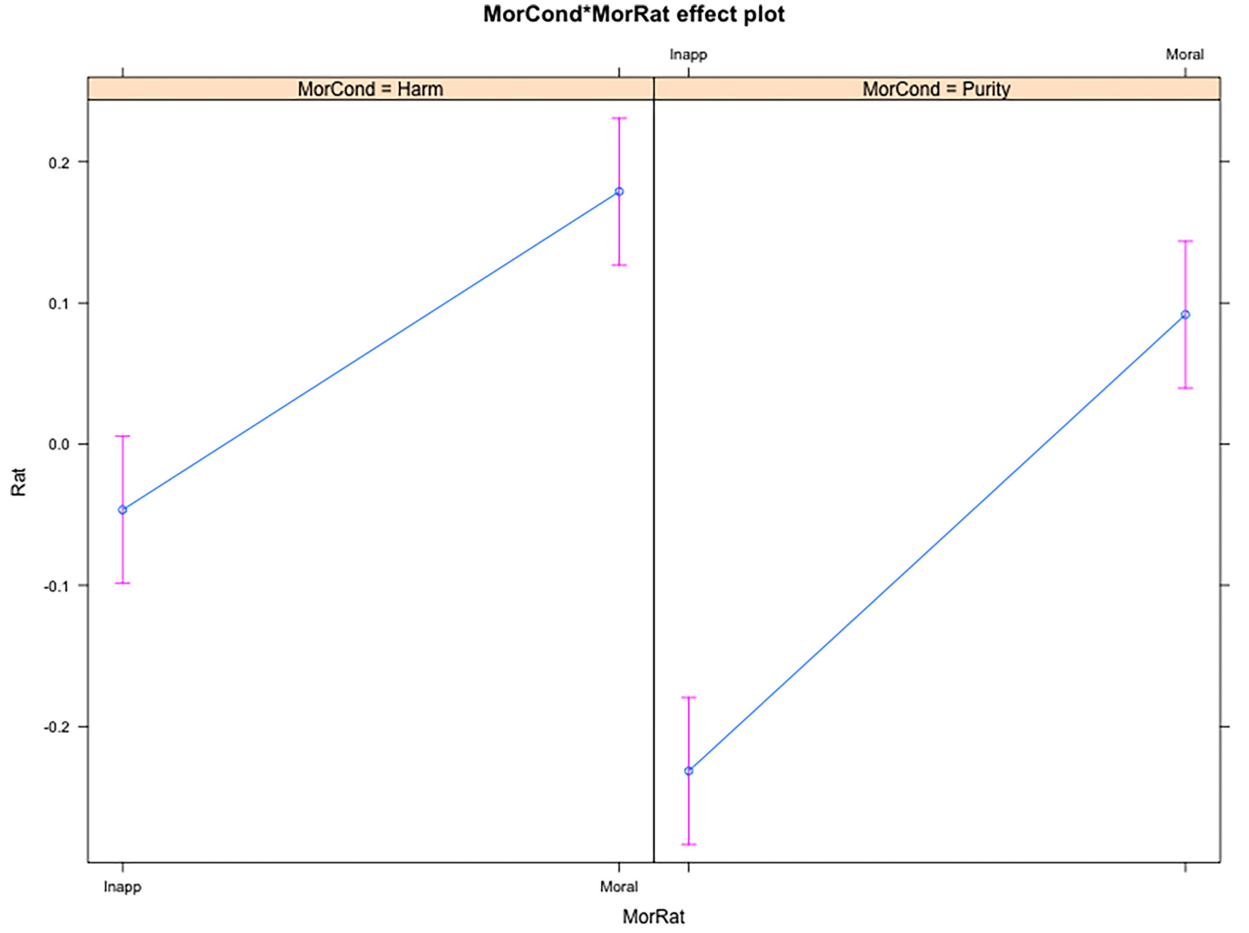

FIGURE 3 | Interaction effect of Moral Condition and Moral Ratings on condemnation ratings. MorCond, Moral Condition (Harm vs. Purity); MorRat, Moral Rating; Moral, Morally Wrong; Inapp, inappropriate.

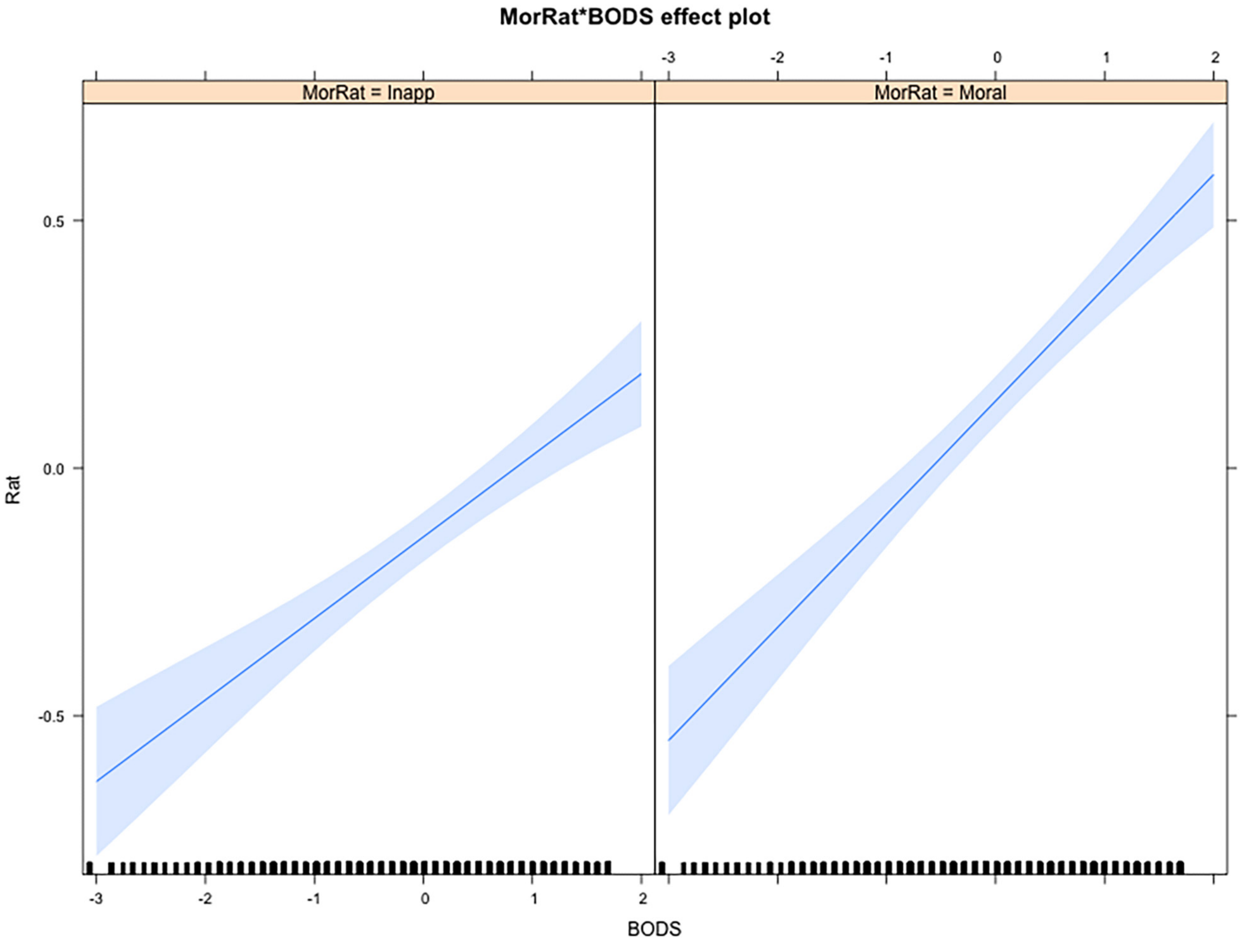

FIGURE 4 | Interaction effect of BODS scores and Moral Ratings on condemnation ratings. BODS, Body Odor Disgust Scale; MorRat, Moral Rating; Moral, Morally Wrong; Inapp, inappropriate.

compared to Harm transgression ("You see a teacher hitting a student's hand with a ruler for falling asleep in class."), elicited a greater Disgust reaction, as compared to Anger. This finding fits well with those of Wagemans et al. (2018a), who investigated effects of trait anger and trait disgust on moral judgments. Our findings, however, extend their results to situation-specific affective reactions.

Although we expected that people scoring higher in BODS would show a more pronounced Disgust reactivity (vs. Anger reactivity) to purity violations (vs. harm violations), the Purity condition instead revealed a stronger relationship between BODS and anger ratings, compared to disgust ratings. A closer look at the results, however, suggests that the interaction might be artificially determined by ceiling effects in the disgust ratings for purity violations among people high in BODS (see **Figure 1**, and the results of the ERS × Moral Condition × Rated Emotion interaction). In other words, it appears that people scoring high in the BODS already provided nearly maximal ratings of disgust in the Purity condition, and therefore there was not enough leverage for providing even higher ratings. The failure to find the expected moderation role of the BODS on the interaction between disgust and Moral Condition might therefore due to limitations concerning the measurement of this BIS-related underlying construct. Alternatively, our negative finding might be partially consistent with the results from Landy and Piazza (2017), who failed to find a stronger relationship between trait disgust and moral condemnation, as compared to other negative emotions.

Nonetheless, we found a stronger association between BODS and affective reactivity (regardless of the specific emotion) in the purity violations scenarios, as compared to the association observed in the harm violations scenarios. This effect remained significant even when controlling for general emotional reactivity. This finding is consistent with the idea that people who exhibit higher levels of trait disgust may react more strongly to moral violations in general (Jones and Fitness, 2008), and that disgust prompts stronger reactions to moral violations (Rozin and Fallon, 1987; Rozin et al., 2009; Tybur et al., 2013) in accordance with a neo-sentimentalist stance on moral judgment (Haidt, 2001).

In order to gain specificity and differentiate moral condemnation from social appropriateness, we collected ratings on both dimensions. Gray and Keeney (2015) have suggested that what differentiates the Purity scenarios from the Harm ones is not their more intimate relation with disgust, but rather their weirdness (e.g., having sex with a frozen chicken). Wagemans et al. (2018a), however, did not find any association between sensitivity to deviation (Okimoto and Gromet, 2016) and moral condemnation. In a study specifically designed to test whether weirdness of disgust sensitivity items predict their relationship to moral judgments of purity transgressions, Wagemans et al. (2018b) found that eliminating the weirdest items from disgust sensitivity measures did not eliminate the more pronounced association between disgust sensitivity and moral judgments for purity transgressions. In addition, our results show that actually, our participants rated the Purity violations less – not more – inappropriate/weird than the Harm violations (**Figure 3**). Furthermore, we found that the BODS scores are more strongly associated with Moral Wrongness ratings than Inappropriateness (**Figure 4**). Hence, it seems unlikely that the weirdness of Purity transgression explains the higher condemnation among people with higher levels of BIS-related traits. However, it should be noted that the validity of the inappropriateness rating to measure weirdness may be questioned. In fact, some participants may interpret inappropriateness as a synonym of moral wrongness. This potential limitation cannot be ruled out in this study.

In the current study, we included only the TDDS pathogen subscale as a control (TDDS-p, e.g., 'Sitting next to someone who has red sores on their arm'), in order to provide the closest and most relevant comparison to body odor disgust. Subscales measuring sexual disgust (e.g., 'Watching a pornographic video') and moral disgust (e.g., 'A student cheating to get good grades') were not included because they are trivially related to moral judgment. Therefore, controlling for them would have undermined our inference because we would have controlled for a mediator (Rohrer, 2018).

Although the current study has the strength of being well-powered and pre-registered, the results were not as straightforward as expected. For instance, although the effect of disgust sensitivity on emotional reactivity to violations appears to be stronger in the Purity (vs. Harm) Condition, we did not find the effect to be specific to disgust ratings. Moreover, whereas the BODS scores were more strongly related to a Moral wrongness judgment (vs. Inappropriateness), this effect did not interact with the Moral scenario.

The inconclusiveness of our findings might be related to the some limitations in our measures of disgust sensitivity. In fact, when measuring disgust sensitivity through supposedly disgust evoking items, other emotions might be evoked as well. In the future, we may ask participants to rate also how much each of the BODS items evoke other negative emotions, following the same strategy as by Landy and Piazza (2017). This might provide a more fine-grained picture on the supposed selective relationship between disgust and moral condemnation of specific moral violations related to the preservation of purity.

Overall, our data suggest that body odor disgust sensitivity (part of the BIS) might in part explain affective reactions to a victimless moral violation that threatens the moral foundation of purity. Such a link might be expected because responses to purity violations have been linked to disease-avoidance concerns (Haidt and Graham, 2007). However, because of the lack of specificity in terms of elicited emotion (Disgust vs. Anger), we cannot rule out the hypothesis that individual differences in disgust sensitivity may covary with a greater tendency to provide extreme ratings. Such a finding might be in line with what found by Landy and Piazza (2017). The fact that this relationship appears to be stronger in response to Purity violations, is in line with the observation that these violations elicit a more automatic, less flexible response (Russell and Giner-Sorolla, 2011; Sabo and Giner-Sorolla, 2017).

CONCLUSION

Individuals with high body odor disgust sensitivity experience stronger affective reactions to moral violations, especially when Purity principles are violated, and strongly condemn morally deviant actions, suggesting a link between chemosensory functions and emotions driving moral judgments of the behaviors of others.

DATA AVAILABILITY

Data associated with this research are available on the Open Science Framework at https://osf.io/tk4x5/.

AUTHOR CONTRIBUTIONS

MTL, TL, SC-M, and JO designed the research. MTL and TL conducted the research. MTL analyzed the data. MTL, TL, and JO wrote the manuscript. All authors approved the final version of the manuscript.

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Implicit Attitudes About Agricultural and Aquatic Products From Fukushima Depend on Where Consumers Reside

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Japanese consumers are still hesitant to purchase products from Fukushima, although 7 years have passed since the Fukushima nuclear disaster, and these products are officially considered safe. In this study, we examined whether Japanese consumers have negative implicit attitudes toward agricultural and aquatic products from the Fukushima region and whether these attitudes are independent of their explicit attitudes. Japanese students completed an implicit association test and a questionnaire to assess their implicit and explicit attitudes toward products from Fukushima relative to another region. The results of two experiments reliably demonstrated that the public has negative implicit attitudes toward Fukushima products, whereas their explicit attitudes are consistently positive. These observations predominantly held for participants living close to Fukushima (Tokyo) as opposed to participants living far away (Hiroshima): Experiment 1 ($n = 40$). Furthermore, individual differences in aversion to germs contributed to the implicit attitudes; the implicit negative attitudes were attenuated among the participants with a relatively low aversion to germs: Experiment 2 ($n = 60$). These results suggest that the implicit attitudes associated with the behavioral immune system, which is conceptualized as a suite of psychological mechanisms designed to proactively resist pathogenic threats, may underlie the hesitation to purchase products from Fukushima.

Keywords: Fukushima nuclear disaster, purchase hesitation, implicit attitude, perceived vulnerability to disease, behavioral immune system

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INTRODUCTION

Although more than several years have passed since the Tohoku Earthquake and the Fukushima Daiichi nuclear power plant disaster, which occurred in 2011, Japanese consumers are still hesitant to purchase agricultural and aquatic products from Fukushima (Hangui, 2014; Fukushima Prefecture, 2016; Consumers Affairs Agency, 2017). It may have been advisable to refrain from consuming Fukushima products immediately after the disaster because of the widespread and unreliable, reputational damaging information regarding radioactive contamination. However, these products are now officially safe to buy (Fukushima Prefecture, 2013). Hence, consumers no longer have any grounds for avoiding them. Nevertheless, this hesitancy, which is a response to the social stigma against Fukushima products, persists; social stigma is defined as the disapproval of someone or something based on perceivable social characteristics used to differentiate it from others (Crocker and Major, 1989). This is causing serious economic damage (i.e., a collapse in the price, Central Union of Agricultural Co-operatives, 2011; Fukushima Minyu Shimbun Sha, 2012; Ichinose, 2012). For example, the market prices of beef, peaches, and rice, which are specialties from the Fukushima region, have continuously decreased since 2011 (e.g., by 9.3, 4.9, and 23.3% in 2017) with respect to the national average because of the disaster (Reconstruction Agency, 2018).

Such hesitancy in purchasing products from Fukushima can be interpreted in the context of error management theory (Haselton and Buss, 2000). According to this theory, an individual makes two possible errors (type I being false-positive and type II being false-negative errors) when making a decision in an uncertain scenario. Essentially, consumers tend to be afraid of making a type II error judgment, in which they mistake products that are dangerous as being safe. Instead, type I error judgments, where safe products are mistaken as dangerous, are more likely. In short, this hesitancy is caused by consumers' vigilance about products from Fukushima.

To prevent reputational damage to products from Fukushima and correct consumers' overcautious attitudes toward them, local and national governments have repeatedly released information regarding their safety, evidenced by screening for radioactive contamination (Ministry of Health, Labour and Welfare, 2018). Due to such attempts, the latest survey research demonstrates that the number of consumers who care about the production area has drastically decreased and that nearly 80% of consumers have no concerns about the safety of Fukushima products (Ministry of Agriculture, Forestry, and Fisheries, 2018). Furthermore, consumers do not currently have "explicitly" negative attitudes toward products from Fukushima, at least on paper (Miura et al., 2016; Kudo and Nagaya, 2017). If this is so, then why do they still hesitate to purchase these products? It appears that another factor, which we consider to be their "implicit" attitudes, underlies this hesitation. It has been suggested that explicit and implicit attitudes differ from one another, particularly with respect to social stigma (Wilson et al., 2000). Thus, we hypothesized that implicit and explicit attitudes toward products from Fukushima are dissociated from one another and that, rather than explicit attitudes, negative implicit attitudes underlie the hesitancy regarding the purchase of Fukushima products.

However, before we can resolve this major hypothesis, it is necessary to validate the basic aspects of our hypothesis, namely: whether consumers indeed have negative implicit attitudes toward agricultural and aquatic products from the Fukushima region and whether these attitudes are independent of their explicit attitudes. We used the implicit association test (IAT), which is a well-known method for measuring implicit attitudes related to a target attribute relative to another (Greenwald et al., 1998). In this study, the participants completed both an IAT and a questionnaire to assess their implicit and explicit attitudes toward products from Fukushima relative to products from another region.

Note that recent research based on the IAT has already reported that Japanese people show somewhat positive, not negative, implicit attitudes toward products from Fukushima (Kudo and Nagaya, 2017). However, we believe that the interpretation of the data from that is limited for the following two reasons. First, the study focused on the effects of a persuasive message on consumers' attitudes, and thus, the implicit attitudes were only measured after manipulating the participants with this message, and the questionnaire measures explicit attitudes. Thus, it was likely that the participants' implicit attitudes had been biased by the exposure to the preceding message and/or the questionnaire. Second, the authors did not provide any information regarding where the participants lived. Because the importance of (or the amount of exposure to) the Fukushima brand increases as the consumers' physical distance from the area where the disaster occurred decreases (Miura et al., 2016), it is plausible that consumers' attitudes toward Fukushima depend on where they live. It has not yet been determined whether consumers' implicit attitudes are modulated by where they live. In this study, excluding the potential confounding factors mentioned, we investigated whether explicit and implicit attitudes vary as a function of location. This is obviously an important factor to be taken into account when marketing products from Fukushima.

EXPERIMENT 1

In the first experiment, we investigated (1) whether consumers have negative implicit attitudes toward products from the Fukushima region, (2) whether these are independent of their explicit attitudes, and (3) whether a consumer's attitude is modulated by where they live. First, the participants completed the IAT. This provided a measure of their implicit attitudes. Then, they answered a questionnaire that measured their explicit attitudes. We recruited participants from two geographically distant areas (Hiroshima and Tokyo, which are 811 and 239 km away from Fukushima as the crow flies). Then, we compared the participants' attitudes.

Method

Ethics Statement All of the experiments carried out in this study were reviewed and approved by the Institutional Review Boards of Hiroshima University (Hiroshima) and Rissho University (Tokyo), Japan. Written informed consent was obtained from all participants before and after the experiment.

Participants We recruited 20 Japanese participants (12 female, mean age = 20.60 years, *SD* = 1.43 years) from Hiroshima and 20 Japanese participants (10 female, mean age = 20.00 years, *SD* = 0.45 years) from Tokyo with the aim of investigating human cognition. We ran the experiments in Hiroshima and Tokyo in parallel, and they took place between November 2017 and April 2018. The participants were blinded to the purpose of the study.

Stimuli We used 12 full-color images as stimuli: four of aquatic products and eight of agricultural products (four flowers and four rice). All images were made in our laboratory. Two aquatic products, two flowers, and two rice images were randomly selected and labeled with the kanji for "Fukushima product." We labeled the products because the images themselves do not convey information regarding where they were produced. The other six images were labeled with the kanji for "Saga product." The word label was white and was placed below the image. In addition, we used five positive word labels and five negative word labels (10 words total) as stimuli, based on Ishii and Numazaki (2009). These labels were written in white with kanji or hiragana scripts. Each stimulus was presented twice within a block. The visual angle of each image subtended 11 × 11° and each character subtended approximately 1.5 × 1.5°. The stimuli were presented at the center of the screen on a black background. The participants' viewing distance was about 57 cm.

We selected Saga prefecture, which is 1,048 km away from Fukushima prefecture, as the reference region. This is because Saga was ranked at a very similar position to Fukushima in the Japanese prefecture attractiveness rankings (Brand Research Institute, 2016) and that, like Fukushima, Saga specializes in agricultural and aquatic products. The participants of our pilot study ($n = 8$ in Hiroshima, $n = 8$ in Tokyo) also evaluated Saga neutrally; participants in Hiroshima rated 3.00 on average ($SD = 0.50$) and those in Tokyo rated 2.88 on average ($SD = 0.60$) to the question, "How much do you favor Saga prefecture relative to Fukushima prefecture? (1 = not favorable at all, 5 = very favorable)."

Procedure The participants performed the IAT task individually. The IAT was conducted in a laboratory under dimmed lighting conditions. We followed the IAT procedure developed by Greenwald et al. (1998), which consists of seven blocks. In each of the blocks, the participants were required to categorize the presented target stimulus by pressing either the left (F) key or the right (J) key on the keyboard using their two index fingers as quickly and accurately as possible. The target stimulus remained on the screen until participants provided a response. A red cross appeared in the center of the screen when participants pressed the wrong key.

In Block 1, which consisted of 24 training trials, the participants were trained to discriminate between products labeled from Fukushima and products from Saga: the left key indicated a Fukushima product and the right key indicated a product from Saga. In Block 2 (20 training trials), the participants were trained to determine whether the meaning of the word label was positive or negative: pressing the left key for positive words and the right key for negative words. In Block 3, which consisted of 22 practice trials, and Block 4, which included 44 test trials, we combined Fukushima/Saga and positive/negative discriminations: pressing the left key for Fukushima or positive words and the right key for Saga or negative words. In the following blocks, the participants learned the opposite category-key mapping to that of Blocks 1, 3, and 4. In Block 5 (24 training trials), they were trained to indicate whether the product image was labeled as being from Saga or Fukushima: pressing the left key for Saga and the right key for Fukushima. Then, in Block 6 (22 practice trials) and Block 7 (44 test trials), the participants pressed the left key when the presented stimulus was labeled as being from Saga or with a positive word, whereas they pressed the right key when the stimulus was labeled with Fukushima or a negative word. The order of the combinations was counterbalanced between the participants; blocks 1, 3, and 4 were switched with blocks 5, 6, and 7 for half of the participants.

Before each block, the participants were fully informed of the next task. Furthermore, we reminded the participants of the category-key mapping for each block as it came, and cue words were presented on the left-top or right-top of the screen for each trial. After completing the IAT, the participants were requested to answer a questionnaire on paper, consisting of two items that assessed the absolute likeability of Fukushima and Saga on an 11-point Likert scale and one item that assessed their relative likeabilities on a 7-point Likert scale: (1) How much do you like products from Fukushima? (−5 = "I do not like Fukushima products at all," +5 = "I like Fukushima products very much"). (2) How much do you like products from Saga? (−5 = "I do not like Saga products at all," +5 = "I like Saga products very much"). (3) Which production area do you prefer? (−3 = "I strongly prefer Saga to Fukushima," +3 = "I strongly prefer Fukushima to Saga"). The neutral point was 0 for all three questions.

Data Analyses

As traditional null hypothesis significance tests do not allow for evidence in favor of the null hypothesis (Wagenmakers, 2007; Cumming, 2013), we used default Bayesian tests (Rouder and Morey, 2012) to determine whether the production area had any effect or whether attitudes leaned to one side (positive or negative) or not (neutral). We treated the Bayes factors as measures of evidence for or against the effects of interest. Briefly, a Bayes factor (B_{10}) indicates the ratio of the likelihood that the data obtained favor a statistical model, including the effects of interest, to the likelihood that they favor a model that excludes these effects. We use the terminology from Jeffreys (1961) and Wagenmakers et al. (2011) to denote the magnitude of the effects. A B_{10} value >1 provides evidence for a statistical effect, whereas a B_{10} value <1 provides evidence for the null hypothesis.

As an index of the positivity/negativity of the implicit attitudes toward Fukushima products relative to Saga products, we calculated the D score for each participant based on the reaction times (RTs) during the IAT (Greenwald et al., 2003; Lane et al., 2007, for more details). First, we excluded incorrect trials and trials with RTs < 300 ms and > 10,000 ms from the following analyses; consequently, 4.08% of the trials were excluded on average. Second, for each pair of practice (blocks 3 and 6) and test blocks (blocks 4 and 7), we subtracted the mean RTs from the Fukushima-positive/Saga-negative combined task from the mean RTs from the Fukushima-negative/Saga-positive combined task. Third, each difference was divided by the overall standard deviation of the RTs for that pair of blocks. Finally, we calculated the equal weight average from the two ratios (mean differences/standard deviation) to obtain the D score. That is, a D score < 0 means that the Fukushima-negative/Saga-positive association is stronger than the Fukushima-positive/Saga-negative association, whereas a D score > 0 means the reverse.

To compute internal consistency, we first separately subtracted each trial's RT in the Fukushima-negative/

Saga-positive combination block from the RT of the corresponding trial of the Fukushima-positive/Saga-negative block. We then computed Cronbach's alpha (Cronbach and Meehl, 1955) of these different scores, following Bosson et al. (2000). Cronbach's alpha is the most routinely used method to estimate the reliability of internal consistency (Parsons et al., 2018). Alpha indicates the internal consistency in the tendency to associate Fukushima-related stimuli with a negative word (or impression) relative to Saga-related stimuli.

Results

Implicit Attitudes The mean *D* scores of participants from Hiroshima and Tokyo were both less than 0, as shown in **Figure 1**. According to the results of a Bayesian one sample *t* test, there was moderate evidence that the score favored the null hypothesis in Hiroshima (B_{10} = 1/3.03, Cohen's *d* = 0.20), whereas there was moderate evidence that the score was less than 0 in Tokyo (B_{10} = 4.66, Cohen's *d* = 0.62). The Cronbach's alpha values were 0.91 for the IAT results of Hiroshima and 0.57 for Tokyo.

Explicit Attitudes We calculated the mean rating scores of absolute likeability (**Figure 2A**) and relative likeability (**Figure 2B**). For the participants from Hiroshima, Bayesian one sample *t* tests demonstrated moderate and strong evidence that the rating scores of absolute likeability were greater than 0 for products from Fukushima (B_{10} = 5.05, Cohen's *d* = 0.63) and Saga (B_{10} = 79.55, Cohen's *d* = 0.95). There was strong evidence that the participants from Tokyo rated the absolute likeability of Fukushima with a score greater than 0 (B_{10} = 39.96, Cohen's *d* = 0.87), but anecdotal evidence that the absolute likeability of products from Saga favored the null hypothesis (B_{10} = 1/1.29, Cohen's *d* = 0.38). In the case of the relative likeability, Hiroshima residents held moderately neutral attitudes (B_{10} = 1/4.34, Cohen's *d* = 0.05), whereas Tokyo residents anecdotally preferred Fukushima to Saga (B_{10} = 2.53, Cohen's *d* = 0.55).

Discussion

In Hiroshima, the Fukushima-negative/Saga-positive implicit association was equivalent to the Fukushima-positive/Saga-negative implicit association, suggesting that Hiroshima residents have neutral (or Saga-level) implicit attitudes toward Fukushima products; internal consistency was acceptable based on Cronbach's alpha. They held explicitly positive attitudes toward products from both regions. These results are consistent with those of previous work (Miura et al., 2016; Kudo and Nagaya, 2017) that found that Japanese consumers in general do not currently have negative implicit or explicit attitudes toward products from Fukushima.

On the other hand, the Fukushima-negative/Saga-positive implicit association was stronger than the Fukushima-positive/Saga-negative implicit association in the case of Tokyo residents; internal consistency was slightly low, which may have been due to the small sample size (but see acceptable evidence observed in Experiment 2 below). This suggests that they have negative implicit attitudes toward products from Fukushima relative to those from Saga. Interestingly, their explicit attitudes were inconsistent with their implicit attitudes, which were consistently positive toward Fukushima. This discrepancy is in line with the previous suggestion (Wilson et al., 2000) that explicit and implicit attitudes can differ from one another, particularly with respect to social stigma.

Although we presented identical stimuli and tasks and used identical recruiting of participants in Hiroshima and Tokyo, the results of the IAT were different. This demonstrates that our current findings cannot be attributed to the physical characteristics of the stimulus images. Therefore, the results of Experiment 1 suggest that consumers have relatively negative implicit attitudes toward products from Fukushima, although their explicit attitudes are positive. This divergence was predominantly observed in the region near to Fukushima (i.e., Tokyo). These findings support our hypothesis that it is implicit negative attitudes rather than explicit negative attitudes that underlie the hesitancy to purchase products from Fukushima.

We built on the findings from Experiment 1 in the next experiment, in which we explored the individual differences between the negative implicit attitudes toward products from Fukushima held by Tokyo residents. We focused on the *perceived vulnerability to disease* (PVD, Duncan et al., 2009), which is defined as an individual's beliefs about their subjective vulnerability to the transmission of infectious diseases (*perceived infectability*) and an individual's tendency to experience emotional discomfort when exposed to potential disease transmission (*germ aversion*). Because negative implicit and explicit social attitudes are associated with individual differences between chronic and temporary concerns about disease transmission (Faulkner et al., 2004; Schaller and Duncan, 2007; Duncan et al., 2009; Duncan and Schaller, 2009; Huang et al., 2011; Murray et al., 2013), it is possible that consumers' implicit attitudes toward products from Fukushima, or radioactive contamination in Fukushima, would vary with their PVD.

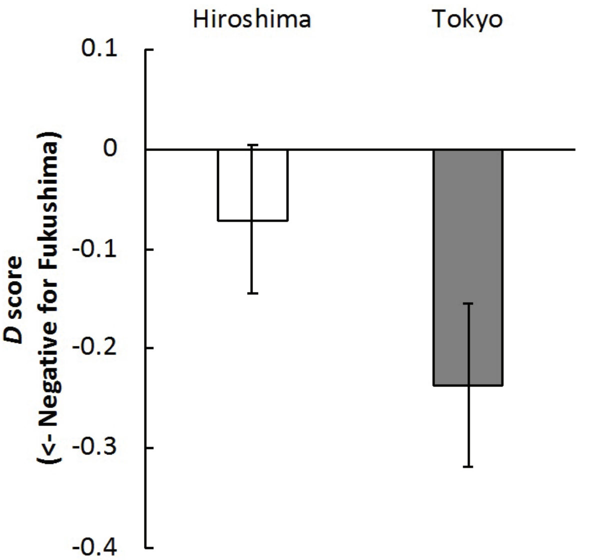

FIGURE 1 | Mean *D* scores in Hiroshima and Tokyo in Experiment 1. Error bars indicate standard error of the mean.

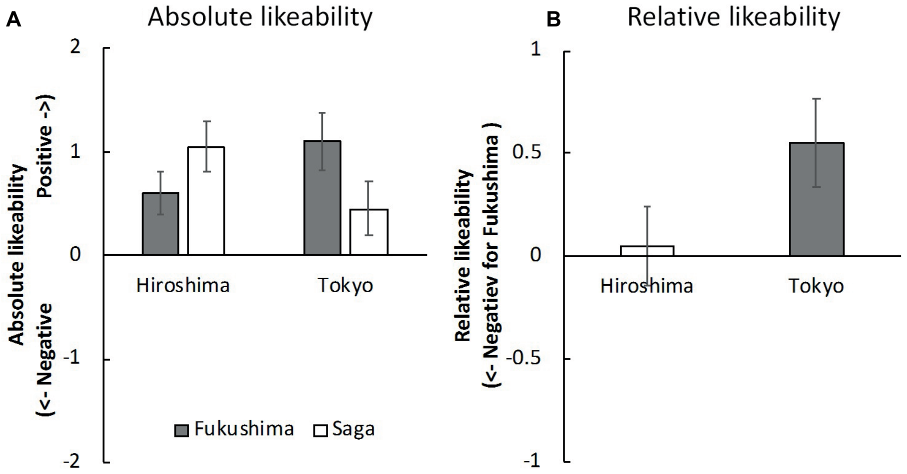

FIGURE 2 | Mean rating scores of **(A)** absolute likeability of Fukushima and Saga in Hiroshima and Tokyo and **(B)** relative likeability of Fukushima to Saga in Hiroshima and Tokyo. The neutral point is zero. Error bars indicate standard error of the mean.

Although the effects of radiation are not infectious, they are parallel to pathogenic threats in terms of being invisible. Previous research on evolutionary psychology proposes an adaptive strategy, which is conceptualized as the *behavioral immune system*. This allows us to detect and avoid objects perceived as a threat to health (Kurzban and Leary, 2001; Schaller and Duncan, 2007; Schaller and Park, 2011). Within this context, we predicted that the implicit attitudes toward Fukushima products may depend on the individual differences between the participants' aversive affective responses to an invisible threat, particularly germ aversion, in terms of their PVD.

EXPERIMENT 2

Method

Participants We recruited 60 Japanese participants (44 female, mean age = 19.88 years, $SD = 6.84$ years) from Tokyo with the aim of investigating human cognition. The experiment was run between April 2018 and July 2018. The participants were blinded to the purpose of this study.

Stimuli and Procedure These were almost the same as those used in Experiment 1, except that the participants completed the Japanese version of the PVD questionnaire (Fukukawa et al., 2014) at the end of the experiment. This was composed of two subscales used to assess perceived infectability and germ aversion, as in Duncan et al. (2009).

Results

PVD The perceived infectability ranged from 1.00 to 6.14 ($M = 3.75$, $SD = 1.29$), and germ aversion ranged from 2.13 to 6.38 ($M = 4.14$, $SD = 0.98$).

Implicit Attitudes and PVD We first calculated the D score, as in Experiment 1, which demonstrated extreme evidence that the score was less than 0 ($M = -0.28$, $SE = 0.04$, $B_{10} = 391.99 \times 10^3$, Cohen's $d = 0.82$); Cronbach's alpha was 0.92. The correlation between the D score and perceived infectability demonstrated moderate evidence for the null hypothesis ($B_{10} = 1/5.46$, $r = -0.07$). The correlation between the D score and the germ aversion score also demonstrated moderate evidence for the null hypothesis ($B_{10} = 1/3.64$, $r = -0.14$), though it was negative.

To assess the influence of perceived infectability from a different perspective, we divided the participants into a low group and a high group (with average scores of 2.70 vs. 4.80, $n = 30$ in each group, see **Figure 3A**). We conducted Bayesian one sample t tests, which revealed strong evidence that the D scores were less than 0, independently of perceived infectability ($B_{10} = 107.18$, Cohen's $d = 0.75$ for low-score group; $B_{10} = 808.47$, Cohen's $d = 0.90$ for high-score group). In terms of the germ aversion score (3.36 vs. 4.91 in average, $n = 30$ in each group, as shown in **Figure 3B**), the high-score participants demonstrated extremely negative implicit attitudes toward products from Fukushima ($B_{10} = 539.93 \times 10^2$, Cohen's $d = 1.20$). There was only moderate evidence among the low-score participants ($B_{10} = 9.72$, Cohen's $d = 0.57$).

Explicit Attitudes and PVD We calculated the absolute and relative likeabilities, which demonstrated extreme evidence that all of the scores were above 0 ($M = 2.33$, $SE = 0.18$, $B_{10} = 247.20 \times 10^{13}$, Cohen's $d = 1.63$ for the absolute likeability of Fukushima; $M = 1.27$, $SE = 0.20$, $B_{10} = 424.55 \times 10^3$, Cohen's $d = 0.82$ for the absolute likeability of Saga; $M = 0.60$, $SE = 0.13$, $B_{10} = 830.98$, Cohen's $d = 0.59$ for the relative likeability of Fukushima to Saga). The correlation between the explicit attitudes and perceived infectability demonstrated evidence for the null hypothesis ($B_{10} < 1/1.16$, $r = -0.24$ to 0.12). The correlation between the explicit attitudes and germ aversion also demonstrated evidence for the null hypothesis ($B_{10} < 1/3.33$, $r = -0.15$ to -0.05).

We calculated the mean rating scores, in terms of perceived infectability and germ aversion, for the absolute and relative likeability for both the low group and the high group. The results of our Bayesian one sample t tests demonstrated strong evidence that the absolute likeability rating scores were greater than 0 (**Figure 4A**). These were less influenced by the perceived infectability (B_{10} = 133.30 × 10^6, Cohen's *d* = 1.81 for Fukushima in the low-score group; B_{10} = 15.12, Cohen's *d* = 0.60 for Saga in low-score group; B_{10} = 138.40 × 10^4, Cohen's *d* = 1.45 for Fukushima in the high-score group; B_{10} = 232.34 × 10^2, Cohen's *d* = 1.14 for Saga in the high-score group). We have strong evidence that the relative likeability rating was greater than 0 among the low-perceived-infectability participants (**Figure 4B**, B_{10} = 37.93, Cohen's *d* = 0.67), whereas this evidence was moderate among the high-perceived-infectability participants (B_{10} = 4.24, Cohen's *d* = 0.49).

The absolute likeability rating scores were much greater than 0 (**Figure 4C**), being less influenced by germ aversion (B_{10} = 708.40 × 10^4, Cohen's *d* = 1.57 for Fukushima in the low-score group; B_{10} = 64.21, Cohen's *d* = 0.71 for Saga in the low-score group; B_{10} = 208.80 × 10^5, Cohen's *d* = 1.66 for Fukushima in the high-score group; B_{10} = 151.18 × 10, Cohen's *d* = 0.95 for Saga in the high-score group). We have strong evidence that the relative likeability rating was greater than 0 among the low germ aversion participants (**Figure 4D**, B_{10} = 355.65, Cohen's *d* = 0.84), whereas our evidence was anecdotal in the case of the high germ aversion participants (B_{10} = 1.12, Cohen's *d* = 0.36).

Correlation Between Implicit and Explicit Attitudes Because, prior to the PVD questionnaire, the procedure was identical to that of Experiment 1, we combined the data concerning the implicit and explicit attitudes of Tokyo residents gathered in Experiments 1 and 2. The correlation between the *D* scores and the relative likeability ratings for products from Fukushima was weakly negative ($n = 80$, $B_{10} = 1/1.45$, $r = -0.20$), although the evidence anecdotally favored the null hypothesis.

Discussion

First, the implicit attitudes toward agricultural and aquatic products from Fukushima were again negative relative to those from Saga; internal consistency was now acceptable. Second, the explicit attitudes toward products from Fukushima were consistently positive and hence dissociated from the implicit attitudes. Thus, the findings of Experiment 1 were robustly supported by those of Experiment 2.

Third, as predicted, we found a negative correlation between the *D* score and germ aversion, but it was not statistically supported. We consider that the absence of the statistical support is likely to be due to the extreme *D* score; that is, the correlation was undetectable due to the ceiling effect. After dichotomizing the data *via* a median split, we identified moderately negative implicit attitudes toward Fukushima among participants with low aversion to germs compared to participants with high aversion to germs. Furthermore, although this effect was moderate among participants with low aversion to germs, we detected a large effect in the participants with high aversion to germs, based on Cohen (1969). Although the median split is controversial (see Rucker et al., 2015), we would like to emphasize that it demonstrated a consistent trend with the correlation. On the other hand, the negative implicit attitudes toward Fukushima, including the effect size, were independent of the perceived infectability. These results can be interpreted in the context of the behavioral immune system (Kurzban and Leary, 2001; Schaller and Duncan, 2007; Duncan et al., 2009; Schaller and Park, 2011). As the perceived infectability in PVD reflects the self-perceived susceptibility to infection, it might be less relevant to radioactive contamination, which is not contagious. However, the aversion to germs in PVD reflects emotional discomfort in the presence of potential disease transmission vectors. Thus, converging evidence suggests that the participants of this study would have aversive affective responses to products from Fukushima so that they can avoid the invisible threat of radiation.

In terms of the correlation between implicit and explicit attitudes, there was a negative trend among the participants residing in Tokyo, although this was not supported by any statistical evidence. Therefore, current evidence suggests

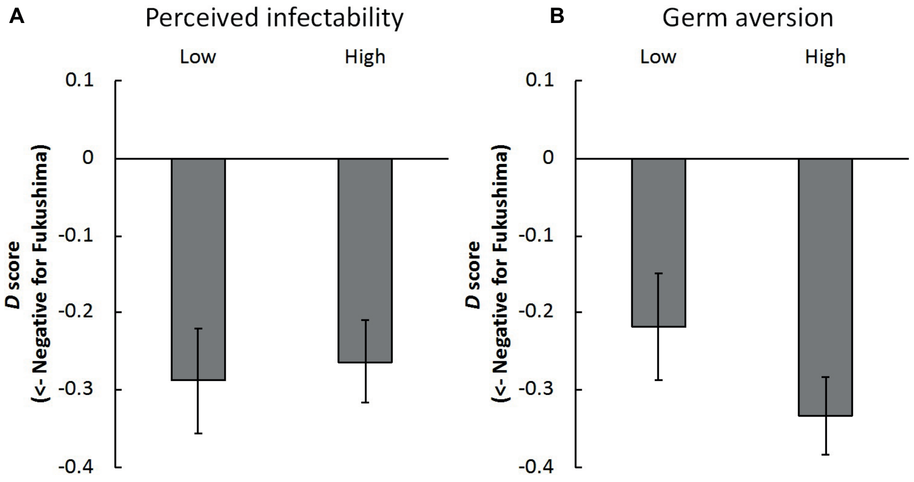

FIGURE 3 | Mean *D* scores among Tokyo residents of **(A)** low/high perceived infectability and **(B)** low/high germ aversion in Experiment 2. Error bars indicate standard error of the mean.

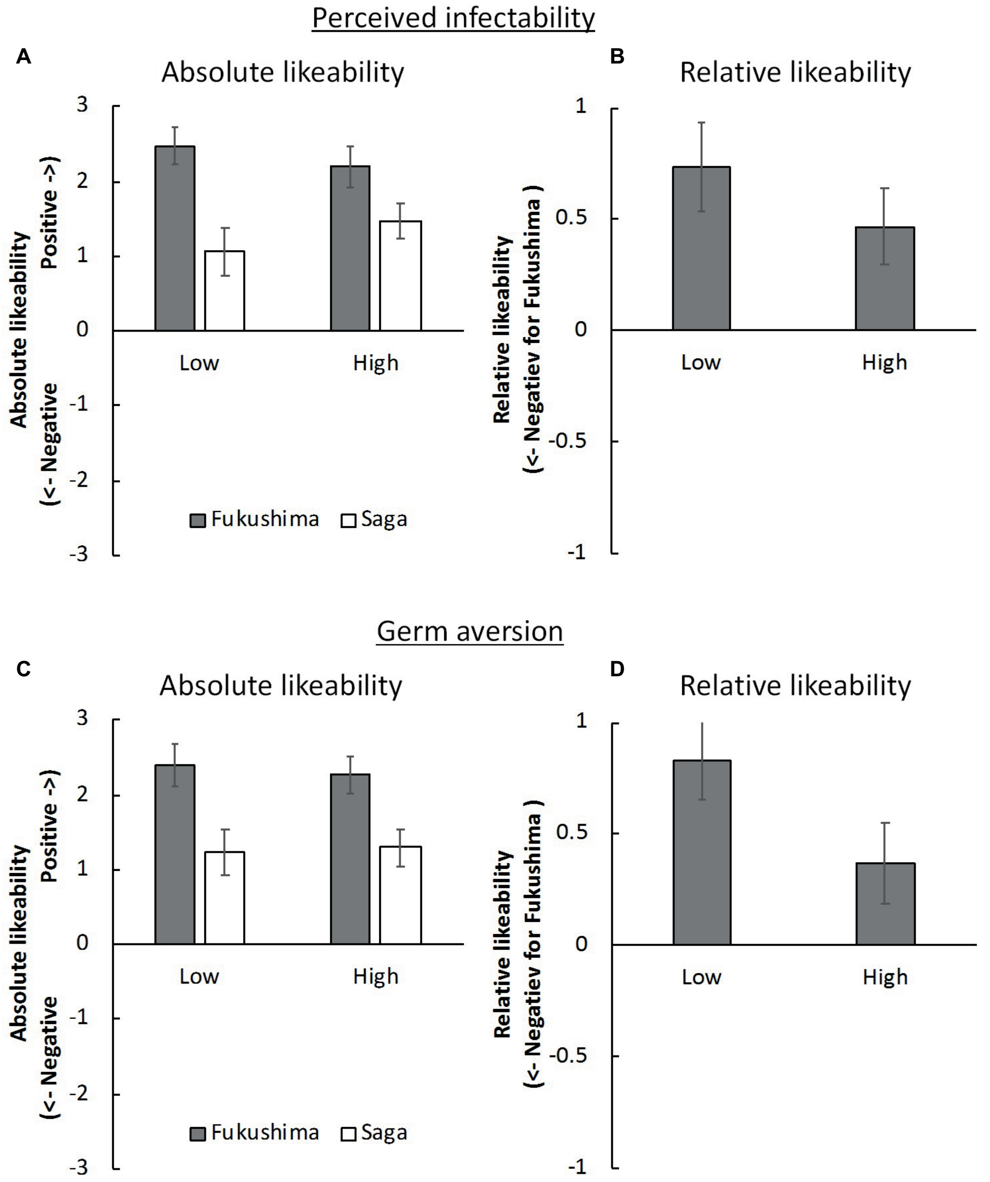

FIGURE 4 | Mean rating scores of **(A)** absolute likeability of Fukushima and Saga and **(B)** relative likeability in each low/high perceived infectability group and of **(C)** absolute likeability and **(D)** relative likeability in each low/high germ aversion group. Error bars indicate standard error of the mean.

that the implicit attitudes were dissociated from, but not opposed to, the explicit attitudes; more work is needed with respect to this issue.

GENERAL DISCUSSION

We investigated the following three questions: (1) Do consumers have negative implicit attitudes toward agricultural and aquatic products from Fukushima? (2) Are these attitudes independent of their explicit attitudes? (3) Are they modulated by residential area? The answers to these questions are all yes. Although Japanese participants consistently had positive explicit attitudes toward products from Fukushima, relative to those from Saga, their implicit attitudes toward Fukushima were reliably negative. These were more predominant in the region near Fukushima (i.e., Tokyo) than in the region further away (i.e., Hiroshima). The results of recent research and market surveys (Miura et al., 2016; Kudo and Nagaya, 2017; Ministry of Agriculture, Forestry, and Fisheries, 2018) suggest that the current consumption situation embraces the apparent contradiction that products from Fukushima are somehow avoided by consumers who have no negative attitudes toward them. Focusing on the implicit attitudes and where consumers live, we succeeded in demonstrating a stepping stone toward the resolution of this paradox. Implicit attitudes may be associated with hesitancy to purchase products from Fukushima.

Furthermore, we explored individual differences in the formation of these implicit attitudes toward products from Fukushima in terms of the PVD (Duncan et al., 2009). The results of our analyses suggest that the negative implicit attitudes toward Fukushima products were attenuated (but still persistent) in participants with relatively low germ aversion in PVD. However, there was a large effect size among participants with high aversion to germs. Previous research suggests that we establish negative implicit attitudes toward foreigners or outside groups based on threat-connoting cues (Faulkner et al., 2004; Duncan et al., 2009; Huang et al., 2011). In this study, the label "Fukushima products" might serve as a threat-connoting cue, which then activates the behavioral immune system. This is our evolutionary adaptive disease-avoidance mechanism (Kurzban and Leary, 2001; Schaller and Duncan, 2007; Schaller, 2011; Schaller and Park, 2011). Because radiation is a serious threat to our health and survival that is also invisible, like a pathogen, it is plausible that consumers promote aversive, cautious (sometimes overcautious) attitudes toward products from Fukushima to minimize the impact of errors in judgment (they avoid making a type II false-negative error in terms of error management theory, Haselton and Buss, 2000). As a result, consumers' attitudes are generally biased toward type I false-positive errors. This response is caused by the behavioral immune system (Oaten et al., 2009; Schaller, 2011; Kouznetsova et al., 2012; Miller and Maner, 2012). It has been suggested that the aversive, cautious response varies not only between individuals but also across external contexts, such as geographical region (Schaller and Murray, 2008). Our current findings (i.e., that negative implicit attitudes reliably observed in the region near Fukushima compared to the region far away) are consistent with this psychological survival function. Thus far, it has been shown that individuals' anxiety and knowledge regarding radiation risk interactively influence their attitudes toward products from radioactive contamination areas (Miura et al., 2016). Developing this knowledge, the results of this study suggest that it is not just these factors but also individual differences in PVD that contribute to consumers' attitudes.

It is noteworthy that implicit measures have been criticized for their proneness to measurement error, faking, or context dependency (see Gawronski and De Houwer, 2014; Gawronski and Hahn, 2019, for review). Although we used the conventional instrument in this study, it is important to investigate implicit attitudes with other instruments in future research, which would strengthen the current evidence.

Our results provide fundamental evidence supporting our hypothesis that it is implicit rather than explicit negative attitudes that elicit hesitancy about purchasing products from Fukushima. Future research is needed to validate our hypothesis more thoroughly. We will investigate whether the findings presented in this paper do indeed underpin the hesitation toward products from Fukushima. In fact, PVD has previously been reported to relate to consumers' intentions to buy secondhand products (Kapitan and Bhargave, 2013). This supports our hypothesis. Future studies should determine whether a more negative implicit attitude toward Fukushima products is associated with a greater hesitancy to purchase these products.

AUTHOR CONTRIBUTIONS

OT and AA contributed conception and design of the study; OT, JQ, and DT conducted the experiments. OT, DT, and AA performed the statistical analysis. OT wrote the first draft of the manuscript. All authors read and approved the submitted version.

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The Inclusive Behavioral Immune System

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Although living in social groups offers many advantages, it comes at a cost of increased transmissible disease. The *behavioral immune system* (BIS) is thought to have evolved as a first line of defense against such infections. It acts by minimizing the contact of yet uninfected hosts with potential pathogens. The BIS has been observed in a wide range of animals including insects, amphibians and mammals, but most research has focused on humans where the BIS is guided by complex cognitive and emotional processing. When researchers discuss the evolutionary origin of the BIS, they assess how it raises individual fitness. What would happen though if we shift our attention to the evolutionary unit of selection – the gene? Success would be measured as the change in the gene's prevalence in the entire population, and additional behaviors would come to our attention – those that benefit relatives, i.e., behaviors that raise *inclusive fitness.* One widely-recognized example of the inclusive BIS is *social immunity*, which is prevalent among eusocial organisms such as bees and ants. Their colonies engage in a collaborative protective behavior such as grooming and the removal of infected members from the nest. Another example may be *sickness behavior,* which includes the behavioral, cognitive and emotional symptoms that accompany infection, such as fatigue, and loss of appetite and social interest. My colleague and I recently suggested that sickness behavior has evolved because it reduces the direct and indirect contact between an infected host and its healthy kin – improving inclusive fitness. These additional behaviors are not carried out by the healthy individuals, but rather by whole communities in the first case, and by already infected individuals in the second. Since they step beyond the classical definition of BIS, it may be useful to broaden the term to *the inclusive behavioral immune system*.

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LIVING IN GROUPS COMES WITH RISKS – PATHOGEN EXPOSURE

Living in large social groups offers several advantages (Shultz et al., 2011). It reduces the risk of predation, simplifies the care for offspring and improves food foraging and food protection. Yet, it also has its drawback – it increases the risk for transmissible infections (McCallum et al., 2001). Pathogens can spread more easily among members of groups that exhibit social contact, share food and move around in the same territory (Cote and Poulin, 1995). Accordingly, both in animals and humans, social isolation is a common intervention that can contain infectious diseases by reducing transmission. Thus selective culling (Fèvre et al., 2006), quarantine (Fraser et al., 2004;

Tognotti, 2013), school closures (Earn et al., 2012) and bans on travel and public gathering (Hatchett et al., 2007; Markel et al., 2007) have proven successful in containing epidemics.

Additional anecdotal support for the importance of social exclusion as a barrier for transmission comes from recent observations in bats, mice, and spiders. Recently, a fungal disease called White Nose Syndrome decimated several bat populations in North America (Blehert et al., 2009; Lorch et al., 2011). As some species approached the verge of extinction, several bat colonies escaped this fate by adopting a solitarily hibernating pattern in which individuals distanced themselves from their neighbors (Langwig et al., 2012). Relatedly, in mice and spiders, experiments have shown that "bold" individuals, which had more encounters with other conspecifics, had higher infection rates than "shy" individuals (Dizney and Dearing, 2013; Dearing et al., 2015; Keiser et al., 2016).

PATHOGENS EXERT A STRONG SELECTIVE PRESSURE

Benefiting from modern medicine, complete with vaccinations, antibiotics, hygiene, and health care, we easily forget that until recently pathogens have been the leading cause of human mortality (Armelagos et al., 1996). Even our recent history is punctuated by repeated outbreaks of deadly epidemics (e.g., influenza, cholera, smallpox, polio, and HIV). Globally, life expectancy more than doubled during the past two centuries (Oeppen and Vaupel, 2002) and combatting infectious diseases was the leading cause for this increase.

Encounters with pathogens throughout our evolutionary history are heavily represented in our genome. Approximately 8% of the human genome is comprised of DNA originating from retroviruses (Griffiths, 2001), a subgroup of viruses that incorporate their genes into the DNA of host cells. Even this high percentage is a significant underestimation of our encounters with retroviruses since to be preserved in our DNA these retroviruses had to infect our germ cells and their integration needed to become fixed (Griffiths, 2001). Genetic variation among different geographically-distributed human populations also echoes the massive burden of infections as it is mostly attributed to pathogen exposure (Fumagalli et al., 2011). During the 100,000 years since humans migrated out of Africa and populations settled in different places, they encountered distinct pathogens which differently shaped their genome.

Clearly, pathogens exerted a tremendous selective pressure on humans and other animals. To avoid and survive infections, we had to evolve sophisticated mechanisms to resist them.

DEFENSE MECHANISMS

There are several lines of defense that evolved to protect us against infections. These defense mechanisms interact with each other and act in a collaborative but also serial manner.

Physical and Chemical Barriers

This so called "first line of defense" is comprised of surface barriers that block pathogen entrance into tissues. It includes the skin which serves as a physical barrier and mucous membranes that secrete buffering mucus and molecules that destroy many pathogens (e.g., gastric acid).

The Physiological Immune System

If pathogens bypass the first line of defense and invade the body, than the physiological immune system comes into play. This is the most acknowledged and most studied pathogen defense mechanism. The proteins it utilizes are encoded by more than 7% of our genome (Kelley et al., 2005), reflecting the strong selective pressure from pathogens.

When a pathogen invades the body, the innate arm of the immune system acts immediately. If this response is insufficient, the adaptive immune system is called into play. It produces specialized cells and antibodies that specifically attack particular pathogens. Although effective in the long run, on the first time a pathogen is encountered there is a substantial delay until a specific immune response is fully deployed. Pathogens can exploit this delay to replicate rapidly and overwhelm their hosts.

On the longer run, pathogens develop strategies to evade the host's immune response. In this ongoing arms race between pathogens and hosts the former enjoy a clear advantage: unlike humans who take decades to reproduce, most pathogens do so within hours or minutes so they rapidly evolve new strategies to evade or resist immune responses. The growing threat from bacterial resistance to antibiotics (Gootz, 2010) and the difficulty in developing highly efficient HIV and influenza vaccines (Carrat and Flahault, 2007; Barouch, 2008) are two examples for the rapid evolution of bacteria and viruses.

Overall, although the immune system is sophisticated and dynamic, its ability to combat pathogens is inherently limited. Perhaps a better way to oppose pathogens is simply to avoid contacting them.

The Behavioral Immune System

In 2006, with this idea in mind, Schaller conceptualized a complementary defense system – the behavioral immune system (BIS) (Schaller, 2006). BIS is considered to be a motivational system that evolved to modify behavior and reduce contact with infectious agents. It is described as a coordinated suite of detection mechanisms, which allow individuals to identify potential sources of pathogens, and of emotional and cognitive mechanisms, which respond to those cues and guide behaviors that distance the individual from contagious sources (Schaller and Park, 2011).

Behavioral immune system likely has deep evolutionary roots. It is evident in a wide range of species: from insects through amphibians to mammals. Social lobsters and bullfrog tadpoles detect and avoid conspecifics infected with a lethal pathogen (Kiesecker et al., 1999; Behringer et al., 2006). In mice and rats several studies show that healthy individuals keep distance and reduce interactions with individuals whose immune system is activated (due to injections of the bacterial extract LPS) (Arakawa et al., 2011; Boillat et al., 2015). Mandrill monkeys avoid grooming infected conspecifics and refrain from the fecal matter (Poirotte et al., 2017). Thus, various groups of animals have developed behavioral strategies to detect and limit contact with pathogens and infectious individuals.

In humans, most support for the existence the BIS comes from extensive studies of the emotional and physical reaction commonly referred to as "disgust" (Curtis et al., 2004, 2011; Oaten et al., 2009; Tybur et al., 2013). We grimace, distance ourselves, and sometimes vomit in response to sights and smells of carcasses, decomposing food, bodily secretions, etc. Disgust often arises in response to potentially contagious elements and usually drives us away from them.

Additional support for the existence of the BIS in humans comes from studies showing that we can detect sick individuals through various cues. For example, the clothes of subjects whose immune system was activated (using LPS) can be sniffed out (Olsson et al., 2014; Regenbogen et al., 2017), and their gait and physical appearance are perceived as less healthy (Sundelin et al., 2015) and desirable (Regenbogen et al., 2017). Although not experimentally demonstrated, it is presumed that these signs lead to reduced contact with the potentially contagious individuals. One study has shown that priming with disease cues led individuals to describe themselves as less extrovert and less open to new experiences (Mortensen et al., 2010).

Since social psychologists were the leading researchers of the BIS, the field naturally centered on humans and its main interests became its effects on the social implications of erroneous detection (e.g., social categorization, prejudice and xenophobia, cross-cultural differences) (Park et al., 2003, 2007; Faulkner et al., 2004; Miller and Maner, 2012). Little experimental attention was given to how the BIS changes behavior toward infectious individuals and on the health outcomes of these dynamics.

SO WHAT ARE WE MISSING?

Since the idea of the BIS as precautionary behavior seemed straightforward, not much consideration has been given to its precise definition. When Schaller first coined the term, he envisaged an anti-pathogenic defense system that detects potentially infectious organisms and objects and leads to a change in behavior (Schaller, 2006). Schaller was interested in how such a system that evolved to detect sick individuals affects social perception. He therefore focused on individual fitness – the emotions, cognitions, and behaviors that evolved to protect healthy individuals from contracting infections (Neuberg et al., 2011). If we recognize, as Schaller did, that an evolutionary process is driving the emergence of the BIS, than we must also acknowledge broader notions of natural selection. These have long placed the "unit of selection" at the level of gene, not the individual.

This shift in focus took form as Hamilton's "inclusive fitness theory" over 50 years ago (Hamilton, 1964). This theory, also known as "kin selection" (Smith, 1964) was based on the realization that evolution occurs through the differential survival of competing genes. From the gene's point of view, evolutionary success depends on leaving behind the maximum number of copies of itself in the population. Genes (more precisely, alleles – variants of a specific genes) whose phenotypic effects tend to increase their frequency will propagate through the population – regardless of which individual carries that gene. Thus, a gene may increase its evolutionary success by indirectly promoting the reproduction and survival of other individuals who also carry that gene and may do so even if they reduce the fitness of the individual originally displaying the phenotypic behavior. This idea is summarized by Hamilton's rule which states that natural selection favors a gene that is costly to the individual carrying it whenever $r^*b > c$, where r represents the genetic relatedness, b represents benefits, and c represents costs (Hamilton, 1964). Thus, if the reproductive success of relatives of individuals weighed by the probability of those relatives carrying the gene in question is larger than the cost to the survival and reproduction of that individual, this gene will be positively selected for.

But how could such a shift from the individual to the gene change our understanding of the BIS? It would broaden its definition to include behaviors that increase the fitness of genetically-related individuals who are likely to carry that gene. Thus, if an animal expresses a phenotype that reduces the transmission of a fatal disease to its kin, these kin (who are likely to also carry that gene and express this phenotype) would enjoy better chances to live and reproduce. Consequently, these genes would increase in frequency and this phenotype would be preserved even at the expense of the individual expressing it.

Social/Collective Immunity

Social immunity is a term originally used to describe the collective defense mechanisms observed in eusocial insects (e.g., ants, bees, termites, and wasps) that result in avoidance, control, or elimination of infections (Cremer et al., 2007). The hallmark of these defense mechanisms is that single individuals cannot perform them efficiently. They require the collaboration of several individuals and are usually mounted for a collective benefit (Cremer et al., 2017). Although the term describes physiological, organizational as well as behavioral adaptations (Cremer et al., 2007), here I will only discuss their behavioral aspect.

Eusocial insects are clearly unique in their social interactions and tend to develop collaborative behaviors and altruism. Comprised of many closely-related sterile workers whose only path to reproductive success is to support their fertile queen and male kin, they act as a super-organisms (Wheeler, 1911; Boomsma and Gawne, 2018). The workers practice division of labor, collectively care for the brood, collect foraged food in communal stores and may sometimes defend the nest to their death (Shorter and Rueppell, 2011).

These colonies are very vulnerable for pathogen transmission as they live at high density, in constant physical contact with each other and even exchange food orally (Aubert and Richard, 2008). Their high genetic similarity also poses an additional risk as more individuals are susceptible to similar pathogens. Thus, eusocial insects are optimal candidates to develop social immunity. One interesting form of social immunity is social fever, which has been observed in honeybees (Starks et al., 2000). Fever has been acknowledged to improve survival following infections (Kluger et al., 1998). Its benefits have most convincingly been shown in exothermal animals such as lizards and fish (Kluger, 1991). Exposing them to sub-optimal environmental temperatures reduced their survival following infection. Fever is thought to improve resistance by depriving pathogens from the optimal temperature for growth as well as by improving the immune response (Kluger et al., 1998; Evans et al., 2015). In honeybees, workers decouple their wings and contract their flight muscles at high speed to elevate their temperature collectively speed and eliminate heat sensitive pathogens (Cremer et al., 2017). Thus, the behavior of healthy workers can eliminate pathogens affecting other members. It remains to be studied whether mammals also use social behavioral thermoregulation like huddling while infected.

In recent years the term social immunity has occasionally been broadened to mechanisms observed in non-eusocial animals. Allogrooming, in which individuals groom other conspecifics, is the most familiar form of behavioral social immunity. It has been observed in species ranging from insects, through birds, to a variety of mammals (primates, rodents, and ruminants). Although it serves an important function in establishing social networks and relationships, it clearly contributes to the hygiene of the animals by removing parasites. Although the behavior of the donor seems to contribute to the health of the recipient at the cost of the donor's time and energy, allogrooming has been suggested to benefit the donor as well. In social ants for example, social contact including allogrooming of infected ants has been shown to immunize the naïve donor and increase survival upon later exposure to the same pathogen (Ugelvig and Cremer, 2007; Konrad et al., 2012). Thus, although this behavior has traditionally been interpreted in terms of kin selection in social insects, other forms of selections may take role in its evolvement. In vertebrates, reciprocal altruism is thought to play a larger role (Clutton-Brock, 2009), although kin selection may also have some function (Ju and Lee, 2016).

Aside from grooming, several studies of social insects have shown additional hygiene behaviors that reduce the spread of infections. These include removal, killing and burial infected nestmates (Cremer et al., 2017), sometimes of even before they become contagious (Pull et al., 2018).

In social immunity, healthy conspecifics engage in behaviors that reduce or eliminate the risk for infection in the colony. Although it has some costs for the healthy individual (e.g., it may increase its risk of being infected, consume time, or deplete energy), some forms of social immunity may provide direct benefit to the donor, making it more likely that social immunity is not limited to eusocial animals and can be found also in sub-social insects (Van Meyel et al., 2018). Whether or not vertebrate behaviors can also be interpreted using similar terms is still contentious.

Could Sickness Behavior Be Understood as Part of the Behavioral Immune System?

When infected with a pathogen, many species display behavioral responses termed "sickness behavior" (SB) (Hart, 1988; Aubert, 1999; Dantzer and Kelley, 2007). SB includes depression, lethargy, hypersomnia, anorexia, reduced drinking, diminished libido, social withdrawal, and reduced grooming. Although some pathogens (e.g., rabies, toxoplasma) may manipulate behavior directly (Poulin, 2010), SB is in fact a well-orchestrated reaction produced by the host's immune system (Dantzer et al., 2008; McCusker and Kelley, 2013). Infectious agents display a variety of pathogen-associated molecular patterns (PAMPs) that are recognized by receptors (e.g., Toll-like receptors) on various cells of the innate immune system (e.g., macrophages and dendritic cells). As a results these cells release proinflammatory cytokines (e.g., interleukin-1 and tumor necrosis factor alpha) that affect the brain through neuronal and humoral routes and induce SB (McCusker and Kelley, 2013). Even non-infectious agents (e.g., LPS, inactivated vaccines) that stimulate the immune system can induce SB. Blockade of the proinflammatory cytokines released by immune cells prevents SB, giving the ultimate support that SB is indeed induced by the host's immune system (Bluth et al., 1992; Dantzer, 2006). The fact that SB is triggered by most infections, is orchestrated by the immune system, and persisted throughout evolution, suggests that it plays some important adaptive role in host defense (Hart, 1988).

We are so used to the manifestations of SB that we consider them the essence of being sick. In fact they are quite baffling as they carry significant adaptive costs to healthy animals (Moret and Schmid-Hempel, 2000; Hanssen et al., 2004). They can put the animal at higher risk of predation, of losing its territory and its social position, of dehydration and of starvation. In addition, these behaviors decrease parental care, and waste opportunities for reproductive success. To be preserved throughout evolution, these costs must be balanced by advantages.

My colleague and I (Shakhar and Shakhar, 2015) have recently proposed that SB has evolved because it reduces the risk of transmitting an infectious disease to offspring or other kin – a theory termed the Eyam Hypothesis after the English mining community that isolated itself to contain an outbreak of bubonic plague in 1666. Three-quarters of the villagers reportedly died, but the surrounding communities were saved (Massad et al., 2004).

Accordingly, self-imposed isolation characterizes most aspects of SB. For some symptoms it is obvious that they reduce the interactions of the infectious host with conspecifics. Such symptoms include depression, lethargy, hypersomnia, social withdrawal, and reduced grooming. Similarly, reduced libido limits courtship and mating behaviors. It is less clear how some symptoms, such as anorexia and reduced drinking, reduce contact and transmission. Presumably, when animals lose their appetite and thirst they share fewer meals with group members, do not contaminate the food or water supplies of the group, and defecate and urinate less, thus spreading less contagious pathogens to the environment.

Since SB often overlaps with the most infectious period of illnesses (Fraser et al., 2004; Carrat et al., 2008; Charleston et al., 2011), the reduced social interactions and contamination of the environment during this period likely reduce the transmission of pathogens. A study in mice has shown that 40% of mice injected with LPS reduced their social interactions with unchallenged mice (Lopes et al., 2016). Using a mathematical model that was developed based on these results the authors predicted that even if only 10% of mice had reduced their interaction, it would result in reduced transmission rate (Lopes et al., 2016). Although the change in behavior did not depend on genetic relatedness (Lopes et al., 2018), this species tends to live in close proximity to its kin (Rusu and Krackow, 2004) and thus social co-habituation may serve as a proxy for kinship.

Thus, if we redefine BIS according to the modern genetic perspective, it could incorporate SB. Individuals carrying genes for pronounced SB limit their social interactions when sick and protect their relatives (along with others) within the local group. SB could actually be a protective behavior that increases inclusive rather than individual fitness.

Accordingly, in eusocial insects, where genetic relatedness is very high and colonies are crowded, we can expect the behavior of infected individuals to be more dramatic. Indeed, social ants and bees infected with a pathogen or treated with (LPS) move less (Aubert and Richard, 2008), interact less with other ants (Bos et al., 2012), avoid contact with brood (Ugelvig and Cremer, 2007; Bos et al., 2012), spend more time outside their nest (Bos et al., 2012) and perhaps even sacrifice themselves (Rueppell et al., 2010). A recent study in ants demonstrated that after exposure to fungi spores, both exposed and non-exposed individuals adjusted their behavior to reduce the risk of contaminating their social network (Stroeymeyt et al., 2018). Clearly the case of super-organisms is unique as selection may occur at colony level (Wheeler, 1911; Boomsma and Gawne, 2018) but the extremity of such acts may provide support to the strong selective pressure pathogens have put on the behaviors of sick individuals in looser social networks.

Since the idea that SB may be part of the BIS and may have evolved to protect our kin from being infected is relatively new, only few studies that examine its premises exist. If this idea is true, we would expect SB to be stronger when pathogens are more virulent, when there is a greater chance of transmission either due to environmental characteristics (e.g., living in dense colonies) or pathogen's characteristics (e.g., infectivity), and when the average genetic relatedness within group is higher than in the a. In addition, if SB is suppressed (e.g., through anti-inflammatory drugs), we would expect transmission rates to increase.

Could Signaling Behavior by Infected Individuals Trigger BIS Responses by Healthy Recipients?

The BIS concept began with the notion that healthy people can detect contagious individuals. It is assumed that evolution equipped healthy individuals with the ability to detect cues of infection. But the concepts of social immunity and the Eyam hypothesis suggest a complementary possibility: that infected individuals actively emit "sickness signals" to warn their conspecifics and keep them away.

Findings from eusocial insects may support this concept. Termites that have contacted fungal spores vibrate to signal their group members that they have been infected. In response, other termites keep their distance from the infected area (Rosengaus et al., 1999). The health state of infected honeybee larvae and pupae can be smelled by the worker bees, leading to their weeding out from the hive, a phenomenon termed "hygiene behavior" (Wilson-Rich et al., 2009; Baracchi et al., 2012). Not only social insects, but mammals as well may signal their health status. Several studies in mice and rats show that LPS-treated individuals emit olfactory signals that drive other group members away and discourage interactions (Kavaliers et al., 2005). It is easy to accept that the detection of infected conspecifics has evolved as a protective mechanism against transmission. But, through kin selection, evolution may have favored not only individuals who can detect such cues but also individuals who display them. This is a subtle issue as infectious animals need to hide their status from predators but convey it to their kin. Experimentally testing this idea is difficult as it is hard to tease apart whether behavioral and sensory signs are perceived so only because of selection at the level of the non-infected individual (i.e., detection) or also at the level of the infectious individual (i.e., signaling).

CONCLUSION

The BIS is a recently developed concept used to describe anti-pathogenic behaviors that evolved because they reduce the risk of infection. It has been assumed that this system evolved because it increases individual fitness. This paper proposes that individuals can also increase their inclusive fitness by protecting relatives (including offspring) from infection through kin selection. Thus, BIS can evolve due to its benefit not only to the individual fitness but also by indirect fitness of the individual by helping others.

Adopting this new outlook broadens the definition of the BIS to include additional behaviors such as social immunity and SB. Whether carried out by a healthy individual in the first case or by infected hosts in the second, these two kinds of behaviors are unique – they benefit others at the expense of the individual displaying them. Perhaps it is time to step beyond the idea of BIS and broaden the term to "inclusive behavioral immune system."

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The author confirms being the sole contributor of this work and has approved it for publication.

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Disease Threat and the Functional Flexibility of Ingroup Derogation

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While the findings from previous studies directly relate the ingroup derogation phenomenon to the evolved response of the behavioral immune system, there are three major limitations in the previous studies on the functional flexibility of ingroup derogation. The present study further investigated the functional flexibility of ingroup derogation by conducting three behavioral experiments on Chinese participants. In Experiment 1, we tested whether exposing to situational disease primes leads to an exaggerated ingroup derogation attitude by adopting a more rigorous control. In Experiment 2, we manipulated the source of disease threats to test whether the ingroup derogation mechanism adjusts its response according to the specific perceived vulnerabilities to the disease threats posed by ingroup and outgroup members. In Experiment 3, we tested whether recent illness promotes the expression of ingroup derogation attitudes. Results of the three experiments consistently showed that, the Chinese participants adjusted their ingroup derogation attitudes according to the external environmental disease cues (Experiments 1 and 2) and the internal physiological disease cues (Experiment 3). The results also showed that the ingroup derogation mechanism was sensitive to the specific perceived vulnerabilities to the ingroup disease threat and the outgroup disease threat (Experiment 2). Taken together, these results support the evolutionary hypothesis of ingroup derogation and suggest that the ingroup derogation found in East Asian cultures could be accounted by a functionally flexible disease-avoidance mechanism.

Keywords: ingroup derogation, behavioral immune system, disease threat, smoke detection principle, functional flexibility principle

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INTRODUCTION

In the long history of human species, group living is essential to one's reproductive fitness. To simplify the social world's complex structure, people regularly parse the social world into "us" and "them" (Hewstone et al., 2002). They usually display a systematic tendency to favor one's own membership group (the ingroup) over a non-membership group (the outgroup) (Hewstone et al., 2002). This bias is referred as ingroup favoritism (or ingroup bias) in social psychology. It can be found among the actual social groups in which there are real differentiations between "us" and "them" (Sosis and Ruffle, 2003; Whitt and Wilson, 2007; Rand et al., 2009; Petersen, 2017). It also can be found among the artificial minimal social groups (i.e., by using minimal group paradigm) in which only a heuristic cue of the differentiation between "us" and "them" is provided (Tajfel et al., 1971; Brewer, 1979; Bernstein et al., 2007; Paladino and Castelli, 2008; Montalan et al., 2012; Makhanova et al., 2015).

Although the mainstream psychology has documented the universal tendency of ingroup favoritism, a similar but completely opposite phenomenon of ingroup derogation (or sometimes be referred as outgroup favoritism) has also been reported. That is, some participants were found to show a preference for outgroup members relative to ones' ingroup members (Jost et al., 2002; Ma-Kellams et al., 2011; Zhao et al., 2012; Liu et al., 2015; March and Graham, 2015; Wu et al., 2015, 2016; Barker and Barclay, 2016; Zuo et al., 2018; Bettache et al., 2019). This counterintuitive bias was initially found in minorities or inferior social groups (Allport, 1958; Jost et al., 2002; Livingston, 2002; Rudman et al., 2002; Ashburn-Nardo et al., 2003; Umphress et al., 2008; March and Graham, 2015; Axt et al., 2018). Studies also revealed that participants rated the deviant ingroup members more negatively compared with their outgroup counterparts (i.e., the black sheep effect; see Marques et al., 1988; Reese et al., 2013; Kunstman et al., 2016; Bettache et al., 2019). In addition, studies also showed that, in East Asian cultures, even though the participants were not minorities or deviants, they still seemed to possess a general, status irrelevant, and pervasive negative posture toward ingroup members (Jahoda et al., 1972; Hewstone and Ward, 1985; Lee and Ottati, 1993, 1995; Diener et al., 1995; Heine and Lehman, 1997; Endo et al., 2000; Snibbe et al., 2003; Cuddy et al., 2009; Ma-Kellams et al., 2011; Zhao et al., 2012; Liu et al., 2015; Wu et al., 2015, 2016; Zuo et al., 2018; Xie et al., 2019). For example, researchers found that the Chinese implicitly associated Westerners with more positive traits and more civilized behaviors than their own ethnic group members (Ma-Kellams et al., 2011; Liu et al., 2015), and they were more prone to make outgroup-favoring and ingroup-disfavoring attributions (Hewstone and Ward, 1985). It was also reported that the Chinese perceived the faces and names of outgroup members as more beautiful and better (Zhao et al., 2012; Wu et al., 2016), and were more inclined to cooperate with outgroup members (Wu et al., 2015, 2016), when actually both the ingroup and outgroup members were having the same neutral average looks.

Few studies have examined the causal origins of ingroup derogation. Researchers found that it was difficult to explain ingroup derogation in terms of proximate cause (Ma-Kellams et al., 2011; Zhao et al., 2012; Wu et al., 2015, 2016). In addition, the existence of ingroup derogation is also a paradox in an evolutionary sense (Wu et al., 2015, 2016). Individuals who preferred ingroups should have been favored by natural selection, whereas individuals displaying ingroup disfavoring tendencies should be eliminated from the gene pool over time (Brewer, 2007; Fincher and Thornhill, 2008a,b, 2012a,b; Van Vugt and Park, 2009; Schaller and Murray, 2010; Neuberg et al., 2011; Schaller and Neuberg, 2012; Thornhill and Fincher, 2014; Neuberg and Schaller, 2016; Ji et al., 2019). Thus, from an evolutionary perspective, preference for outgroup members should be considered as a maladaptation, which makes it difficult of explain the prevalence and persistence of ingroup derogation.

Behavioral Immune System and Ingroup Derogation

The behavioral immune system is composed of mechanisms that evolved as a means of inhibiting contact with disease-causing parasites and facilitating behaviors that minimized infection risk and enhanced fitness (Schaller and Neuberg, 2012; Schaller et al., 2015; Murray and Schaller, 2016). Recent studies have demonstrated that this system has unique consequences for many aspects of human social cognition and behaviors (Fincher and Thornhill, 2008a,b, 2012a,b; Van Vugt and Park, 2009; Schaller and Murray, 2010; Neuberg et al., 2011; Schaller and Neuberg, 2012; Thornhill and Fincher, 2014; Schaller et al., 2015; Murray and Schaller, 2016; Neuberg and Schaller, 2016; Bonin et al., 2019; Mullett et al., 2019). One of the main impacts of the behavioral immune system is its involvement in the emergence of the ubiquitous tendency of ingroup favoritism. Researchers proposed that, since the physiological immune system of an organism is primarily shaped by the local pathogen ecology, the outgroup members may often harbor the novel pathogens that are infectious to an individual and its immunologically similar ingroup members (Fincher and Thornhill, 2008a,b, 2012a,b; Schaller and Murray, 2010; Thornhill and Fincher, 2014). Therefore, under ecological conditions of high disease stress, a psychological mechanism facilitating the aggregation of ingroup members but inhibiting contacts with outgroup members is adaptive for its functional value of avoiding novel pathogens and minimizing local infectious risks and thus should be favored by natural selection[1] (Fincher and Thornhill, 2008a,b, 2012a,b; Van Vugt and Park, 2009; Schaller and Murray, 2010; Neuberg et al., 2011; Schaller and Neuberg, 2012; Thornhill and Fincher, 2014; Schaller et al., 2015; Murray and Schaller, 2016; Neuberg and Schaller, 2016; Ji et al., 2019; Zakrzewska et al., 2019).

Not only the ingroup favoritism can be explained by the functionality of behavioral immune system, but also the existence of ingroup derogation is possible to be accounted by the system's pathogen defense function. Recently, researchers proposed a novel evolutionary hypothesis to explain the general ingroup derogation tendency found in East Asian cultures (Wu et al., 2015). Specifically, it was proposed that the assumption of the disease threat posed by outgroup members was much greater than the disease threat posed by ingroup members is problematic. For example, if there are outbreaks of some emerging diseases in the local habitat of ingroup members, or somehow the pathogen load within the local habitat of ingroup members become much higher than the pathogen load within the local habitat of outgroup members (such as environmental change), it would be much more easier to catch an infectious disease *via* an ingroup member than *via* an outgroup member. Under such circumstances, it would be more adaptive to derogate, to dislike, and to avoid ingroup members than to bond with them. If such situations did occur recurrently in the evolutionary

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[1] Some of the studies on ingroup favoritism mainly focused on the aspect of outgroup negativity, whereas some of the studies mainly focused on the aspect of ingroup preference. To simplify the discussion, in the present research, we call all these related phenomena as ingroup favoritism.

history of the human race, a psychological mechanism that facilitates ingroup derogation responses under particular ecological conditions should be favored by nature selection. Thus, this hypothesis suggests that the East Asians derogate their ingroups because they are responding to heuristic cues indicating the disease threat incurred by the ingroup members has become stronger than the disease threat incurred by the outgroup members (Wu et al., 2015).

Some indirect evidence suggests that this hypothesis could be supported. For example, besides being an area where ingroup derogation attitudes are prevalent (Ma-Kellams et al., 2011; Zhao et al., 2012; Liu et al., 2015; Wu et al., 2015, 2016; Zuo et al., 2018), evidence also indicates that China may have higher pathogen prevalence than other areas (e.g., Europe) by both historical and contemporary measures (Fincher et al., 2008; Chang et al., 2011). Theoretical works also suggest that in face of high pathogen load, ingroup investment is not optimal and thus should be reduced (Thornhill and Fincher, 2014), and they also suggest that individuals may prefer to cooperate with outgroup members instead of ingroup members if the infection risk associated with outgroup members is low (Brown et al., 2016) or when the infection risk associated with ingroup members is high (Hu et al., 2018). Consistent with these theoretical works, empirical studies also reported that the associations between pathogen load and ingroup favoritism attitudes were found to be inconsistent or to be none. Studies also revealed that the relationship between these two variables is better to be described by a quadratic function than by a simple linear model (i.e., the ingroup favoritism drops when the pathogen load rises to a certain level; e.g., Fincher and Thornhill, 2012a,b; Cashdan and Steele, 2013; Hruschka and Henrich, 2013; Talhelm et al., 2014). Studies on generalized social trust also revealed that both the ingroup trust and outgroup trust are negatively associated with local pathogen load (Aarøe et al., 2016), and the outgroup trust actually rises when the local pathogen load exceeds a certain threshold (Zhang, 2018).

Direct evidence for this hypothesis also has been obtained. Researchers found that mere social categorization alone is already sufficient to elicit ingroup derogation among Chinese participants, which suggests that ingroup derogation follows the smoke detector principle of behavioral immune system (i.e., the behavioral immune system responds to heuristic cues which imply the presence of diseases and thus is prone to make false-positive errors; Wu et al., 2015, 2016). In addition, they also found that the ingroup derogation attitude was positively associated with the perceived vulnerability to diseases, and such an intergroup bias was found to be exaggerated if there were diseases cues in the immediate environment (Wu et al., 2015). Further evidence indicates that the positive correlation between the perceived vulnerability to diseases and ingroup derogation among mainland Chinese was mainly driven by the negative correlation between ingroup attitude and perceived vulnerability to diseases, and the results also showed that the Chinese participants responded more strongly to the diseases cues mediated by ingroup members rather than to the diseases cues mediated by outgroup members (Wu et al., 2015). These results suggest that the ingroup derogation follows the functional flexibility principle of behavioral immune system (i.e., under circumstances in which individuals are easy to be infected or merely perceive themselves to be vulnerable to infection, the activation of behavioral immune system is stronger; Van Vugt and Park, 2009; Schaller et al., 2015; Murray and Schaller, 2016). Taken together, these results suggest that the ingroup derogation in East Asian cultures is related to a specialized response of behavioral immune system and it is designed to deal with a special ecological condition in which the greater threat of diseases is incurred by ingroup members (instead of by outgroup members).

The Current Study

Although the current evidence seems to be consistent with the evolutionary hypothesis of ingroup derogation, it is still necessary to be cautious and consider the evidence as preliminary. Specifically, there are three major limitations in the current evidence concerning the functional flexibility of ingroup derogation (Wu et al., 2015). First, the functional flexibility principle dictates that the behavioral immune system should be sensitive to individuals' apparent vulnerability to pathogen threat and modulates the threat-minimizing responses accordingly (Van Vugt and Park, 2009; Schaller et al., 2015; Murray and Schaller, 2016). Therefore, as an evolved response, the ingroup derogation attitude should be adjusted according to external disease cues (Wu et al., 2015). However, until now, researchers had only examined the effects of pathogen threat on ingroup derogation attitudes by employing a no-threat control (Wu et al., 2015). This was not rigorous enough to completely rule out other plausible explanations. For example, it is possible that the observed effects of pathogen threat were actually caused by the byproduct of unspecific emotional arousal. Second, in the study of Wu et al. (2015), researchers had only investigated the functional flexibility of ingroup derogation under situations in which the relative risk of infection between ingroup and outgroup was fixated. However, if ingroup derogation is indeed an evolved response of the behavioral immune system, the ingroup derogation mechanism should be able to adjust its responses according to the specific perceived vulnerabilities to the ingroup disease threat and the outgroup disease threat. Third, the activation of the behavioral immune system has been shown to be closely related to the biological immune system (Murray et al., 2019). If ingroup derogation is indeed a functionally flexible response of the behavioral immune system, the ingroup derogation attitude should not only be adjusted when there were external disease cues. It also should be more exaggerated when the biological immune system is inhibited since such a condition indicates a heightened susceptibility to diseases (Miller and Maner, 2011; Lund and Miller, 2014; Kandrik et al., 2017; Oaten et al., 2017; Gassen et al., 2018; Bradshaw et al., 2019; Murray et al., 2019). However, this important feature of ingroup derogation tendency has not been investigated in the previous study (Wu et al., 2015) in which the researchers had only examined the roles of subjective and situational disease cues in the expression of ingroup derogation.

To address these limitations, we conducted three experiments in the current study to further investigate the functional flexibility of ingroup derogation. We mainly focused on the ingroup derogation among mainland Chinese. In Experiment 1, we tested whether exposing to a situational disease prime leads to an exaggerated ingroup derogation attitude by adopting a more rigorous control. In Experiment 2, we manipulated the source of disease threat to test whether the ingroup derogation mechanism can adjust its response according to the specific perceived vulnerabilities to the different disease threats posed by ingroup and outgroup members. Since being recently ill temporarily lowers the physiological immune function and consequently activates the behavioral immune system (Miller and Maner, 2011; Lund and Miller, 2014; Kandrik et al., 2017; Oaten et al., 2017; Murray et al., 2019), we also tested whether recent illness promotes the expression of ingroup derogation attitudes in Experiment 3.

According to the evolutionary hypothesis of ingroup derogation, mere social categorization alone – a heuristic cue that implies the differentiation between "us" and "them" – should be sufficient to bring the bias of ingroup derogation (i.e., smoke detector principle; e.g., Wu et al., 2015, 2016). As a wide-accepted paradigm to study intergroup bias in the laboratory, the minimal group paradigm categorizes people into arbitrary social categories or groups, such as whether they have a "red" personality type or a "green" personality type based on bogus personality tests, which provides group-categorization heuristics to one's actual social group membership (Tajfel et al., 1971; Brewer, 1979; Bernstein et al., 2007; Paladino and Castelli, 2008; Makhanova et al., 2015; Wu et al., 2015, 2016). Studies employing this paradigm have shown strong cognitive, motivational, and behavioral differences in responses to these arbitrarily constructed ingroups and outgroups[2], which were very similar to the responses elicited by actual social groups (e.g., Tajfel et al., 1971; Brewer, 1979; Bernstein et al., 2007; Paladino and Castelli, 2008; Makhanova et al., 2015; Wu et al., 2015, 2016; Zuo et al., 2018; Dang et al., 2019). Therefore, following the studies of Wu et al. (2015) and Wu et al. (2016), we also employed the minimal group paradigm to elicit the ingroup derogation phenomenon.

Studies on ingroup favoritism have shown that participants incline to affiliate to and cooperate with their ingroup members (Sosis and Ruffle, 2003; Ruffle and Sosis, 2006; Whitt and Wilson, 2007; Rand et al., 2009; Van Vugt and Park, 2009; Yamagishi and Mifune, 2009; Neuberg et al., 2011; Schaller and Neuberg, 2012; Fincher and Thornhill, 2012a,b), while studies of ingroup derogation found the reversed patterns. For example, it was reported that the mainland Chinese were more inclined to cooperate with outgroup members if they were asked to choose their partners based on the facial information and group membership, while actually both the ingroup and outgroup members were having the same neutral average looks (Wu et al., 2015, 2016). Following these studies, we used the degree of acceptance (i.e., acceptance of a specific group member as a partner to work with) as the measure of participants' preference for a specific group membership in the present study. If the participants were more inclined to work with outgroup members, then they harbored an ingroup derogation attitude. If the pattern was reversed, then they displayed an ingroup favoritism attitude (for same measures of intergroup bias, see Navarrete and Fessler, 2006; Wu et al., 2015, 2016).

EXPERIMENT 1

As a specialized response of behavioral immune system, the ingroup derogation mechanism should follow the functional flexibility principle. This means that the activation of ingroup derogation mechanism should be promoted when there are cues of diseases in the immediate environment. The previous study (Wu et al., 2015) has shown that Chinese participants displayed more exaggerated ingroup derogation attitudes when they were placed in a disease environment (i.e., finishing the experiment with a very dirty keyboard) or when the ingroup and outgroup members were both displaying the cues of diseases. However, researchers had only compared the effects of pathogen threat to a no-threat control in the previous study (Wu et al., 2015). This kind of control is not rigorous enough to completely rule out other alternative explanations. For example, the effects of pathogen threat found by Wu et al. (2015) might actually be caused by the high arousal state created by pathogen threat rather than by the specific disease features of pathogen threat. It is also possible that the ingroup derogation mechanism is nonspecifically responding to all kinds of threats rather than specifically responding to the disease threat. To rule out these possibilities, we extended and replicated the study of Wu et al. (2015) by adopting a more rigorous control in Experiment 1. Specifically, following prior research (Park et al., 2007; Miller and Maner, 2012; Wu and Chang, 2012; Lund and Miller, 2014; Makhanova et al., 2015; Nussinson et al., 2018; Wang and Ackerman, 2019), we experimentally primed Chinese participants with either disease-connoting images or images of non-disease-related threats. Consistent with previous studies on ingroup derogation (Zhao et al., 2012; Wu et al., 2015, 2016), we measured the ingroup derogation attitudes of Chinese participants by asking them to finish a face appraisal task in which only the facial information and group membership were provided. Given that Chinese participants were responding to a special ecological condition in which the greater threat of disease was posed by ingroup members, immediate disease cues in the environment should elicit more avoidance responses to ingroup members than to outgroup members in these participants. Therefore, we predicted that, compared with the non-disease-threat priming, Chinese participants should exaggerate their ingroup derogation attitudes after the disease prime even when the overall affective valence and arousal were well matched between the two different priming conditions.

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[2] In the minimal group paradigm, the targets who belong to the same assigned category of participants are called ingroup members, whereas the targets who do not belong to that category are called outgroup members (Tajfel et al., 1971; Brewer, 1979; Bernstein et al., 2007; Paladino and Castelli, 2008; Montalan et al., 2012; Makhanova et al., 2015).

Method

Participants and Design

G*Power Version 3.1.9.2 software (Faul et al., 2009) was used to acquire an *a priori* estimate of the required sample size. Using the parameters (power = 0.99, effect size f = 0.21[3], $\alpha = 0.05$; Richard et al., 2003) and giving the current experimental design, the analysis estimated a sample size of 108. We finally recruited a total of 120 Chinese undergraduate or postgraduate students (60 males and 60 females, aged 18–25 years). Sensitivity power analysis indicated that, the minimal detectable effect (power = 0.99) for this sample size is $f = 0.197$. This experiment was carried out in accordance with the recommendations of the IRB of the Institute of Psychology, Hunan Normal University, with written informed consent from all participants. All participants gave written informed consent in accordance with the Declaration of Helsinki. The protocol was approved by the IRB of the Institute of Psychology, Hunan Normal University.

A 2 (category label: ingroup, outgroup) × 2 (priming condition: disease prime, control) mixed-model experimental design was used, with priming condition being the between-subjects factor and category label being the within-subjects factor.

Materials and Procedure

Following previous studies (Bernstein et al., 2007; Paladino and Castelli, 2008; Makhanova et al., 2015; Wu et al., 2015, 2016), a bogus personality test was employed to create the minimal groups. This test consisted of 40 questions taken from the Eyesenck Personality Questionnaire (Eysenck and Eyesenck, 1975). The computer ostensibly analyzed participants' responses and then randomly informed the participants that they had either a "red" or "green" personality type. Participants were then told that each personality type was not necessarily better than the other personality type and the purpose of this experiment was to investigate psychological differences between these two different personality types. Given no further explanation, participants were given a green or red identity tag to wear, and told it was to identify their particular personality type (see Wu et al., 2015, 2016, for the same procedure).

Eighty gray-scale facial images of Chinese adults displaying neutral facial expressions were chosen as the stimuli (directly adopted from Zhao et al., 2012). These images were completely novel to all participants and they consisted of two image sets (with 40 faces in each set) which were matched on the degrees of beauty (all were average looking faces; Zhao et al., 2012) and acceptance (Wu et al., 2015). The facial stimuli were presented in the same way as in Wu et al. (2015) and Wu et al. (2016). Each face was presented in the center of the screen and a label of personality type (red or green) was placed at the top of the background in order to label the face. The background color of the screen was set to be identical to the personality label (red or green). These two image sets were counterbalanced across background color (and its personality label) on a between-subjects basis. Thus, each image set has an equal probability of being labeled as ingroup or outgroup members.

Participants were randomly assigned either to a disease priming condition or to a control condition. Participants in each condition were instructed that they would take a computerized personality test at first. Then, they were told that they were going to complete another unrelated task before completing the "formal experiment." Following prior researches (Park et al., 2007; Miller and Maner, 2012; Wu and Chang, 2012; Lund and Miller, 2014; Makhanova et al., 2015; Nussinson et al., 2018; Wang and Ackerman, 2019), participants in the disease priming condition watched a slideshow consisting of 10 images that portrayed information about germs, infections, and other diseases. Participants in the control condition watched a slideshow of 10 images portraying information about common accidents and hazards (e.g., car accidents, air crash) that were non-disease related threats. Each image was shown for 6 s and participants were asked to watch closely to answer questions about them. Each participant was asked to use 9-point scales to rate the valence (1 = "very unpleasant" and 9 = "very pleasant") and arousal (1 = "very calming" and 9 = "very arousing") of his/her current emotional state after slide watching. Then, participants were told that they had to complete the "formal experiment" which was a face appraisal task. Participants were instructed that they would view faces on the screen, and that the background color and the label displayed on the top of the screen would denote the target's personality type. Their task was to rate "to what extent would you want to work together with the person shown on the screen in the next experiment" on an 8-point scale (1 = "definitely not" to 8 = "definitely like to") for these faces. The faces were presented one at a time, and each face remained on the screen until the response was made. Faces were randomly presented for each participant.

Results and Discussion

Independent t-tests showed that there were no significant differences between the two priming conditions for the overall affective valence [disease prime: $M = 1.85$, SD = 1; control: $M = 2.12$, SD = 1.12; $t(118) = -1.37$, $p = 0.17$] and arousal [disease prime: $M = 6.57$, SD = 1.59; control: $M = 6.2$, SD = 1.15; $t(107.39) = 1.45$, $p = 0.15$]. Thus, the manipulation was successful at creating intended differences in threat contents but without creating differences in overall affect.

A 2 (category label) × 2 (priming condition) mixed model analysis of variance (ANOVA) on rating scores of face appraisal task showed that the main effect of category label was significant [$F(1, 118) = 61.95$, $p < 0.001$, $\eta_p^2 = 0.344$], and the main effect of priming condition [$F(1, 118) = 20.88$, $p < 0.001$, $\eta_p^2 = 0.15$] and the interaction between category label and priming condition [$F(1, 118) = 8.37$, $p = 0.005$, $\eta_p^2 = 0.07$] were significant. Simple effects analysis showed that participants under all priming conditions were consistently more inclined to affiliate with outgroup members than with ingroup members [disease prime: $F(1, 118) = 57.93$, $p < 0.001$, $\eta_p^2 = 0.33$; control: $F(1, 118) = 12.39$, $p = 0.001$, $\eta_p^2 = 0.1$] (see **Figure 1**). It also revealed that participants in the disease prime condition showed less favorable attitudes toward both ingroup [$F(1, 118) = 30.61$, $p < 0.001$, $\eta_p^2 = 0.21$] and outgroup [$F(1, 118) = 8.84$, $p = 0.004$, $\eta_p^2 = 0.07$] members than participants in the control condition (see **Figure 1**).

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[3] We employed the mean effect size in social psychology (Richard et al., 2003) as our estimation of effect size.

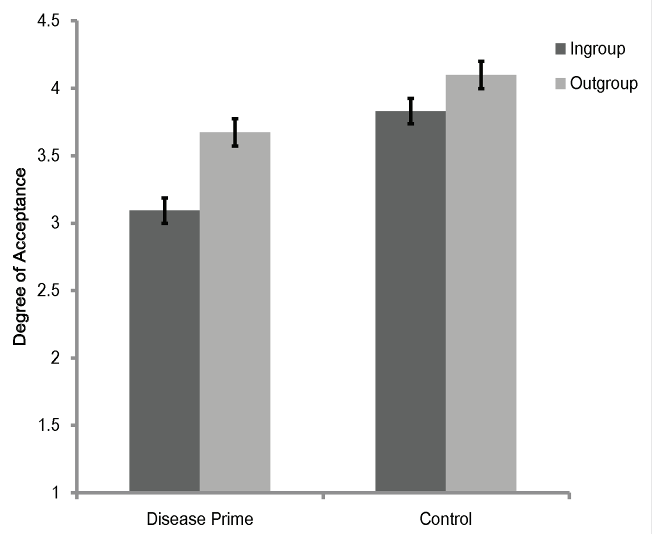

FIGURE 1 | Degree of acceptance of faces labeled as ingroup members and outgroup members in Experiment 1. Error bars represent standard errors.

To further illustrate the interaction between category label and priming condition, rating scores of outgroup members in the face appraisal task were subtracted by that scores of ingroup members to create a composite score of ingroup derogation, and we subjected this score to a one-way ANOVA (with the priming condition being the independent variable). The results showed that the main effect of priming condition was significant [$F(1, 118) = 8.37$, $p = 0.005$, $\eta_p^2 = 0.07$], with participants showing more ingroup derogation attitudes in the disease prime condition ($M = 0.58$, SD = 0.63) than in the control condition ($M = 0.27$, SD = 0.55).

In sum, by adopting more a rigorous control, Experiment 1 replicated the results of previous studies of ingroup derogation (e.g., Zhao et al., 2012; Wu et al., 2015, 2016). These results of Experiment 1 indicated that, compared with a non-disease-threat prime, participants displayed stronger ingroup derogation attitude after a disease prime even with the overall affective valence or arousal was well controlled, and this effect was caused by the more exaggerated ingroup avoiding responses. They suggest that ingroup derogation mechanism is a mechanism that responds exclusively to the threat of disease and thus support the hypothesis that ingroup derogation found in East Asian cultures is an evolved response of the behavioral immune system.

EXPERIMENT 2

The ingroup derogation mechanism should not be a simple and rigid mechanism that can only be more activated when there are cues of diseases in the immediate environment (as shown in Experiment 1). As a flexible mechanism, it has to be sensitive to the specific perceived vulnerabilities to ingroup/outgroup disease threats to better adjust to the changing benefits and costs associated with approaching/avoiding the ingroup or outgroup members. Therefore, to facilitate the ingroup avoiding response, the ingroup derogation attitude should become more exaggerated when there are cues of diseases indicating that the ingroup members are infectious, whereas a reversed pattern should be observed when the environmental cues indicate that the outgroup members are very infectious. These possibilities were tested in Experiment 2. Specifically, we predicted that the Chinese participants would exaggerate their ingroup derogation attitudes after watching a disease prime in which the ingroup members are depicted as infectious (compared with a disease-related control prime), whereas participants receiving a disease prime which depicts the outgroup members as infectious should reduce their ingroup derogation attitudes accordingly.

Method

Participants and Design

G*Power Version 3.1.9.2 software (Faul et al., 2009) was used to acquire an *a priori* estimate of the required sample size. Using the parameters (power = 0.95, effect size $f = 0.21$, $\alpha = 0.05$; Richard et al., 2003) and giving the current experimental design, the analysis estimated a sample size of 93. We finally recruited a total of 90 Chinese undergraduate students (46 males and 44 females, aged 18–22 years). Sensitivity power analysis indicated that, the minimal detectable effect (power = 0.95) for this sample size is $f = 0.21$. This experiment was carried out in accordance with the recommendations of the IRB of the Institute of Psychology, Hunan Normal University, with written informed consent from all participants. All participants gave written informed consent in accordance with the Declaration of Helsinki. The protocol was approved by the IRB of the Institute of Psychology, Hunan Normal University.

A 2 (category label: ingroup, outgroup) × 3 (disease prime condition: ingroup disease prime, outgroup disease prime, control) mixed-model experimental design was used, with disease prime condition being the between-subjects factor and category label being the within-subjects factor.

Materials and Procedure

Participants were randomly assigned to one of the three disease prime conditions. Then participants were instructed to finish a bogus personality test (as described in Experiment 1) in order to create the minimal groups. After that, participants were instructed that they were going to complete another unrelated task before completing the "formal experiment." Specifically, participants were instructed that they would view several medical cases and they had to watch closely in order to answer several questions about these cases after finishing the "formal experiment." Participants in the ingroup and outgroup disease prime conditions were further instructed that these medical cases were selected from the persons that were identical to (ingroup disease prime condition) or opposite to (outgroup disease prime condition) their own personality type. They were also told that the background color of the screen and the label displayed on the top of the screen would denote the personality type of the target person. Then, participants under all disease prime conditions directly watched the corresponding disease primes.

In the control condition, the disease-related control prime consisted of eight slides displaying images of Chinese adults (half of the targets were male, while the other half were female) who were infected with skin diseases (e.g., herpes, scabies, tinea corporis). The images within each slide consisted of one facial image (with a neutral facial expression) of the target person and one image of the infected part of the target's body. The images were placed on the upper half of the screen, with the facial image being placed on the left and the image of the infected part being placed on the right. The background of the slide was set to be gray, and a paragraph of text was placed on the bottom of screen to describe the target's symptoms. Twenty participants who did not participate in the formal experiment rated the contents of these disease primes. They had to rate that whether these slides portrayed relevant information about disease threat, sexual activity, and other threats (i.e., aggression, deception, and natural disaster) on 7-point scales (−3 = "definitely not," 0 = "I'm not sure," 3 = "definitely yes"). One sample *t*-test showed that the disease prime in control condition clearly conveyed information about diseases ($M = 2.76$, SD = 0.33), $t(19) = 37$, $p < 0.001$, but they did not contain relevant information about sexual activity ($M = -2.73$, SD = 0.5), $t(19) = -24.25$, $p < 0.001$, and other threats ($M = -2.61$, SD = 0.43), $t(19) = -27$, $p < 0.001$. The contents of disease primes under ingroup and outgroup disease prime conditions were identical to those in control condition, but with the background color being set to be identical (ingroup disease prime) or opposite (outgroup disease prime) to the color of the participant's assigned personality type (red or green). A label (red personality type or green personality type) which was identical to the background color was placed on the top of the slide in order label the target person depicted in the slide. Each slide was presented for 20 s under all disease prime conditions.

After the disease threat priming, participants were asked to finish the "formal experiment" which was a face appraisal task (as described in Experiment 1). Facial images of the target persons in the disease primes were not included in the 80 facial stimuli (as described in Experiment 1) of the face appraisal task.

Results and Discussion

Rating scores for ingroup and outgroup members were subjected to a 2 (category label) × 3 (disease prime condition) mixed-model ANOVA. The results showed that the main effect of category label [$F(1, 87) = 13.03$, $p = 0.001$, $\eta_p^2 = 0.13$] and the interaction between category label and disease prime condition [$F(1, 87) = 13.86$, $p < 0.001$, $\eta_p^2 = 0.24$] were significant. The main effect of disease prime condition was not significant [$F(2, 87) = 0.17$, $p = 0.84$, $\eta_p^2 = 0.004$]. Further simple effects analysis showed that participants in the ingroup disease prime condition [$F(1, 87) = 33.64$, $p < 0.001$, $\eta_p^2 = 0.28$] and participants in the control condition [$F(1, 87) = 4.4$, $p = 0.04$, $\eta_p^2 = 0.05$] were more inclined to affiliate with outgroup members than with ingroup members, but there were no significant differences between the ingroup and outgroup attitudes [$F(1, 87) = 2.7$, $p = 0.1$, $\eta_p^2 = 0.03$] for participants under the outgroup disease prime condition (see **Figure 2**). The results also showed that

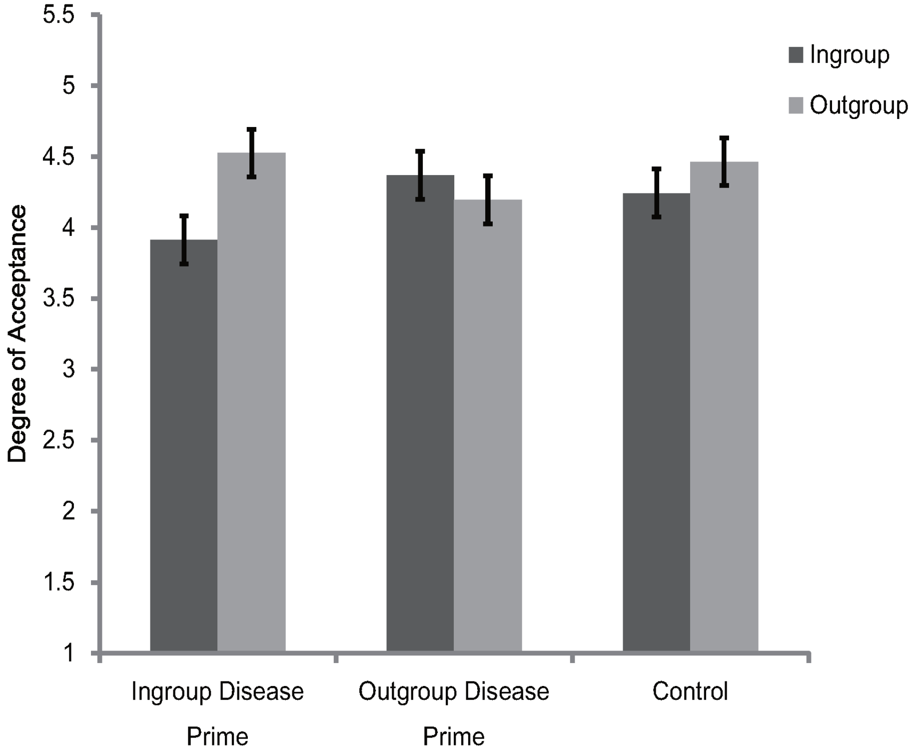

FIGURE 2 | Degree of acceptance of faces labeled as ingroup members and outgroup members in Experiment 2. Error bars represent standard errors.

the effects of disease prime condition were not significant for ingroup members [$F(2, 87) = 1.93$, $p = 0.15$, $\eta_p^2 = 0.04$] and outgroup members [$F(2, 87) = 1.1$, $p = 0.34$, $\eta_p^2 = 0.03$].

To further illustrate the interaction between category label and disease prime condition, an ingroup derogation score (as described in Experiment 1) was created. The one-way ANOVA showed that the differences of ingroup derogation scores among the three disease prime conditions were significant [$F(1, 87) = 13.86$, $p < 0.001$, $\eta_p^2 = 0.24$]. Further *post hoc* comparisons (Bonferroni) showed that, participants in the ingroup disease condition were more likely [$t(87) = 2.6$, $p = 0.03$] to derogate their ingroup member ($M = 0.61$, SD = 0.58) than participants in the control condition ($M = 0.22$, SD = 0.42). In addition, the results also showed that, compared with participants in the ingroup disease prime [$t(87) = 2.65$, $p = 0.03$] and control prime [$t(87) = 5.26$, $p < 0.001$] conditions, participants in the outgroup disease prime condition endorsed less ingroup derogation attitudes ($M = -0.17$, SD = 0.69).

Collectively, the results of Experiment 2 indicated that the Chinese participants exaggerated their ingroup derogation attitudes after receiving the ingroup disease prime, but the tendency of ingroup derogation was eliminated after receiving the outgroup disease prime. These results suggest that ingroup derogation is a functional flexible mechanism which can adjust its response according to the specific perceived vulnerabilities to disease threats posed by ingroup and outgroup members. These results were consistent with our prediction and thus provide support for the evolutionary hypothesis of ingroup derogation.

EXPERIMENT 3

To protect the body from severe tissue damage and facilitate the recovering from recent infections, our biological immune system produces an anti-inflammatory response after being recently sick (Mocellin et al., 2003), which temporarily inhibits the physiological defenses against new pathogens (Jakab, 1985; LeVine et al., 2001; van der Sluijs et al., 2004) and consequently promotes the activation of behavioral immune system (Miller and Maner, 2011; Lund and Miller, 2014; Kandrik et al., 2017; Oaten et al., 2017; Murray et al., 2019). Therefore, as a functionally flexible response of the behavioral immune system, the ingroup derogation attitude should not only be exaggerated when there are external cues of diseases in the immediate environment (as shown in Experiments 1 and 2). It also should be more exaggerated when the responses of the biological immune system are inhibited since such a condition indicates a heightened susceptibility to diseases. In Experiment 3, we examined whether recent illness would lead Chinese participants to exaggerate their ingroup derogation attitudes.

Method

Participants and Design

G*Power Version 3.1.9.2 software (Faul et al., 2009) was used to acquire an *a priori* estimate of the required sample size. Using the parameters (power = 0.99, effect size $f = 0.21$, $\alpha = 0.05$; Richard et al., 2003) and giving the current experimental design, the analysis estimated a sample size of 108. A total of 122 Chinese undergraduate or postgraduate students (60 males and 62 females, aged 18–24 years) were finally recruited by advertisement. Specifically, 60 participants had been sick within the previous week (recently sick), and 62 participants had not been recently sick (i.e., the last time they had been sick was more than 1 week ago). Sensitivity power analysis indicated that, the minimal detectable effect (power = 0.99) for this sample size is $f = 0.196$. This experiment was carried out in accordance with the recommendations of the IRB of the Institute of Psychology, Hunan Normal University, with written informed consent from all participants. All participants gave written informed consent in accordance with the Declaration of Helsinki. The protocol was approved by the IRB of the Institute of Psychology, Hunan Normal University.

A 2 (category label: ingroup, outgroup) × 2 (illness recency: recently sick, not recently sick) mixed-model experimental design was used in Experiment 3, with illness recency being the between-subjects factor and category label being the within-subjects factor.

Materials and Procedure

Following previous studies (Miller and Maner, 2011; Lund and Miller, 2014; Prokosch et al., 2019), participants were categorized into two groups, a recently sick group (those who reported that they had been sick within the previous week) and a not recently sick group (those who reported that the last time they had been sick was more than 1 week ago). This categorization reflects the typical window of the biological system's heightened susceptibility to new diseases after infection (Jakab, 1985; Miller and Maner, 2011; Lund and Miller, 2014; Murray et al., 2019). Participants in all groups were asked to take a bogus personality test at first and then to finish a face appraisal task. The bogus personality test which was used to create minimal groups and the face appraisal task that was employed by this experiment were identical to those of Experiment 1. After completing the face appraisal task, all participants were asked to complete the Perceived Vulnerability to Disease scale (PVD) (Duncan et al., 2009) to assess conscious concerns about disease. Participants responded to each item on a 7-point scale (with endpoints labeled "strongly disagree" and "strongly agree"). Following previous studies (e.g., Wu and Chang, 2012; Wu et al., 2015; Díaz et al., 2016; Liuzza et al., 2016), we used PVD as a single scale ($\alpha = 0.64$) in Experiment 3. Higher scores on these measures indicate greater perceived vulnerability to diseases.

Results and Discussion

The 2 (category label) × 2 (illness recency) mixed model ANOVA on the rating scores of face appraisal task indicated that the main effect of category label [$F(1, 120) = 44.82$, $p < 0.001$, $\eta_p^2 = 0.27$] and the interaction between category label and illness recency [$F(1, 120) = 6.09$, $p = 0.02$, $\eta_p^2 = 0.05$] were significant. Consistent with Experiments 1 and 2, participants of the two illness recency groups consistently preferred the outgroup members over ingroup members [recently sick: $F(1, 120) = 41.3$, $p < 0.001$, $\eta_p^2 = 0.26$; not recently sick: $F(1, 120) = 9.09$, $p = 0.003$, $\eta_p^2 = 0.07$] (see **Figure 3**). The main effect of illness recency was not significant [$F(1, 120) = 0.48$, $p = 0.49$,

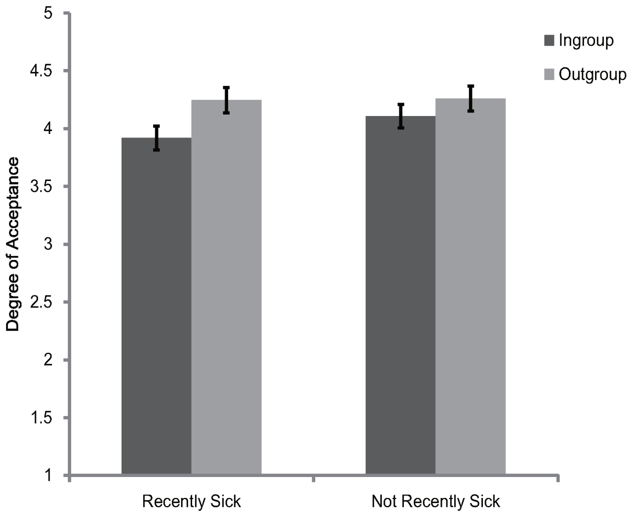

FIGURE 3 | Degree of acceptance of faces labeled as ingroup members and outgroup members in Experiment 3. Error bars represent standard errors.

η_p^2 = 0.004]. To better illustrate the interaction between category label and illness recency, the ingroup derogation score as described in Experiment 1 was created. Independent *t*-test showed, ingroup derogation attitudes were exaggerated for recently sick participants [recently sick: M = 0.33, SD = 0.35; not recently sick: M = 0.15, SD = 0.43; $t(120)$ = 2.47, p = 0.02]. Further analysis revealed that the main effect of illness recency on ingroup derogation score remained significant even after controlling for PVD [F(1, 119) = 4.77, p = 0.03, η_p^2 = 0.04]. Thus, the results of Experiment 3 indicated that recent illness was accompanied by an exaggerated ingroup derogation tendency among Chinese participants. These results suggest that during a period of heightened susceptibility to new diseases after infection, the activation of ingroup derogation attitude would become stronger, and such effect was over and above the effects of overt concerns about disease vulnerability. Consistent with previous studies (Miller and Maner, 2011; Lund and Miller, 2014; Kandrik et al., 2017; Oaten et al., 2017; Gassen et al., 2018; Bradshaw et al., 2019; Murray et al., 2019), these results also suggest that the behavioral immune system will be more activated if the biological immune system is temporarily inhibited.

GENERAL DISCUSSION

In previous studies (e.g., Jost et al., 2002; Ashburn-Nardo et al., 2003; Zhao et al., 2012; Liu et al., 2015; March and Graham, 2015; Bettache et al., 2019), researchers mainly investigated the ingroup derogation phenomenon among actual social groups. With three behavioral experiments, the present study investigated the bias of ingroup derogation by using the minimal group paradigm. Although there were no real differences between the minimal groups, and no group members were labeled as deviants, the results of the three experiments in the current study still consistently showed that the Chinese participants derogated their ingroup members when they were asked to choose their partners purely based on the facial information and group membership. These results directly replicated the results of previous studies in which the Chinese participants were also found to be more inclined to cooperate with outgroup members under the minimal group paradigm (Wu et al., 2015, 2016). Similar results were also reported by researches using other tasks under minimal group paradigm (Zuo et al., 2018; Dang et al., 2019). For example, researchers found that East Asian participants allocated more resources to the outgroup members than to ingroup members when there were intragroup competitions within the minimal groups (Zuo et al., 2018). Taken together, the results of the current study showed that mere social categorization alone was sufficient to elicit ingroup derogation among Chinese participants, indicating that the ingroup derogation follows the smoke detector principle.

As an evolved response of behavioral immune system, except for being prone to make false-positive errors, the ingroup derogation also should follow the functional flexibility principle (Wu et al., 2015). Specifically, as a special adaptation to a particular situation in which ingroup members pose more threat of diseases than outgroup members, the ingroup derogation mechanism should modulate its responses accordingly when the individuals subjectively feel vulnerable to diseases (Condition 1), when there are cues of diseases in the immediate environment (Condition 2), when the relative risk of infection between ingroup and outgroup has been changed (Condition 3), or when the responses of biological immune system to new pathogens have been inhibited (Condition 4). The previous study had partially examined the functional flexibility of ingroup derogation under Conditions 1 and 2 (Wu et al., 2015). In the current study, we further investigated the functional flexibility of ingroup derogation under the last three conditions (Conditions 2, 3, and 4). In Experiment 1, we employed a more rigorous control to investigate whether Chinese participants would exaggerate their ingroup derogation attitudes after a disease prime (i.e., Condition 2) to rule out the alternative explanations that cannot be ruled out by the study of Wu et al. (2015). The results did show that the Chinese participants endorsed more ingroup derogation attitudes after a disease prime even when the overall affective valence and arousal were well matched between the disease prime and the non-disease-related threats control prime. In Experiment 2, we tested the Condition 3 by priming the Chinese participants with disease information about different social groups. The results indicated that, Chinese participants exaggerated their ingroup derogation attitudes after being primed with ingroup disease information (compared with a disease-related control prime which conveyed disease information about individuals with unknown group membership). The results also showed that, Chinese participants eliminated their ingroup derogation attitudes after receiving the disease prime which depicted the outgroup as infectious. In Experiment 3, we tested the Condition 4 by examining whether recent illness would promote the activation of ingroup derogation since fighting off one disease temporarily inhibits the physiological defenses against new diseases and consequently promotes the activation of behavioral immune system (Miller and Maner, 2011;

Lund and Miller, 2014; Kandrik et al., 2017; Oaten et al., 2017; Murray et al., 2019). As predicted, the results showed that the ingroup derogation tendency was exacerbated when Chinese participants had been recently ill, and such effect was independent of the conscious concerns about disease. In summary, the results of the three experiments consistently indicate that the activation of ingroup derogation is related to the external disease cues (Experiments 1 and 2) and internal disease cues (Experiment 3). Collectively, these results suggest that ingroup derogation found among East Asian participants is an evolved response of behavioral immune system and it follows the functional flexibility principle.

While the previous study (Wu et al., 2015) suggests that ingroup derogation is a specialized mechanism which disregards explicit disease-relevant information mediated by outgroup members, a different pattern was observed in Experiment 2. Specifically, Experiment 2 showed that the participants eliminated their ingroup derogation attitudes after being primed with slides portraying medical cases of outgroup members. Consistent with the prediction made by previous study (Wu et al., 2015) in its discussion section (i.e., different pattern of results might be obtained if participants were separately facing the ingroup or outgroup members), the results of Experiment 2 was obtained by employing a between-subjects design in which the disease information of ingroup and outgroup members was separately presented (rather than be concurrently presented, as in Wu et al., 2015). Therefore, combined with the results of Wu et al. (2015), the results of Experiment 2 suggest that ingroup derogation is sensitive to the disease cues mediated by both ingroup and outgroup members, and they also suggest that the ingroup derogation mechanism will selectively respond to the disease cues mediated by ingroup members if the cognitive resources are getting depleted. Since the cognitive load was not manipulated either in the current study or in the study of Wu et al. (2015), this speculation still demands more investigation in the future. In addition, according to the evolutionary hypothesis of ingroup derogation, the ingroup derogation attitudes found among Chinese participants should be reversed to ingroup favoritism if the Chinese were primed with information depicting extremely strong outgroup disease threat. In Experiment 2, we only found that the ingroup derogation could be eliminated after receiving outgroup disease primes. Therefore, researchers still need to test this hypothesis by employing stronger disease threat primes. Cross-culture comparisons are also needed for a more thorough test of the evolutionary hypothesis of ingroup derogation. For example, researchers could try to prime the Western participants with ingroup disease primes to examine whether the ingroup favoritism attitudes can be reduced accordingly or be reversed to ingroup derogation attitudes.

In the previous study (Wu et al., 2015), researchers mainly focused on the effects of contextual cues. The current results provided the first empirical evidence for the hypothesis that temporary inhibition of the biological immune system facilitates the activation of ingroup derogation mechanism (as shown in Experiment 3). Recent studies have shown that the biological immune system and the behavioral immune system are connected on the cellular level, such as through the signals of proinflammatory cytokines (Il-6, Il-1β, and TNF-α), white cells, and stress and sex hormones (Kandrik et al., 2017; Gassen et al., 2018; Bradshaw et al., 2019; Murray et al., 2019). However, the current study was not designed to answer questions about the specific physiological mechanisms linking the biological immune system and the ingroup derogation mechanism. In addition, although we ruled out the effects of conscious disease concerns, we did not directly investigate the potential role of nonconscious goals. To clarify the biological and psychological processes mediating the link between the biological immune system and ingroup derogation, future research should address these limitations.

As a functionally coherent disease defense mechanism, the behavioral immune system can generate a series of consistent changes in down-stream perceptual, affective, cognitive, and behavioral processes (Schaller and Neuberg, 2012; Schaller et al., 2015; Murray and Schaller, 2016). Although previous studies have investigated the ingroup derogation phenomenon in East Asian cultures by using many different tasks, such as the face perception task (Jahoda et al., 1972; Zhao et al., 2012; Wu et al., 2016), emotion judgment task (Wu et al., 2016; Xie et al., 2019), memory task (Zhao et al., 2012), trait rating task (Ma-Kellams et al., 2011; Liu et al., 2015), attribution task (Hewstone and Ward, 1985), cooperation and allocation task (Wu et al., 2015, 2016; Zuo et al., 2018; Dang et al., 2019), etc., the current study had only examined the effects of infectious disease on ingroup derogation attitude in the domain of cooperation. If ingroup derogation is indeed an evolutionarily based disease defense mechanism, its activation should result in other functionally related changes, such as altered attention and avoidance response to threat-related targets (e.g., Miller and Maner, 2011). These questions demand further investigations in the future. In addition, in the current study, we mainly examined the effects of infectious disease on artificially constructed minimal groups. To thoroughly test the evolutionary hypothesis of ingroup derogation, we also have to examine these effects on natural social groups.

While the results of the current study suggest a potential link between disease threat and ingroup derogation in East-Asian cultures, the exact mechanisms that account for this link have not been identified by the present research. Although Experiment 2 showed that ingroup derogation could be modulated by specific environmental cues and thus it suggests that ingroup derogation is caused by the differential activation of functionally flexible neurocognitive mechanisms, other possible mechanisms still demand investigation (e.g., differential genetic selection and differential developmental trajectories). In addition, since the present studies only intended to offer an ultimate explanation for the ingroup derogation phenomenon, they are not able to offer any explanations in terms of proximate cause. It is entirely possible that the differential activation of behavioral immune system is proximately accomplished through the differential cultural transmission of learned behaviors (Chang et al., 2011; Scott-Phillips et al., 2011; Lewis et al., 2017).

Currently, the only plausible proximate explanation for the ingroup derogation phenomenon found in East Asian cultures is the dialectic theory in which researchers proposed that individuals with East Asian culture background are inclined to appraise both bad and good for the same object (Ma-Kellams et al., 2011). However, this theory can only explain why the criteria of appraisal for East Asians are stricter, but it cannot explain why East Asian participants still derogated their ingroup members when they held the same dialectical belief toward both ingroup and outgroup members (Zhao et al., 2012; Wu et al., 2015, 2016). Can other cultural-specific factors (e.g., different value emphases, different social relationships; for review, see Chang et al., 2011) mediate or moderate the relationship between disease threat and ingroup derogation? Researchers should look into this question in the future. In addition, it should also be noted that while we mainly investigated the ingroup derogation phenomenon among mainland Chinese participants, the current findings are not directly applicable to the ingroup derogation found in minority groups (e.g., Allport, 1958; Jost et al., 2002; Livingston, 2002; Rudman et al., 2002; Ashburn-Nardo et al., 2003; Umphress et al., 2008; March and Graham, 2015; Axt et al., 2018) or to the ingroup derogation found against deviant ingroup members (Marques et al., 1988; Kunstman et al., 2016; Bettache et al., 2019). Although the theory of behavioral immune system may offer the ultimate explanation for the black sheep effect, explaining the ingroup derogation found in socially disadvantaged groups would be another story (e.g., Wu et al., 2015, 2016).

Previous studies on ingroup favoritism mainly support the theory that ingroup favoritism is an adaptive response from the behavioral immune system (Fincher and Thornhill, 2008a,b, 2012a,b; Van Vugt and Park, 2009; Schaller and Murray, 2010; Neuberg et al., 2011; Schaller and Neuberg, 2012; Thornhill and Fincher, 2014; Schaller et al., 2015; Murray and Schaller, 2016; Neuberg and Schaller, 2016; Ji et al., 2019; Zakrzewska et al., 2019). However, some recent studies have also found that the negativities toward outgroups may not be an adaptive outcome but a byproduct of the behavioral immune system. That is, the behavioral immune system is sensitive to any type of deviation and the outgroups happen to look dissimilar (Petersen, 2017; van Leeuwen and Petersen, 2018). By demonstrating that the behavioral immune system is sensitive to source of disease threat in Experiment 2, the current study supports the adaptation account and suggests that the behavioral immune system contains perceptual mechanisms for which some features that correlate with ingroup and outgroup memberships are part of proper domain. However, we should also be noted that the adaptation account and the byproduct account are not necessarily exclusive to each other and actually both of these two causes may contribute to the intergroup bias we found in human societies (Ji et al., 2019). In fact, by the results of Experiment 2 alone, we are not able to completely rule out the possibility that the byproduct cause also contributes to the ingroup derogation we found in the current study. That is, due to the low inter-regional mobility within East Asian countries and the high pathogen loads faced by East Asians (Chang et al., 2011), the behavioral immune system of East Asian participants is calibrated to detect the dissimilarities between ingroup members which makes them become less tolerant toward their ingroup members. This possibility should be tested by future works.

The present work adds more evidence to the disease prevalence account of cultural differences (Fincher et al., 2008). Previous studies mainly focused on the social behaviors on this aspect. For example, researchers have found that nations with greater pathogen loads are more religious, more collectivistic, more likely to conform, more conservative, etc. (Fincher et al., 2008; Schaller and Neuberg, 2012; Thornhill and Fincher, 2014; Schaller et al., 2015; Murray and Schaller, 2016). By testing the effects of disease threat on the ingroup derogation attitude among Chinese participants, the current study suggests that East Asians are responding to a special ecological condition in which in which the greater threat of diseases is incurred by ingroup members and thus they may have a unique pattern in their activation of behavioral immune system. Given the importance of behavioral immune system in shaping our basic cognitions (e.g., Miller and Maner, 2011, 2012; Makhanova et al., 2015; Liuzza et al., 2016; Murray and Schaller, 2016; Nussinson et al., 2018; Bonin et al., 2019; Prokosch et al., 2019; Wang and Ackerman, 2019), we may expect to find other functionally related differences between Easterners and Westerners in the processes of perception (Nussinson et al., 2018), memory (Bonin et al., 2019), emotion (Xie et al., 2019), decision (Prokosch et al., 2019), etc. These are important directions for future research.

CONCLUSION

Ingroup derogation is a counterintuitive phenomenon that apparently contradicts both expert and lay beliefs. The current findings suggest that the activation of ingroup derogation mechanism is related to external environmental disease cues and internal physiological disease cues. Such a mechanism is also sensitive to the specific perceived vulnerabilities to ingroup disease threat and outgroup disease threat. Thus, the current research supports the evolutionary hypothesis of ingroup derogation and suggests that the ingroup derogation found in East Asian cultures may be explained by a functionally flexible disease-avoidance mechanism.

DATA AVAILABILITY

The datasets generated/analyzed for this study can be found in the figshare: https://figshare.com/s/f811b11f9e17121346cc. Password: 20190628hunnu.

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by The IRB of the Institute of Psychology, Hunan Normal University. The patients/participants provided their written informed consent to participate in this study.

AUTHOR CONTRIBUTIONS

QW and PZ conceived and designed the experiments. QW and SY performed the experiments and analyzed the data. QW drafted the paper. All the authors participated in the revising of the paper, approved the version's publishment, and agreed to be accountable for all aspects of the work.

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Pathogens and Immigrants: A Critical Appraisal of the Behavioral Immune System as an Explanation of Prejudice Against Ethnic Outgroups

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The last two decades have seen the development of a body of literature in evolutionary psychology that seeks to attribute negative attitudes to ethnic and racial minorities and other outgroups to an evolved behavioral immune system (BIS). It hypothesizes that disgust sensitivity, which evolved as protection against pathogen threats, also triggers reactions to cues that are not viscerally disgusting, such as people with unfamiliar features, and thus can explain prejudice toward members of these groups. Such an explanation seems to limit the influence of education, public policy, and rhetoric on those attitudes. Our conceptual analysis shows that this is not the case. Existing hypotheses about why the BIS would be triggered even in the absence of visceral disgust elicitors suggest that general unfamiliarity or atypicality act as cues for this hypersensitive threat detection system. This implies that the impact of the BIS must depend on the cultural and societal context in which people learn not only what is disgusting but also what is typical. The social context of personal interaction with mass media representation of and political debate about immigrants consequently needs to be considered as a decisive factor for any effect of the BIS on attitudes and behavior toward ethnic and racial outgroups. The BIS is therefore not a separate or even superordinate explanation of prejudice, compared to those coming from the social sciences. We conclude that it can offer valuable insights into processes of stigmatization and prejudice, once the role of social learning in the developmental unfolding and activation of psychological mechanisms is taken seriously.

Keywords: behavioral immune system, pathogen threat, disgust, contagion avoidance, ethnic outgroups, prejudice, xenophobia, evolutionary psychology

INTRODUCTION

Why do people have a propensity to exclude or otherwise discriminate against certain groups of other people? Evolutionary approaches to stigmatization assume that the tendency to exclude individuals with certain characteristics results from psychological mechanisms that evolved by natural selection because they solved specific problems faced by our human ancestors (Kurzban and Leary, 2001). The last two decades have seen the development of a body of literature in evolutionary psychology that attributes many present-day political attitudes, such as social or political conservatism (Terrizzi et al., 2013), ethnocentrism (Navarrete and Fessler, 2006), and xenophobia (Faulkner et al., 2004), to evolved threat-management mechanisms (Neuberg and Schaller, 2016). Much of this research has focused on the behavioral immune system (BIS), which is hypothesized to produce automatic disgust reactions as an evolved response to the threat of pathogens (Schaller, 2006; Terrizzi et al., 2013). The BIS is considered an example of how the hypersensitivity of threat detection mechanisms can produce prejudices against people who do not actually pose a threat.

Social psychology and sociology have mostly looked in other directions to explain stigmatization, although more recently Phelan et al. (2008) have recognized evolutionary explanations as a promising route for understanding stigma associated with non-infectious diseases and disabilities. Mostly, contributions from these disciplines have pointed to uncertainty about the right way to interact with people who for various reasons look or behave differently from what is considered to be normal (Goffman, 1963), or dominant cultural beliefs that lead to negative stereotyping and othering of certain groups (Link and Phelan, 2001, pp. 368–370). Power differentials and efforts to preserve them have often been identified as the driving force behind stigmatization and prejudice (Elias and Scotson, 1965; Link and Phelan, 2014; Tyler and Slater, 2018).

The BIS approach to negative attitudes toward ethnic outgroups and immigrants superficially ties in with sociological research on dehumanization and disgust-eliciting language in public discourse (Esses et al., 2013; Utych, 2018). The observation that the implicit or explicit equation of immigrants and vermin in public discourse contributes to their rejection resonates with the BIS literature's focus on associations between parasite stress or pathogen threat and ingroup assortative sociality (Fincher and Thornhill, 2012), anti-immigrant attitudes (Aarøe et al., 2017), and xenophobia (Faulkner et al., 2004). However, different from sociological perspectives, the BIS approach investigates why cues that are not viscerally disgusting traits produce reactions of disgust. It does not try to explain why some people may *consciously* express disgust toward other ethnic groups (Hodson et al., 2013). Instead, the focus is on *unconscious* disgust responses. Higher individual disgust sensitivity, which evolved by natural selection as protection against pathogen threats, is hypothesized to lead to more negative attitudes toward strangers and immigrants even in the absence of consciously detected cues of such threats.

With a growing interest from political science in this line of research, policy implications of its findings are increasingly discussed. The reference to humans' evolutionary past as the ultimate explanation for some contemporary attitudes and behaviors depicts those not only as unintentional but also as largely outside conscious reflection. Such an explanation can also be misunderstood to mean a limited influence of education, public policy, and rhetoric on those attitudes and behaviors. For example, Kam and Estes (2016) suggest that disgust sensitivity can explain individuals' policy opinions and preferences and thus influence the demand for protective policies in such diverse policy fields as food safety and immigration, i.e., "policies that most overtly lend themselves to concerns about bodily and societal contamination" (Kam and Estes, 2016, p. 493). Clifford and Jerit (2018), after finding that disgust reactions impair memory and information-seeking of crucial facts related to a perceived threat (in their studies an infectious disease), suggest a possible generalization to public reactions to stigmatized social groups, such as immigrants and ethnic outgroups: "[D]isgust may be an obstacle to perspective taking and learning about other groups/cultures – two common methods for countering prejudice and intolerance" (Clifford and Jerit, 2018, p. 277). An article focusing on explaining anti-immigrant attitudes makes the similar but stronger claim that "the evolved features of the BIS fundamentally change the politics of ethnic inclusivity and frustrate the integrationist route to tolerance as multiculturalism increases in the Western world" (Aarøe et al., 2017, p. 290).

In this article, we show that such a conclusion is not justified, even if one accepts both the theoretical assumptions and the empirical findings of a link between disgust sensitivity and attitudes toward immigrants. This is because the existing literature has not sufficiently considered the interplay between evolved psychological mechanisms and the present social world in which these mechanisms affect behavior. As a result, research linking BIS or disgust to attitudes toward immigrants and other outgroups suffers from two conceptual shortcomings, although to varying degrees. Some take social context into account, but only in the form of individual-level variables such as education, income, or political ideology (e.g., Aarøe et al., 2017). They thus treat the potential role of societal-level factors such as political rhetoric and media coverage in shaping disgust reactions as somewhat irrelevant. Others take media coverage and the emotions it evokes as their starting point (Clifford and Jerit, 2018) and emphasize that many elicitors of disgust are socially constructed (Kam and Estes, 2016). At the same time, however, they treat the psychological mechanism that underlies disgust reactions as a black box and do not consider the possibility of non-visceral triggers of disgust that the BIS concept includes.

By placing the concept of the BIS in the context of arguments from both evolutionary psychology and sociology, we show that its contribution to understanding prejudice against ethnic outgroups is not a separate or even superordinate explanation to those focusing on social context. On the contrary, any effect of the BIS on attitudes and behavior toward ethnic and racial outgroups is mediated by the social context of personal interaction with mass media representation of and political debate about immigrants. For this reason, an evolved BIS is no fundamental obstacle to policies that stress efforts at integration and social learning of tolerance toward unfamiliar people, such as those based on intergroup contact (e.g., Pettigrew and Tropp, 2006). However, in conjunction with social context, the concept can offer a deeper understanding of the circumstances under which prejudice and xenophobia are reproduced.

In section "Disgust and the Behavioral Immune System," we describe how the BIS concept of disgust relates to and differs from social-psychological and social-anthropological approaches to the role of disgust in shaping attitudes toward ethnic outgroups and immigrants. In section "Ethnic Outgroups and Cues of Pathogen Threat," we take a closer look at the hypotheses about the BIS and identify a theoretical ambiguity regarding its presumed response to cues of outgroup membership, which can only be resolved by a recourse to social context. We subsequently show in section "Bringing Back the Social Context" that any effect that the BIS may have on attitudes toward ethnic outgroups and immigrants is deeply entwined with the impact of media and political discourse and therefore not a separate or even superordinate explanation for negative attitudes. We conclude that the concept of the BIS can offer valuable insights into how processes of stigmatization and prejudice can be influenced by a psychological mechanism that elicits disgust reactions. It is however essential that it is embedded in a discussion of the contemporary social and political factors that create the context in which that mechanism is triggered.

DISGUST AND THE BEHAVIORAL IMMUNE SYSTEM

The BIS is considered to be a suite of emotions, cognitions, and behavior that acts reactively and proactively to protect humans from pathogens (Schaller, 2006). It responds to potential cues of disease with the emotion of disgust and thereby triggers avoidance and/or protective behavior in order to reduce the likelihood of contagion or contamination from close contact. Due to the potentially high costs of pathogen contamination, and error in mapping pathogen cues onto actual pathogen threats (e.g., because of a latency between infection and the presentation of symptoms, or because cues are ambiguous), the BIS is expected to be hypersensitive and generate false positive reactions, which means that it can be triggered by cues of pathogens even if there is no actual pathogen threat (Nesse, 2005).

Briefly, a feature of threat detection mechanisms in general (from the BIS and our physiological immune system to animals' alarm calls in response to predators) is that they are selected to produce "false positives": this is because the cost of mistakenly responding to a potential threat is less than the cost of ignoring it (error management theory: Haselton and Buss, 2000; Haselton and Nettle, 2006). While these apparent errors are ultimately adaptive, with modern hygiene, many potentially threatening situations do not pose a pathogen risk. Just as the physiological immune system can overreact to generally harmless stimuli (as in food allergies), the first hypothesized step in the false-positive BIS disgust reaction is to misclassify an unfamiliar person or other stimulus as a pathogen threat. The strength of reaction varies across individuals, who consequently can be more or less disgust-sensitive (Tybur et al., 2018).

The concept of the BIS is one important result of a surge in research interest in the emotion of disgust that took off in the late 1990s (Rozin et al., 2016). Its focus on pathogen avoidance as an evolved function of disgust distinguishes it from other attempts to understand the evolutionary origins and social functions of disgust. Although there is wide agreement that pathogen avoidance initially played a fundamental role in the evolution of disgust, there are different views regarding its relevance for understanding the scope of disgust elicitors in contemporary humans.

Most conceptualizations of disgust agree that its evolutionary origin is (partly or entirely) an adaptation to avoid pathogens contained in contaminated food (Rozin et al., 2016). There is less unanimity regarding the question of how to categorize a range of other disgust elicitors within an evolutionary framework. The first influential scale for measuring disgust (Haidt et al., 1994) distinguished seven domains of disgust (food, animals, body products, sex, envelope violations, death, and hygiene) as well as a cross-cutting domain of magical thinking that triggers disgust reactions based on visual similarity with or imagined contagion from disgusting items. A revised disgust scale (Olatunji et al., 2007), based on a psychometric analysis of the initial one, reduced the domains of disgust to three, by merging the disgust elicitors food, animals, and body products into a domain of core disgust, reconceptualizing disgust of death and envelope violation as animal-reminder disgust, and introducing contamination as a separate domain, related to hygiene and aspects previously understood as magical thinking. Another three-domain framework (Tybur et al., 2009) reinterpreted core disgust as pathogen disgust and added sexual and moral disgust as domains in which disgust reactions solve distinct adaptive problems, namely avoiding substances that could cause diseases, avoiding sexual partners and behaviors with a negative impact on long-term fitness, and avoiding individuals with anti-social behaviors that endanger one's social group.

In particular, the notion of moral disgust and its psychological correlate are controversial. One argument is that verbal expressions of disgust as a reaction to someone's actions or character are not more than a metaphor (Nabi, 2002) and facial expressions of disgust just signaling devices, communicating reproach and a wish for social distancing (Royzman and Kurzban, 2011; Tybur et al., 2013). Another argument forges a link with cultural anthropology (Douglas, 1966) and conceives moral disgust as a reaction to the threat of spiritual pollution, i.e., a particular type of moral transgression, and thus as a culturally evolved abstraction from non-moral disgust of potentially contaminating substances (Rozin et al., 1999, 2016). Hutcherson and Gross (2011) suggest that there is considerable overlap between disgust, anger, and contempt as negative social emotions related to judgments of others' attitudes and actions; yet, they find disgust to be most strongly felt in response to transgressions that affect others (as opposed to self) and are not due to incompetence but violate the ethic of community.

The BIS literature, though certainly aware of the conceptual complexities involved in understanding the emotion of disgust (e.g., Lieberman et al., 2012; Clark and Fessler, 2014), by definition focuses on the adaptive function of pathogen avoidance. It looks for and interprets associations between disgust and particular attitudes or behaviors based on the hypothesis that such findings will be related to the function of disgust in avoiding pathogens.

When it comes to linking disgust and attitudes toward ethnic outgroups and immigrants, social science research suggests two ways to make the connection. On the one hand, a politics of disgust can use stereotypical characterizations of certain groups to elicit the emotion of disgust in processes of "othering" (Douglas, 1966; Tyler, 2013; Round and Kuznetsova, 2016).

The BIS could be understood as the psychological basis that ensures the effectiveness of such a politics. On the other hand, people perceive immigrants as posing different threats, such as economic, cultural, or security threats (Stephan and Stephan, 2000; McLaren and Johnson, 2007; Hellwig and Sinno, 2017) – a list that could be complemented by adding pathogen threat.

The BIS literature however follows a different route. It seeks a link that precedes public discourse and the labeling of certain groups as pathogen threats. Although not incompatible with the notion of explicit stereotypes about dirtiness and revolting behavior triggering disgust reactions (Clifford and Piston, 2017), the BIS approach focuses on unconscious, non-discursive cues. The assumption is that the BIS uses cues from the environment that are correlated with pathogen risk or were correlated with it in the environment in which this psychological mechanism was selected. We now turn to the arguments that ethnic outgroups are one such cue to which a hypersensitive BIS might react.

ETHNIC OUTGROUPS AND CUES OF PATHOGEN THREAT

If the BIS can be triggered by ethnic outgroups, it must categorize them as posing a risk of infection. Several hypotheses are given for a psychological mechanism that has evolved to react to cues of general unfamiliar appearance which ethnic outgroups present. The first hypothesis is that contact with previously unknown groups could increase the risk of exposure to novel pathogens. Since such pathogens have not co-evolved with the local population, locals' physical immune system lacks defenses against them (Thornhill and Fincher, 2014). Consequently, avoidance of even healthy-looking strangers could have provided fitness benefits for our ancestors (Faulkner et al., 2004; Navarrete and Fessler, 2006). This would have made foreigners or strangers a relevant category for our ancestors' survival and reproduction, which is why the human mind would have evolved an automatic disgust reaction to unfamiliar-looking outgroups.

The notion that the BIS reacts to cues of outgroup membership *per se* (rather than unfamiliarity, of which outgroup membership is one aspect) has met criticism. First, it is questioned whether pathogens carried by outgroups are generally more dangerous to locals than co-evolved pathogens (De Barra and Curtis, 2012). Second, ancestral humans did not travel large enough distances to encounter outgroups with pathogens radically different from their own (van Leeuwen and Petersen, 2018). Third, avoiding individuals from outgroups would not have protected against novel pathogens if some ingroup individuals interacted with members of an outgroup, which was likely due to other fitness benefits that could be gained from such interaction (Robinson and Barker, 2017); infectious pathogens originating in the outgroup would still have spread in the ingroup, but those avoiding outgroup contact would have forgone the benefits from it (van Leeuwen and Petersen, 2018). Empirical studies also raise doubt about the BIS directly reacting to outgroup membership (Tybur et al., 2016; Petersen, 2017).

A second, complementary hypothesis is that the BIS reacts to outgroups because individuals from such groups could be more likely to behave in ways that violate local customs implicitly relevant for avoiding diseases from local parasites, such as rules regarding hygiene or food preparation (Faulkner et al., 2004; Tybur et al., 2016). Such rules could even be considered a part of the BIS, since their (cultural) evolution once brought fitness benefits by neutralizing pathogen threats (Thornhill and Fincher, 2014). Thus, a hypersensitive BIS could take cultural unfamiliarity (rather than outgroup membership itself) as a cue of potential rule violation, triggering a disgust reaction (Aarøe et al., 2017).

A third hypothesis is that the BIS reacts to physical unfamiliarity not because it is a cue for outgroup membership *per se* but because physically unfamiliar traits resemble cues that were once correlated with disease. A hypersensitive BIS might react to general unfamiliarity, including cues of foreignness, because it mistakes atypical appearance for physical features that infected people may display (Aarøe et al., 2017; Petersen, 2017).

To what extent could atypical physical characteristics (parts of the body or bodily movements) be correlated with disease? This can be seen as a continuum, ranging from direct signs of disease, such as sores or swellings (Oaten et al., 2011; Lieberman et al., 2012), on one end, to a less well-defined other end with traits that were or are at least weakly correlated with pathogen threats. For example, some bodily features of obesity resemble symptoms of infectious conditions likely to have been present in ancestral environments (Park et al., 2007).

When it comes to ethnic differences, general physical unfamiliarity is implied to be a cue weakly correlated with disease threats. But the relevant aspects of unfamiliarity are often not specified. Aarøe et al. (2017), p. 278) offer the example of skin color to illustrate how immigrants may be physically unfamiliar in a way relevant to the BIS. As some diseases do indeed affect the color and appearance of human skin, this example illustrates a specific trait that the BIS could classify as relevant. Other ways in which physical unfamiliarity of ethnic outgroups might trigger the BIS are an open question that is ripe for future research.

To whatever understanding of unfamiliarity one subscribes, it is crucial to note that the assessment of whether a trait is typical or atypical, and how well it is correlated with disease, presupposes previous learning. Distinguishing between what is familiar and unfamiliar requires knowledge about what certain physical traits, e.g., faces or body morphology, as well as certain activities, e.g., preparing or eating food, typically look like. Cues of unfamiliarity may also involve the cognition and appraisal of learned labels related to disease (Oaten et al., 2011). In the context of immigration, such knowledge may include stereotypes about whether immigrants live in hygienic conditions (Tsuda, 1998, p. 344) or about the prevalence of infectious diseases in countries from which immigrants typically come. As a psychological mechanism to assess pathogen risk, the BIS would process such stereotypes as disease cues just as it would process physical traits. But stereotypes are cues that are learned in social contexts, in which they may serve many functions that have nothing to do with protection against disease, for example the justification of power differentials (Phelan et al., 2008).

Against this social background, it would seem untenable to conceive the impact of the BIS as independent of the cultural and broader societal context in which people learn what is typical and what is disgusting. Yet the research that considers the link between the BIS or disgust and negative attitudes to ethnic outgroups or immigrants has generally overlooked this fundamental relationship between social context and disgust reaction. It either takes social context into account only as individual-level variables; or it acknowledges the role that social context in the form of political rhetoric and mass media plays as a potential source of disgust elicitors, but only considers explicit elicitors of disgust and not the effect on perceptions of familiarity and typicality to which the BIS may react.

Early examples of the focus on individual-level variables are the studies reported in Faulkner et al. (2004). They test the hypothesis that disease-avoidance mechanisms (the concept of a BIS was not established yet in the field) influence xenophobic attitudes. They examine effects of chronic and temporary perceptions of vulnerability to disease on reactions to subjectively foreign people, based partly on correlational findings and partly on experimental manipulation. The results indicate that a higher perceived vulnerability to disease amplifies xenophobic attitudes, not as a result of a rational risk assessment but of an automatic heuristic. The article stresses that subjective perceptions of familiarity and foreignness seem to be fundamental for the effect and that both individual and situational differences in perceived vulnerability to disease correspond to differences in xenophobic attitudes. Yet the studies do not address the social context in which perceptions of familiarity and foreignness are shaped.

This is of course perfectly justified in terms of a division of labor in research. However, it becomes an issue once the question of policy implications is posed and/or, by leaving out the social and cultural context, a psychological disease-avoidance mechanism is treated as a separate or even competing explanation. An example is Aarøe et al. (2017), who explore the relationship between the sensitivity of the BIS and attitudes toward immigration in the US and Denmark, employing self-report and physiological measures in large-scale surveys and laboratory experiments. The authors find that greater sensitivity of the BIS is associated with greater opposition to immigration, and that cues of disease protection, as well as cues of the physical and cultural familiarity of the immigrant, weaken that relationship. They also find that greater disgust sensitivity is associated with lower approval of situations that involve contact with immigrants who already live in a community, and that cues about the immigrants' willingness and effort to integrate do not affect this relationship. With these findings, the authors claim that the BIS poses a fundamental obstacle to policies that stress efforts at integration and social learning of tolerance toward unfamiliar people.

The theoretical premise of this work and its suggested policy implications is that the hypersensitive BIS reacts to cues of physical and cultural unfamiliarity, which leads to false-positive identification of pathogen threats, resulting in an unconscious disgust reaction that leads in turn to avoidance and rejection of the people perceived to carry the threat. The only suggestion that this unconscious mechanism is mediated by social context can be found in an online appendix making the important qualification that "substantial and continuous personal contact with immigrants living in the society" (Aarøe et al., 2017, online appendix A12) could have the effect of making people more familiar with ethnic and racial differences.

On the other hand, contributions that have a broader notion of relevant social context and consider mass media or political statements tend not to conceive this context as influencing perceptions of familiarity but only as a potential source of disgust elicitors. For example, Clifford and Jerit (2018) characterize the relationship between disgust reactions and learning as one in which a triggering of the former inhibits the latter. Different from Aarøe et al. (2017), they focus on the role of mass media coverage in presenting disgust-eliciting triggers. Yet, also different from Aarøe et al. (2017), they do not discuss the psychological mechanism that underlies the disgust reaction and the possibility of non-visceral cues as triggers. As a result, the role of learning in connection to disgust needs a more comprehensive reflection: on the one hand, unconscious disgust may be an obstacle toward learning (about other groups and in general); on the other hand, the psychological mechanism that is responsible for disgust reactions operates in a social context in which learning about the attributes to which the BIS may react, namely familiarity and typicality, is always already taking place (**Figure 1**).

BRINGING BACK THE SOCIAL CONTEXT

Mass media and the broader social context beyond personal contact play an important role when it comes to perceiving immigrants as familiar or unfamiliar, both physically and culturally. A lack of encounters with immigrants in a relatively homogenous society such as Denmark or a highly segregated society such as the U.S. (Aarøe et al., 2017) is mostly not the result of active avoidance but of their frequent absence in the everyday life of the majority in the first place. However, such settings do not lack exposure to immigration, because that happens to a large degree *via* mass media. Decisions to include or exclude minorities in contexts unrelated to immigration, especially on television, will consequently influence whether they are perceived as unfamiliar. When immigrants *are* depicted in the mass media, their portrayal can either highlight cultural unfamiliarity or contribute to making the unfamiliar familiar by emphasizing commonalities. The existence of such effects is suggested by research on children's television and prejudice reduction (Graves, 1999) and the differential effect of public versus private television consumption on anti-immigrant sentiments (Jacobs et al., 2017).

Mass media and the often stereotypical depiction of immigrants are a key part of the social context in which individuals form attitudes about those immigrants (Esses et al., 2013). These depictions are also influenced by the political debate about immigration. The current political discourse in many countries contains various cues that, based on the logic of the BIS, make favorable attitudes toward immigrants less likely. It tends toward emphasizing difference, in particular religious differences between Islam and Christianity (Yilmaz, 2012).

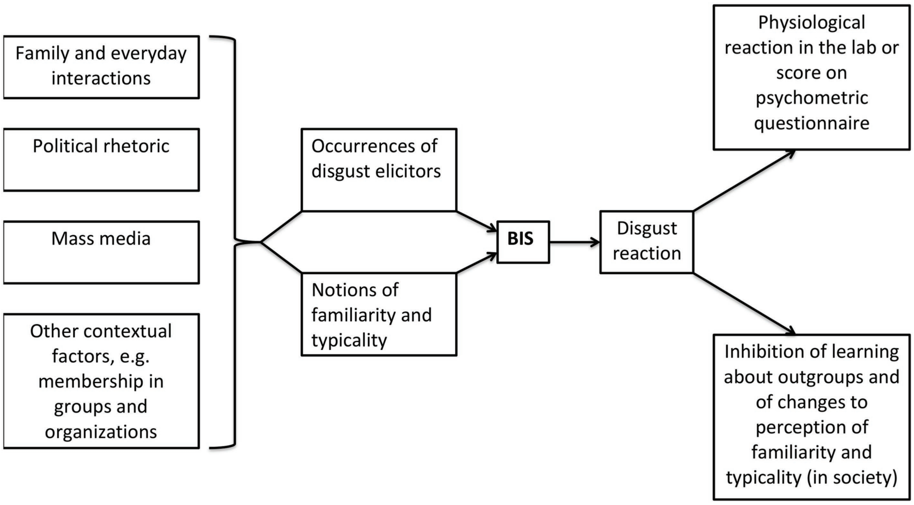

FIGURE 1 | Impact of societal factors on the BIS and (societal) effects of triggered disgust reactions. Individuals are exposed to and learn about disgust elicitors as well as familiar/typical appearance and behavior in social contexts, including family, daily interactions, politics, and mass media. The triggering of an individual's BIS is influenced by both explicit disgust elicitors and notions of familiarity/typicality. This reaction can be quantified by physiological or psychometric measures. Such data imply that the disgust reaction may prevent learning about outgroups and consequently inhibit changes to perceptions of familiarity and typicality in society.

But it may also enhance cues of cultural unfamiliarity in other, more indirect ways. If the original fitness benefits of responding to this type of cue derived from an avoidance of behaviors that violated local norms, some of which had an effect on the likelihood of exposure to pathogens (Murray and Schaller, 2012; Tybur et al., 2016), the depiction of immigrants as norm-violators would foster their perception by the BIS as culturally unfamiliar.

Political discourse has subscribed to such depictions in various forms. It has fed a stereotype according to which immigrants tend to be involved in crime or terrorism (Ceobanu, 2011; Sohoni and Sohoni, 2014). It has focused on the distinction between legal and illegal immigrants, which means that immigrants have regularly been depicted as violating laws about entering and living in a country. Political discourse has also increasingly addressed immigration as a problem in the context of welfare state redistribution, with immigrants being framed as less deserving of welfare benefits than natives (Aarøe and Petersen, 2014; Jorgensen and Thomsen, 2016) or as welfare abusers (Brown, 2016). This is based on an implicit norm of reciprocity, which immigrants violate when they claim benefits without having contributed to the welfare state that grants them.

The relationship between the immigration debate and BIS responses is thus two-way, whereas existing research (Kam and Estes, 2016; Aarøe et al., 2017) only considers how BIS responses might influence the immigration debate. For example, in a vignette experiment and survey with U.S. participants, Aarøe et al. (2017) investigate the correlation between disgust sensitivity and opposition to immigration, and find that it is weakened by cues about the immigrants' physical and cultural familiarity but not by cues about their willingness and effort to integrate. The finding seems to support the BIS hypothesis, since motivation to integrate does not reduce an unconsciously perceived pathogen threat. The authors highlight the motivation to integrate as the main route to increasing tolerance that research has identified. They therefore claim that they are "demonstrating how the behavioral immune system can undermine established pathways to ethnic tolerance in political science research" (Aarøe et al., 2017, pp. 285–286). But they fail to consider that the actual immigration debates to which the participants in their studies have likely been exposed – often emphasizing difference instead of willingness to integrate – may have shaped the reactions of the BIS that they measure in a decisive way.

It is also important to recognize that the geographical origin of an immigrant may act as a cue not only in terms of physical and cultural familiarity, but also in terms of stereotypes about specific regions and their inhabitants (Brader et al., 2008; Hellwig and Sinno, 2017). Once we take the content of the current immigration debate more fully into account, it is clear that it is the debate itself that is an obstacle to more positive attitudes to immigrants, since it tends to depict immigrants as untrustworthy norm violators, i.e., culturally unfamiliar. The BIS approach plays a valuable role in elucidating the psychological mechanism that reacts negatively to such a depiction. But if our evolutionary past gave rise to a BIS sensitive to cultural unfamiliarity as a cue for possible norm violations, it is still our changeable present in which attitudes and behaviors are influenced by explicitly negative depictions of certain groups.

Many empirical studies that have been employed to show the influence of the BIS and pathogen avoidance on various political attitudes (Faulkner et al., 2004; Navarrete and Fessler, 2006; Aarøe et al., 2017) can actually be interpreted in a way that stresses this changeability. These studies typically manipulate cues about disease protection or disease threat to demonstrate their effect on political attitudes. But what they present as support for the claim that pathogen avoidance is a causal factor in the formation of attitudes toward ethnic and racial outgroups can also be read as impressive evidence for the evolved capacity for flexibility of the BIS under changeable environmental conditions. For example, in avoiding contact with others, there is a tradeoff between protecting oneself from pathogens and forgoing social interactions. At times pathogen avoidance may take precedence, whereas under different circumstances the beneficial opportunities of new interactions have more weight (Aarøe et al., 2017, 284). This flexibility, and the ease with which even weak environmental factors – in studies with vignettes, typically verbal cues or hand-washing – alter the influence of the BIS on political attitudes (e.g., Navarrete and Fessler, 2006. pp. 277–278; Huang et al., 2011; Aarøe et al., 2017, p. 285), suggest that we have no reason to assume that the BIS will inevitably come in the way of policies aimed at fostering integration and tolerance. Rather, the behavior resulting from the BIS is highly variable, and depends on the immediately present cues.

CONCLUSION

Far from being an obstacle to "the integrationist route to tolerance" (Aarøe et al., 2017, p. 290), the role of the BIS in attitudes toward immigrants and ethnic outgroups actually highlights both the necessity and feasibility of fostering tolerance, provided that peaceful interaction is the policy goal and not the stigmatization of outgroups for political gain. Familiarity with physical and cultural traits is not genetically inherited but learned, which means that any hypotheses based on the BIS need to take the broader sociocultural context into account to make a contribution to understanding attitudes toward immigrants and ethnic outgroups.

Empirically, the use of non-Western samples is a promising course to sensitize research on the BIS to the role of sociocultural context in the activation of psychological mechanisms. Along these lines, van Leeuwen and Petersen (2018) used samples from the US and India to test the impact of pathogen disgust sensitivity on attitudes toward ethnic outgroups. In a survey with the US sample, presented with photographs of Indians (represented by photographs of adult males with brown skin), they find that people with higher disgust sensitivity were less comfortable with contact with Indians. But they do not find such an association in the Indian sample when respondents were shown photographs of white males. They conclude that the association seems to be a result of processes that are culturally specific for the US or Western countries; importantly, they identify stereotypical beliefs about the trustworthiness and dirtiness of the non-white outgroup as responsible for the association. The possible role of stereotypes about hygienic conditions in an immigrant's country of origin could be explored in a similar way: for example, in a survey administered to a sample from a stereotypically non-hygienic country that is asked about immigrants from a stereotypically hygienic country.

Theoretically, research on the BIS offers valuable insights into how and why stigmatization can be influenced by unconscious sensitivity: here, the focus is on disgust, but other unconscious processes, such as a need for physical safety, could play a role (Napier et al., 2018). Nevertheless, at present a significant part of the novelty appeal of evolutionary psychological approaches to explaining political attitudes and behavior relies on downplaying or omitting the role of social learning in the developmental unfolding and activation of psychological mechanisms. Talking about innate (Petersen and Kennair, 2009) or automatically operating (Aarøe et al., 2017) psychological mechanisms can be misinterpreted to mean an unchangeability of behaviors fixed in our evolutionary past (e.g., Kanazawa, 2001) that is not borne out by the empirical evidence (Varella et al., 2013). A careful consideration of the interplay between evolved psychological mechanisms and the changing and changeable social world in which these mechanisms affect behavior is not only the more fruitful course of research but also the more responsible one when it comes to the policy implications of such research. Understood in this way, research on the BIS could complement existing studies on a dual process model of prejudice and perceived group threat (Devine, 1989; Blinder and Lundgren, 2018) by offering a deeper understanding of automatic, unconscious reactions.

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All authors listed have made a substantial, direct and intellectual contribution to the work, and approved it for publication.

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Interaction Effects of Behavioral Inhibition System/Behavioral Activation System and Cost/Probability Biases on Social Anxiety

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Introduction: Social anxiety disorder (SAD) symptoms are maintained by cognitive biases, which are overestimations of the severity and likelihood of negative social events (cost/probability biases), and by sensitivity to rewards and punishments that are determined according to behavioral inhibition/behavioral activation systems (BIS/BAS). Cost/probability biases might activate the behavioral immune system and exacerbate the avoidance of social events. Earlier studies have proposed that low BIS or high BAS decrease SAD symptoms; BIS/BAS may even change the effects of cognitive biases on SAD symptoms. Hence, the current study investigates the interaction effects of BIS/BAS and cost/probability biases on SAD symptoms.

Method: Seventy-six Japanese undergraduate students completed the Japanese version of the Liebowitz Social Anxiety Scale (LSAS), which comprises Fear and Avoidance subscales, the BIS/BAS Scale, and the Social Cost Probability Scale.

Results: A multiple regression analysis was performed to examine whether cost/probability biases, BIS/BAS, and their interactions affected SAD symptoms; following this, the main effects of cost bias and BIS were determined for LSAS-Fear ($\beta = 0.64$, $p < 0.001$; $\beta = 0.33$, $p < 0.01$) and LSAS-Avoidance ($\beta = 0.49$, $p < 0.001$; $\beta = 0.35$, $p < 0.01$). The interaction effect between cost bias and BAS was significant for LSAS-Avoidance ($\beta = -0.32$, $p < 0.05$). Simple slope analysis showed that the slope of cost bias was significant for low-BAS individuals ($\beta = 0.77$, $p < 0.001$) but not for high-BAS individuals ($\beta = -0.21$, *n.s.*). The interaction effect between probability bias and BAS was significant for LSAS-Avoidance ($\beta = 0.40$, $p < 0.01$) as well. Further, simple slope analysis revealed that the slope of probability bias was significant for low-BAS individuals ($\beta = -0.53$, $p < 0.05$) but not for high-BAS individuals ($\beta = 0.17$, *n.s.*).

Discussion: The study found interesting results with respect to the avoidance of social events. Low-BAS individuals with high cost or low probability biases regarding social events may have a tendency to avoid social events. In contrast, if high-BAS individuals overestimate the cost of social events or underestimate the probability of social events, their anticipation of rewards might prevent them from avoiding social events.

Keywords: social anxiety, cost bias, probability biases, behavioral inhibition system, behavioral activation system

INTRODUCTION

Social anxiety disorder (SAD) is characterized by an excessive fear and avoidance of social situations where individuals feel scrutinized and fearful of being negatively evaluated by others (American Psychiatric Association [APA], 2013). The 12-month prevalence rate of SAD in the United States is approximately 7%, and SAD is associated with an increase in school dropout rates and a decrease in individual well-being, employment, workplace productivity, socioeconomic status, and quality of life (American Psychiatric Association [APA], 2013). Although individuals with SAD experience considerable distress and social impairment, only about half of them in Western societies ever seek treatment, and they tend to do so only after 15–20 years of experiencing the associated symptoms (American Psychiatric Association [APA], 2013). Therefore, it is a public health imperative to understand and reveal the development and maintenance of SAD symptoms.

Cognitive bias is believed to play an important role in the maintenance of SAD symptoms (e.g., Clark and Wells, 1995). Accordingly, Hofmann (2007) reviewed relevant recent laboratory findings and clinical trial results and presented a comprehensive and disorder-specific cognitive behavioral model for SAD. According to this model, individuals with SAD overestimate the severity (cost bias) and likelihood (probability bias) of a negative outcome of a social situation. Thus, individuals with SAD tend to believe that they are in danger of behaving in an inept and unacceptable fashion and that this will result in disastrous consequences. Consequently, they anticipate social mishaps and engage in avoidance and/or safety behaviors (Wells et al., 1995), which reduce unpleasant feelings and prevent future negative outcomes. In addition, these behaviors prevent the disconfirmation of core dysfunctional beliefs (Salkovskis, 1991). In other words, cost/probability biases might activate the behavioral immune system, a motivational system that detects infectious pathogens, triggers disease-relevant emotional and cognitive responses, and promotes avoidance of the infectious pathogens (Schaller and Park, 2011). Further, a recent study reported that the behavioral immune system affects social cognition and social behavior in human societies (Murray and Schaller, 2016). Cost/probability biases might activate individuals' avoidance of social events, which, in turn, might temporarily relieve their anxiety. This cycle helps maintain SAD symptoms.

However, to date, the ways in which the above-mentioned factors (e.g., cognitive bias, avoidance) interact with one another to develop and maintain SAD symptoms remain unclear. Kimbrel (2008) proposed that the revised Reinforcement Sensitivity Theory (rRST; Gray and McNaughton, 2000) can be used to integrate a wide range of factors into a unified and theoretically driven model of social anxiety. The rRST is a biology-based theory of personality that postulates that three major subsystems of the brain underlie many individual differences in personality, psychopathology, and reinforcement sensitivity. These brain systems are referred to as the Fight–Flight–Freeze System (FFFS), Behavioral Inhibition System (BIS), and Behavioral Approach System (BAS). The FFFS is proposed to motivate avoidance and escape behaviors in response to conditioned and unconditioned aversive stimuli, and BIS is believed to cause anxiety and neuroticism and inhibit behavior by attending to threatening stimuli or the expectation of a threat. BIS is the basis of cognitive biases such as negative beliefs and negative expectations regarding a threatening situation (Kimbrel, 2008). In contrast, BAS is proposed to trigger reward-seeking behavior and impulsivity (Gray, 1970) in individuals, since BAS reflects the factors promoting goal-oriented behavior. Kimbrel (2008) proposed that low BAS represents an additional risk factor for social anxiety. Further, FFFS has been proposed as being useful for animals but less common in human daily life, and FFFS is not important in human research (Kunisato et al., 2007). Therefore, if FFFS is expressed as a human temperament, it is expressed as a system similar to BIS (Pickering et al., 1999). Consistent with the position of contemporary research in this area (e.g., Gray and McNaughton, 2000), Kimbrel (2008) and Kimbrel et al. (2012) took the position that the sensitivity of both the BIS and FFFS were combined. In Kimbrel et al. (2012), the term "BIS–FFFS" is used throughout the paper to refer to self-report measures of BIS based on earlier versions of the theory. Therefore, the current study examines BIS and BAS.

Kimbrel et al. (2012) tested the hypothesis that cognitive biases for negative and threatening social information (memory bias, expectancy bias, belief bias, and perception of threat) mediate the effects of BIS and BAS sensitivity on social anxiety among college students. They found that, under the mediation of these cognitive biases, higher BIS or lower BAS have significant indirect effects on social anxiety. However, the magnitude of the standard partial regression coefficient of BAS on cognitive biases ($\beta = -0.20$, $p < 0.001$) was lower than that of BIS on cognitive biases ($\beta = 0.71$, $p < 0.001$). In addition, the correlations between BAS and cognitive biases were weak (memory bias; $r = -0.08$, *n.s.*, expectancy bias; $r = -0.28$, $p < 0.001$, belief bias; $r = -0.23$, $p < 0.001$, and perception of threat; $r = -0.15$, $p < 0.01$). Furthermore, Takahashi et al. (2007) reported that BIS and BAS functioned independently of each other. According to these reports, there are not only people who have high-BAS and low-cost/probability bias but also those have high-BAS and high-cost/probability bias. High-BIS and/or low-BAS individuals may overestimate potential social costs and exaggerate the probability of negative outcomes of social events. Further, cost/probability biases might activate the behavioral immune system and exacerbate the avoidance of social events, which may increase the level of SAD symptoms. In contrast, high-BAS individuals may anticipate rewards and prevent themselves from avoiding social events even when they overestimate the social cost and probability of such events; further, this tendency may not increase the level of SAD symptoms. For example, even if a high-BAS individual overestimates the social cost and probability of one's research presentation at an academic conference, he or she will not avoid but will instead conduct the presentation for growth opportunities and academic achievement. However, to date, no study has directly examined the relationships between BIS/BAS, the cost/probability bias that is strongly related to SAD symptoms, and social anxiety.

Hence, the current study investigates the interaction effects of the BIS/BAS and cost/probability biases on SAD symptoms. The results are expected to contribute to the development of SAD therapies tailored to individual characteristics. Accordingly, we conducted a cross-sectional study to assess BIS/BAS, cost/probability bias, and social anxiety and hypothesized that BIS was positively correlated with cost/probability bias and SAD symptoms. Further, we hypothesized that the coefficient of the interaction effects between BAS and cost bias and that between BAS and probability bias on SAD symptoms are negatively significant. Specifically, for low-BAS individuals, the higher cost/probability bias, the higher the SAD symptoms. Contrastingly, for high-BAS individuals, SAD symptoms do not increase even with an increase in cost/probability bias.

MATERIALS AND METHODS

Participants and Procedures

Participants were 76 undergraduate students (39 women and 35 men, mean age 21.91 ± 5.03 years) of Waseda University, Saitama, Japan. Students were recruited from psychology classes. The inclusion criterion was: (a) being 20 years of age or older. Further, the exclusion criteria were as follows: (a) undergoing counseling, (b) being prescribed medication by a doctor, and (c) having ever continuously visited medical institutions offering psychiatric and psychosomatic medicine. The study did not have invasiveness. Participants were aged over 20 years. Therefore, we omitted the procedures for informed consent in accordance with the recommendations of the Ethical Guidelines for Medical and Health Research Involving Human Subjects. Instead, completion of the questionnaire was considered as informed consent. Further, we provided both verbal and written explanations of informed consent to potential participants based on the recommendations of the Ethical Guidelines for Medical and Health Research Involving Human Subjects. In particular, the questionnaire's first page contained the following information for participants: the research objective, inclusion and exclusion criteria, consideration of questionnaire completion as the consent to participate, free and voluntary nature of survey participation, information that data will be processed statistically and participant information will be kept anonymous and confidential, and information that participation or non-participation is unrelated to the participants' class evaluation.

The participants completed the Japanese version of the Liebowitz Social Anxiety Scale (LSAS), which comprises Fear and Avoidance subscales, the BIS/BAS Scale, and the Social Cost Probability Scale (SCOP). The study was approved by the ethics committee of Waseda University.

Measures

Assessment of Social Anxiety Symptoms

The LSAS, comprising 24 items rated on a scale of severity from 0 to 3, is a valid and reliable social anxiety measure (Liebowitz, 1987). The LSAS consists of Fear and Avoidance subscales. The Japanese version of the LSAS (LSAS-J), which was developed to assess social anxiety in the Japanese population, is psychometrically robust (Asakura et al., 2002) and was used for social anxiety evaluation in the current study.

The LSAS items are descriptions of various social events. Some sample items include "Calling in public" and "Expressing my opinion at a meeting." For each Fear subscale item, the participants were required to rate the degree of fear on a four-point scale. Similarly, for each Avoidance subscale item, they were required to rate the degree of avoidance on a four-point scale.

Assessment of Cost/Probability Bias

The SCOP is a 12-item scale of perceived cost/probability bias in social events, with response options ranging from 1 to 5. SCOP is a valid and reliable measure of cost/probability biases (Shirotsuki and Nomura, 2009).

The SCOP has items describing different social events and respondents' cognition of cost bias in these social events. Some sample items are "I think that my opinion will be misunderstood if I express it in public" and "I think that I will be rejected when I talk with my friend." To assess cost biases, participants were required to score the following question on a five-point scale: "To what extent does the following idea applies to each situation?" Further, to assess probability biases, the participants had to score the following question on a five-point scale: "To what extent do you think the following idea will come true in each situation?"

Assessment of BIS/BAS

Research has proved the validity and reliability of the BIS/BAS Scale, which comprises 20 items rated on a scale of severity from 1 to 4 (Carver and White, 1994). The Japanese version of this scale, which was developed for the Japanese population, is psychometrically robust (Takahashi et al., 2007) and was used to evaluate BIS/BAS in the current study.

Statistical Analyses

Pearson's correlation coefficients were calculated to examine the associations between all the variables. After conducting bivariate analysis, we conducted a multiple regression analysis to examine whether cost/probability biases, BIS/BAS, and their interactions affected SAD symptoms. We used SPSS version 24.0 to analyze the data.

RESULTS

Descriptive Statistics

Table 1 presents the characteristics of the 76 participants. The numbers of participants rated for each severity level of SAD symptoms were as follows: less than mild (0–43 points; $n = 31$), mild (44–79 points; $n = 37$), moderate (80–101 points; $n = 8$), and severe (over 102 points; $n = 0$). Eighty-nine percent of the participants were rated as having mild or less than mild symptoms. In addition, the means and standard deviations of each of the descriptive variables were similar to those of earlier findings on healthy Japanese people (Takahashi et al., 2007; Shirotsuki et al., 2010).

We performed the Kolmogorov–Smirnov test to examine the normality of variables (**Table 1**). The results revealed that all the data were not significant. Therefore, it found that all the variables were normally distributed.

Correlation Between Variables

Pearson's correlation analysis was applied to examine the associations among all the variables (**Table 2**). The results revealed significant positive correlations between fear symptoms of social anxiety and cost bias ($r = 0.61$, $p < 0.001$), probability bias ($r = 0.27$, $p = 0.02$), and BIS ($r = 0.41$, $p < 0.001$). In addition, there were significant positive correlations between avoidance symptoms of social anxiety and cost bias ($r = 0.42$, $p < 0.001$), probability bias ($r = 0.29$, $p = 0.01$), and BIS ($r = 0.44$, $p < 0.001$). Moreover, there were significant positive correlations between BIS and cost bias ($r = 0.37$, $p = 0.001$), between BIS and probability bias ($r = 0.42$, $p < 0.001$), and between BIS and BAS ($r = 0.32$, $p = 0.004$).

Testing Assumptions of Multiple Regression

A multiple regression analysis was conducted to examine whether cost/probability biases, BIS/BAS, and the interactions between these variables predicted SAD symptoms (**Table 3**). Accordingly, significant main effects of cost bias and BIS were found for LSAS-Fear ($\beta = 0.64$, $p < 0.001$; $\beta = 0.33$, $p < 0.01$) and LSAS-Avoidance ($\beta = 0.49$, $p < 0.001$; $\beta = 0.35$, $p < 0.01$). The results suggested that an increase in cost bias and BIS significantly increased SAD symptoms. Further, the interaction effect between cost/probability bias and BAS was not significant for LSAS-Fear (cost bias: $\beta = -0.05$, *n.s.*; probability bias: $\beta = 0.18$, *n.s.*), whereas that between cost bias and BAS was significant for LSAS-Avoidance ($\beta = -0.32$, $p < 0.05$). Simple slope analysis showed that the slope of cost bias was significant for low-BAS ($\beta = 0.77$, $p < 0.001$) but not high-BAS ($\beta = 0.21$, *n.s.*) individuals. Further, the results revealed that the combination of low BAS and high cost bias increased avoidance. The interaction effect between probability bias and BAS was significant for LSAS-Avoidance ($\beta = 0.40$, $p < 0.01$), as well. Further, simple slope analysis showed that the slope of probability bias was significant for low-BAS ($\beta = -0.53$, $p < 0.05$) but not high-BAS ($\beta = 0.17$, *n.s.*) individuals. The results showed that the combination of low BAS and low probability bias increased avoidance. **Figures 1**, **2** illustrate these results.

TABLE 1 | Demographic data for participants and the results of normality test ($N = 76$).

	Mean	***SD***	**Kolmogorov–Smirnov test**	
			Z	***p*-Value**
Social anxiety				
LSAS-Total	50.46	23.13	0.08	0.76
LSAS-Fear	27.97	12.26	0.08	0.67
LSAS-Avoidance	22.49	12.06	0.06	0.93
Cognitive bias				
Cost bias	31.25	8.41	0.09	0.60
Probability bias	31.49	9.00	0.07	0.88
Temperament				
BIS	20.70	4.00	0.08	0.73
BAS	37.67	6.76	0.07	0.83

LSAS = liebowitz social anxiety scale, BIS = behavioral inhibition system, BAS = behavioral activation system.

DISCUSSION

The current study examined the interaction effects between BIS/BAS and cost/probability biases on SAD symptoms. The results of Pearson's correlation analyses revealed significant positive correlations between BIS and cost bias, probability bias, and SAD symptoms. Further, multiple regression analysis detected significant interaction effects between cost bias and BAS and between probability bias and BAS for avoidance of social events. Simple slope analysis revealed that the slope of cost/probability bias was significant for low-BAS but not high-BAS individuals. In particular, low-BAS individuals who estimate that there will be a high cost or low probability of social events tend to avoid them. On the other hand, even if high-BAS individuals overestimate the cost or probability of social events, the anticipation of positive outcome occurrence may supersede their tendency to avoid social events. These results were consistent with the first hypothesis that BIS is positively correlated with cost/probability bias and SAD symptoms. Further, the second hypothesis was that low-BAS individuals with high-cost/probability bias presented increased SAD symptoms. The results of the multiple regression analysis of avoidance of social events partially confirmed the second hypothesis, whereas high-BAS individuals did not experience increased SAD symptoms regardless of the degree of their cost/probability bias.

Regarding the first hypothesis that BIS is positively correlated with cost/probability bias and SAD symptoms, the current results conform to the findings obtained by other researchers. BIS is proposed to trigger response to threatening stimuli or expectation of such stimuli. Thus, high BIS may cause cognitive biases such as negative belief and negative expectation in

TABLE 2 | Pearson's correlations between variables ($N = 76$).

	1	2	3	4	5	6	7
Social anxiety							
1 LSAS-Total	–	0.95*** [90.98]*	0.95*** [90.98]*	0.54*** [22.76]*	0.29* [00.54]*	0.44*** [09.70]*	−0.01
2 LSAS-Fear		–	0.81*** [63.91]*	0.61*** [31.80]*	0.27* [05.47]*	0.41*** [05.67]*	−0.04
3 LSAS-Avoidance			–	0.42*** [07.68]*	0.29* [07.48]*	0.44*** [08.69]*	0.01
Cognitive bias							
4 Cost bias				–	0.52*** [19.75]*	0.37** [09.60]*	0.003
5 Probability bias						0.42*** [07.68]*	0.04
Temperament							
6 BIS						–	0.32** [03.56]*
7 BAS							–

*LSAS = liebowitz social anxiety scale, BIS = behavioral inhibition system, BAS = behavioral activation system. Values enclosed in parentheses represent the 95% confidence interval for each parameter. *p < 0.05, **p < 0.01, ***p < 0.001.*

TABLE 3 | The results of multiple regression analysis ($N = 76$).

Variables	LSAS-Fear		LSAS-Avoidance		VIF
	β	95% Confidence interval	β	95% Confidence interval	
Cognitive bias					
Cost bias	0.64***	0.40–0.88	0.49***	0.23–0.75	1.87
Probability bias	−0.24†	−0.48–0.00	−0.18	−0.44–0.08	1.85
Temperament					
BIS	0.33**	0.11–0.55	0.35**	0.11–0.58	1.51
BAS	−0.10	−0.29–0.10	−0.04	−0.25–0.17	1.20
Cognitive bias × temperament					
Cost bias × BAS	−0.05	−0.29–0.19	−0.32*	−0.58–−0.06	1.84
Probability bias × BAS	0.18	−0.06–0.42	0.40**	0.14–0.66	1.84
Cost bias × BIS	0.17	−0.04–0.38	0.12	−0.11–0.34	1.43
Probability bias × BIS	−0.15	−0.36–0.06	0.01	−0.22–0.24	1.45
R^2	0.42***		0.31***		

*LSAS = liebowitz social anxiety scale, BIS = behavioral inhibition system, BAS = behavioral activation system, VIF = variance inflation factor. †p < 0.10, *p < 0.05, **p < 0.01, ***p < 0.001.*

threatening situations (Kimbrel, 2008) and high-BIS individuals might tend to avoid danger, in general (Peters and Slovic, 2000). Avoidance of danger might mediate the relationship between BIS and SAD symptoms (Lorian and Grisham, 2010). Therefore, high-BIS individuals would overestimate the potential social costs and exaggerate the probability of negative outcomes of social events. The cost/probability biases might activate the behavioral immune system and exacerbate the individuals' avoidance of social events. Avoidance of danger might strengthen the individuals' cognition of negative outcomes (Maner and Schmidt, 2006), and SAD symptoms might be negatively reinforced and maintained in these individuals.

The second hypothesis, that the coefficient of the interaction effects between BAS and cost bias and between BAS and probability bias on SAD symptoms is negatively significant, was confirmed only for cost bias on the avoidance symptoms of SAD. In addition, regarding probability bias, the results showed that a low probability bias might increase the avoidance symptoms of SAD; this result was inconsistent with our hypothesis and earlier reports (e.g., Shirotsuki et al., 2010).

First, we consider the results on cost bias. BAS has been proposed to promote goal-oriented behavior (Gray, 1970). Based on an earlier study on how a low BAS represented an additional risk factor for social anxiety (Kimbrel, 2008), if low-BAS individuals overestimate the cost of social events, their cost bias

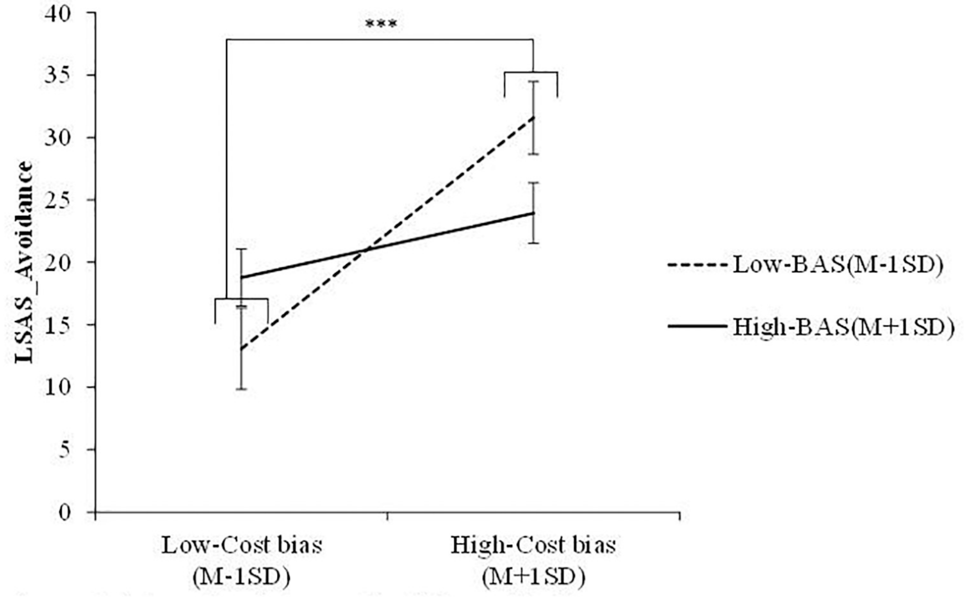

FIGURE 1 | Interaction between cost bias and BAS. *LSAS* = liebowitz social anxiety scale; *BAS* = behavioral activation system. ***$p < 0.001$.

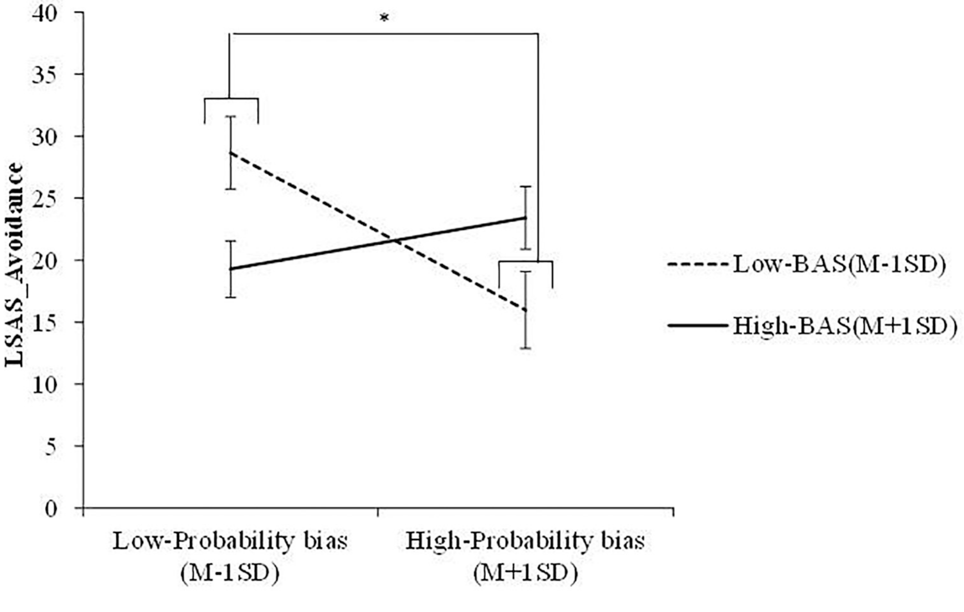

FIGURE 2 | Interaction between probability bias and BAS. *LSAS* = liebowitz social anxiety scale; *BAS* = behavioral activation system. *$p < 0.05$.

might activate the behavioral immune system and exacerbate avoidance of social events. Avoidance of danger might strengthen cognitions of negative outcomes (Maner and Schmidt, 2006) and help maintain SAD symptoms. On the other hand, high-BAS individuals might react strongly to a reward and attempt to achieve it. Even if high-BAS individuals overestimate the cost of social events and fear social events, they might try to attain the reward by experiencing the social events. Consequently, the attempt would indirectly decrease avoidance of social events.

Second, the relationship between probability bias and avoidance of social events was inconsistent with the findings of earlier studies, according to which overestimating the likelihood of a social situation's negative outcome would increase SAD symptoms (Hofmann, 2007). Since this result pertains to a rare occurrence, there is a possible that multicollinearity occurred. In order to confirm whether multicollinearity is an issue, Variance Inflation Factor (VIF) was calculated. The results showed that all values of VIF were less than 2, so multicollinearity is likely not an issue. Nevertheless, in order to confirm the robustness of the results, further studies should recruit a larger sample and examine the current study's findings again. It has been proposed that probability bias leads to social anxiety through factors other than those directly affecting social anxiety (Shirotsuki and Nomura, 2009). Shirotsuki et al. (2010) showed that probability bias increased cost bias and indirectly affected avoidance and anxiety. However, according to the correlation between cost bias and probability bias and the results of the interaction effect between cost bias and BAS on avoidance, there is a possibility that probability bias also leads to avoidance through other factors. Research on cognitive strategies suggests that individuals with unjustified optimism who have a negative cognition of past performance but have set positive expectations for the future tend to adopt self-handicapping or avoidance coping styles (Mitsunami, 2010). In other words, there are cases where individuals estimate future risk low and therefore are less motivated to manage current problems. Reducing future risk may be similar to situations with low probability bias. Our results here suggest that low-BAS individuals with low probability bias may engage in cognitive strategies that downplay future risk, believing that terrible outcomes are rare. For example, students might think that even if they are absent from a public presentation, they are unlikely to fail the class. Because of this bias, they may have little motivation to be exposed to stressful social situations. In contrast, low-BAS individuals with high probability bias may believe the future is very risky. For example, students might think that the absence from a presentation is highly likely to result in failing the class. This mentality drives social engagement as a way to prevent negative outcomes. Therefore, future studies should examine in more detail whether cognitive strategies reducing future risk could influence social avoidance.

Regarding why a difference was observed for avoidance but not fear, Shirotsuki et al. (2010) clarified that avoidance of social events increases fear of social events. Further, McManus et al. (2008) proposed that safety behaviors in SAD individuals might lead to higher anxiety. In contrast, Moitra et al. (2008) showed that anxiety about social events exacerbates avoidance and finally results in depression. However, in the current study, the main outcome was SAD symptoms rather than depression. Therefore, we have adopted the former model, according to which avoidance of social events increases the fear of social events. Since fear of social events might be a secondary reaction following avoidance of events, no difference can be observed in fear of social events in a cross-sectional study.

In addition, the results of Pearson's correlation analyses revealed significant positive correlations between BIS and BAS. Earlier studies have revealed that BIS and BAS are independent of each other (Carver and White, 1994). On the other hand, some studies have also reported correlations between BIS and BAS (e.g., Takahashi et al., 2007), as well. Takahashi et al. (2007) reported a weak correlation ($r = 0.12$, $p < 0.05$) between the BIS and BAS. This weak correlation might be caused by the effect of spurious correlation. Because BIS and BAS were assumed to correlate positively with neuroticism, the partial correlation coefficient between BIS and BAS controlling neuroticism was calculated. Results showed that there was no significant partial correlation coefficient ($pr = -0.05$, $p > 0.50$). Since the current study used the scale developed by Takahashi et al. (2007), the correlation between BIS and BAS in this study might also be affected by the effect of spurious correlation. Future studies should further assess neuroticism and examine the current study's findings.

Limitations and Future Directions

The current study has three main limitations. The first is our use of a student sample. We believe that future studies may benefit from replicating the findings using a clinical sample. Second, we did not conduct a social threat manipulation. Kimbrel (2008) proposed that socially threatening cognitions might occur only among socially anxious individuals under conditions of imminent social threat. Future studies should add a social threat manipulation and contextually examine the current study's findings. Third, the current study used a relatively small sample size. In the multiple regression analysis, although there were eight predictor variables in the model, the number of participants was only 79 (less than 10 participants per predictor), which is generally assumed to be the absolute minimum number (e.g., Wilson Van Voorhis and Morgan, 2007). Hence, further studies should recruit a larger sample and examine the current study's findings.

CONCLUSION

This study found interesting results regarding avoidance of social events. If low-BAS individuals overestimate the cost or underestimate the probability of social events, they tend to avoid them. On the other hand, in the case of overestimation or underestimation by high-BAS individuals, their desire to receive rewards tends to supersede their tendency to avoid social events. Although this topic requires additional research, our findings imply that the cost/probability bias toward social events may be the mechanism through which BIS and BAS exert their influence on SAD symptoms. Future studies should examine the change in avoidance symptoms of SAD while addressing cost/probability bias.

DATA AVAILABILITY STATEMENT

The datasets generated for this study are available on request to the corresponding author.

ETHICS STATEMENT

This study was carried out in accordance with the recommendations of the Ethical Guidelines for Medical and Health Research Involving Human Subjects, Ministry of Education, Culture, Sports, Science and Technology and Ministry of Health, Labor and Welfare. The current study did not involve invasiveness. All the participants were over 20 years of age. Therefore, we omitted the procedures concerning informed consent in accordance with the recommendations of the Ethical Guidelines for Medical and Health Research Involving Human Subjects. Further, completion of the questionnaire was considered informed consent. We provided both verbal and written explanations on informed consent to potential participants based on the recommendations of the Ethical Guidelines for Medical and Health Research Involving Human Subjects. Further, the participants were informed about the study's objectives, notified of the voluntary nature of participation, and assured of their data's anonymity and confidentiality. The protocol was approved by the Research Ethics Committee of Waseda University.

AUTHOR CONTRIBUTIONS

RI, NK, SY, and SS developed the research idea. RI, NK, SY, HI, and YT performed the data collection. RI performed the data analyses and wrote the first draft. All authors contributed to the revision of the manuscript.

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The Effect of Trait and State Disgust on Fear of God and Sin

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There is a growing literature suggesting disgust plays a major role in religiosity. However, the relationships between specific domains of disgust sensitivity and general religious fundamentalism or religious scrupulosity remains unknown and a lack of experimental data prevents the drawing of causal inferences about the potential effects of disgust on religiosity. Two studies are reported that examined the relationship between specific types of disgust sensitivity (i.e., pathogen, sexual, and moral disgust) and specific religious beliefs (i.e., fear of sin and fear of God). In the first study it was found that sexual disgust and pathogen disgust were significantly correlated with fear of sin and fear of God, respectively. In the second study the experimental induction of disgust led to greater fear of sin but not to the fear of God. These findings suggest that pathogen and sexual disgust sensitivities may serve as effective mechanisms for inflated scrupulosity. Taken together the outcomes from both studies converge on a greater understanding of the 'Human Behavioral Immune System' model that can account for social behavior with the evolution of adaptive benefit and perhaps more importantly highlights the possible drivers of specific religious behavior.

Keywords: disgust, scrupulosity, religion, sexuality, Human Behavioral Immune System (HBIS)

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INTRODUCTION

Even in today's secular society there is little doubt that the world's major religions have regulated social behaviors for centuries. There are still a wide range of social behaviors that are regulated in part by religious beliefs such as consumer psychology (Shyan Fam et al., 2004), alcohol consumption (Koopmans et al., 1999) and even organizational decision making (Fernando and Jackson, 2006). Yet despite such a pervasive role in the regulation of our social behavior very little is known about the mechanisms that influence or cause religious scrupulosity.

When considering the Judeo-Christian religion, there are two major factors that are thought to play a major role in motivating and maintaining individual religiosity (Weeden et al., 2008). The first is in-group solidarity, which can provide honest signals of group membership and commitment through complex codes of conduct while also serving as a barrier to out-groups (Fincher and Thornhill, 2008; Thornhill and Fincher, 2014b). The second is reproductive support by providing "low-promiscuity, marriage-centered, heterosexual, high-fertility sexual and reproductive strategies" (Weeden et al., 2008, p. 8). Here, such behavior is sometimes defined as being religious scrupulosity – literally translated to mean the *fearing sin where there is none* – (Abramowitz and Jacoby, 2014). Behaviors that occur as a result of such religious cognitions can be framed as both a fear of moral transgressions, e.g., the fear of committing sins and a fear of a lack of faith and piety, e.g., fear of god (see also Cohen and Rozin, 2001). Within a clinical context religious scrupulosity does have an overlap with obsessive behaviors where patients can manifest with overt behaviors to mitigate the effects of perceived moral transgressions while maximizing their self-perceived piety (Nelson et al., 2006).

In a non-clinical scenario such religious scrupulosity is correlated with conservative or traditional sexual and family attitudes and behaviors with religiosity increasing in the presence of perceived mating competition (Weeden et al., 2008; Li et al., 2010). In other words, religious scrupulosity may operate to prevent risk taking behaviors that might lead, in some circumstances, to pathogen transmission.

Scrupulosity can also be seen to play a major role in religiosity through enhanced self-monitoring of thoughts and behavior. As a result, a religiously scrupulous person is persistently concerned as to whether they have sinned in thought, word, or deed (Abramowitz et al., 2002). Psychometric research has revealed two dimensions of scrupulosity. The first is the fear of sin, in which individuals assess the frequency of their doubts and fears concerning their sins and the degree to which this affects their everyday life. The second dimension is the fear of God, in which the consequences of disobeying God are assessed (Olatunji et al., 2007a,b).

A growing literature has considered the role of disgust on the nature, extent, and expression of religious beliefs (e.g., Ritter et al., 2016). While this literature has focused on disgust sensitivity and general religious fundamentalism (Terrizzi et al., 2010, 2012b; Tybur et al., 2010) or specific forms of religious scrupulosity (Olatunji et al., 2005; Olatunji, 2008), there has been a dearth of research considering the relationship between discrete types of disgust sensitivity or even the emotional state of disgust (as in elevated state disgust) and specific forms of religious beliefs. The studies reported here attempt to address this gap and delineate the role of different types of disgust sensitivity and induced disgust on fear of sin and fear of God.

At first pass it may not be immediately clear how disgust can facilitate religiosity yet as is discussed above religion serves as an adaptive response to environmental threats such as infectious disease. The facilitation of specific reproductive strategies that are operationalized within certain religious codes is an example of a behavioral mechanism of this adaptive response. This class of behaviors can also be described within a theoretical model called the Human Behavioral Immune System (HBIS), which describes behaviors that have a role protecting individuals and groups from pathogens and infections by delineating psychological boundaries that separate the in- and out-group members (Schaller and Murray, 2011; Terrizzi et al., 2012a). There are obvious similarities here with religious organizations that define boundaries that are constructed to maintain a socially conservative value system focusing on "adherence to social norms, in-group cohesion and out-group avoidance" (Terrizzi et al., 2012a, p. 106). Indeed, the HBIS may be seen as operating on individuals through belief and behavior such as promulgating social organizations such as churches, prayer meetings, etc., and thus providing an environmental immune system of sorts; a system of behaviors that prevent contagion within the church by regulating social behavior and providing a social barrier from those outside the church (see Henneberg, 2011; Wiebe, 2013). In other words: "(A)lthough religion apparently is for establishing a social marker of group alliance and allegiance, at the most fundamental level, it may be for the avoidance and management of infectious disease" (Fincher and Thornhill, 2008).

Anti-pathogen behaviors that are promoted by the experience of disgust can foster the separation of members of an in-group population (i.e., the group to which the disgust holder belongs) from members of the outgroup population (i.e., the group which strangers belong). Such a separation would facilitate a general psychological tendency for social conservatism (see e.g., Schaller et al., 2015; Brown et al., 2016). Indeed, there is much evidence supporting the faciliatory role of pathogen stress in the development of social, political and even religious conservatism (e.g., Thornhill et al., 2009; Aarøe et al., 2017). Religious scrupulosity underpins religious fundamentalism yet the mediating role of pathogen stress on scrupulosity has yet to be explored.

Work suggests that disgust is more than a singular defense system that protects the body from pathogens (Rozin et al., 2008). Although multiple models for disgust exist (Rozin and Fallon, 1987; Olatunji et al., 2007c), one recent evolutionary-adaptive framework for disgust may be particularly salient to the understanding of religiosity (Tybur et al., 2009, 2010). Per the evolutionary theory detailed by Tybur et al. (2009), there are three domains for disgust sensitivity; three clusters of situations or contexts in which the basic emotion of disgust operates to facilitate individual, cultural, and evolutionary adaptation to promote survival and reproductive success. This particular model of disgust is comprised of pathogen, sexual, and moral domains of disgust sensitivity (Olatunji et al., 2007c, 2012; Tybur et al., 2009, 2010, 2012)[1].

The importance of disgust is further reinforced by an overview of the neurological substrates that mediate its experience (see Calder, 2003). In their extensive review of the neurological substrates that underpin the experience of the various forms of disgust Vicario et al. (2017) concluded that distinct forms of disgust may be represented by a number of overlapping and distributed networks that each converge at the anterior insula. This neural substrate has long been seen to play a fundamental role in the perception of facial display of disgust as well as the gustatory experience of bad tastes (Phillips et al., 1997, 1998).

The Role of Pathogen Disgust and the Fear of God

The importance of cleanliness is a significant feature in nearly all major religious affiliations (Preston and Ritter, 2012). Pathogen disgust likely mediates the rejection of out-groups that potentially pose the threat of contamination (Schaller and Murray, 2011). Thus, religious beliefs concerning purity may be related to negative attitudes toward out-groups including

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[1] Anecdotal evidence also suggests a possible link between the fear of sin as a regulatory social behavior within the finance industry (Hirshleifer, 2008).

homosexuals (Olatunji, 2008; Inbar et al., 2012; Terrizzi et al., 2012b), foreigners, and immigrants (Navarrete and Fessler, 2006; Hodson and Costello, 2007), and may stem from concern that these groups may potentially transmit pathogens and disease (Tybur et al., 2010). In addition to the direct mediation of attitudes about threatening groups, disgust may operate indirectly through religious beliefs and attitudes (Olatunji, 2008). Core disgust – which is highly akin to pathogen disgust – indirectly influences attitudes toward homosexuals through *fear of sin* and conservative sexual attitudes (Olatunji, 2008). In essence, Christian identification can serve as a marker of in-group conformance with norms of purity (Graham et al., 2009). This in turn can limit the potential for infection by pathogens coming from outsiders. Consistent with this is research suggesting diversity in religious groups increases alongside parasite stress levels (Fincher and Thornhill, 2008; Thornhill and Fincher, 2014a,b). As a result, it is hypothesized that pathogen disgust will predict religious scrupulosity generally and of fear of sin and fear of God specifically.

Sexual Disgust and the Fear of Sin

The link to conservative sexual attitudes and disgust is a relatively consistent finding across a wide body of literature (see e.g., Haidt and Hersh, 2001). Here, heightened disgust sensitivity affects behavior to such a degree that the efforts to keep oneself 'pure' may actually play a role in the formation of a variety of sexual disorders (Borg et al., 2011). The importance of the relationship between disgust sensitivity and the fear of sin in driving self-regulatory behavior can be seen with the work of Zhong and Liljenquist (2006). Here, it was found that threats to an individual's moral behavior which would be likely in the case of sexual conservative attitudes resulted in an increase in the perception of sin which also predicted an increase in cleaning behaviors (see also Fetterman, 2016).

Within social organizations such as religions, sexual disgust may be emphasized to avoid mating with individuals that may jeopardize reproductive success (Tybur et al., 2012). Indeed, specific in-group behaviors that are partially regulated by disgust toward out-group sexual behaviors has been shown to increase true paternity (and corresponding reduction in cuckoldry) in offspring (Strassmann et al., 2012). Such reproductive success is an important function of religions, especially as religions tend to champion high fertility and low promiscuity behaviors (Weeden et al., 2008; Li et al., 2010). According to Tybur et al. (2009) religion enhances fertility by setting, monitoring, and enforcing social group norms and values through "avoiding reproductively costly sexual behaviors, narrowing the pool of sexual behaviors and partners to those likely to contribute to the production of healthy viable offspring" (p. 106). At the same time, sexuality specific avoidance due to disgust allows for a range of beneficial social interactions that might have been precluded by pathogen-based disgust (Tybur et al., 2009; Borg and de Jong, 2012) while also limiting potentially reproductively costly within-group behavior. Due to fear of sin apparently being chiefly concerned with self-regulation to maintain in-group stability, it is hypothesized that sexual disgust sensitivity will be positively related with increased fear of sin.

Moral Disgust and the Fear of Sin

Moral disgust plays an important role for religious organizations by limiting potentially maladaptive behaviors that disrupt social relationships and their cohesion (Tybur et al., 2012; Chapman and Anderson, 2013; Russell and Giner-Sorolla, 2013). Moral disgust may be seen as most divorced from pathogen avoidance and response, yet utilizes many of the same physiological, psychological, and behavioral responses as pathogen and sexual disgust (Tybur et al., 2012). As a result, it is hypothesized that sensitivity to moral disgust will predict both fear of sin and fear of God.

Exploratory Analysis of Anxiety, Anger, Sex, and Religious Identification

Personality traits of anxiety and anger need to be considered in the formation of scrupulosity (Olatunji et al., 2005, 2007a). Trait anger is important for understanding in-group/out-group divisions through aggressive confrontation, not the avoidance propensity seen with disgust. Research considering the three dimensions of disgust has also shown sex or gender differences in response to pathogen, sexual and moral disgust, with females scoring higher in these scales (Tybur et al., 2009, 2010; Olatunji et al., 2012). Furthermore, in a study considering political conservatism, when controlling for the sensitivity to the various forms of disgust as noted above, men had significantly higher levels of religious fundamentalism than women (Tybur et al., 2010). Finally, to examine the effects of personal religious identification, participants were also asked to indicate whether they identified as either Christian or non-Christian.

THE DOMAINS OF DISGUST AND RELIGION

Methods

Participants

Previous research has regularly reported small effect sizes when studying the associations between disgust sensitivity and conservative attitudes. For example, Inbar et al. (2012) reported partial eta-sq. of 0.02 between DS-R total score and self-reported conservatism. Power analysis using G-Power 3.0 (Faul et al., 2007) suggested that, for the proposed multivariate regression, a minimum sample of 539 subjects would be required to detect a significant effect ($a = 0.05$) with moderate power (0.80) and a small effect size ($R^2 = 0.02$). A total of 545 adult (18-years or older) undergraduate students enrolled in introductory psychology courses at a large southern American university took part in this study; 523 participants completed all study questionnaires. The average age reported by participants ($n = 508$) was 19.49 ($SD = 3.29$) with a majority female (60.2%), Caucasian/white (87.8%), and belonging to "a Christian religion" (88.1%).

Measures

Revised Penn Inventory of Scrupulosity (PIOS-R; Abramowitz et al., 2002; Olatunji et al., 2007a) is a 15-item self-report religious scrupulosity scale that consists of two subscales: the 10-item fear of sin scale that measures fears of having committed a religious sin (e.g., 'I am afraid of having immoral thoughts') and the 5-item fear of God scale that measures fears of punishment from God (e.g., 'I worry that God is upset with me'). Items for this scale are based upon 5-point scales ranging from 0 ('never') to 4 ('constantly'). Internal consistencies for the two scales were strong (**Table 1**).

Three Domains of Disgust Scale (TDDS; Tybur et al., 2009) is a 21-item self-report scale that measures pathogen (e.g., 'Standing close to a person who has body odor'), sexual (e.g., Bringing someone you just met back to your room to have sex'), and moral disgust sensitivity (e.g., Forging someone's signature on a legal document'). Each factor is represented by 7 items that are measured on a zero to 6-point scale, ranging from 'not at all disgusting' to 'extremely disgusting.' The TDDS has strong psychometric properties (Olatunji et al., 2012) and is gender invariant (Tybur and de Vries, 2013). Internal consistencies of the TDDS factors in the current study were moderate (**Table 1**).

Trait Anger Scale: The Trait Anger Scale (STAXI-T; Vagg and Spielberger, 1979) is a 10-item self-report scale that measures the degree to which an individual experiences and expresses anger in general (e.g., 'I feel like hitting someone'). The STAXI-T utilizes a 4-point scale ranging from 1 ('almost never') to 4 ('almost always'). The STAXI-T had moderate internal consistency in the present study (**Table 1**).

Trait Anxiety Scale (STAI-T; Spielberger, 1983) is a 20-item self-report scale that assesses an individual's general level of anxiety over the past 2 weeks (e.g., 'I am tense'). The STAI-T uses a 4-point scale ranging from 1 ('not at all') to 4 ('very much so'). Internal consistency of the STAI-T was moderate in the present sample.

Procedure

All data were collected through an online questionnaire, an approach as reliable as in-person data collection (Coles et al., 2007 see also Smith and Senior, 2001). All participants provided IRB approved informed consent prior to completing the online protocol and were awarded course credit in exchange for their participation. The orders of questionnaire presentation were randomized.

Data Analysis

Bivariate correlations (see **Table 1**) were carried out prior to multivariate regression. Fear of sin and fear of God were separately regressed onto pathogen, sexual, and moral disgust, trait anger and anxiety, religious status (Christian vs. non-Christian) and gender (see **Table 2**). All predictors were entered simultaneously. Univariate distributions were normal and checks for multicollinearity revealed no major violations (see Tabachnick et al., 2007).

TABLE 2 | Religious scrupulosity linear regressions the variance inflation factors (VIF) are also shown.

		Fear of Sin	Fear of God
	VIF	β	β
Pathogen Disgust	1.85	0.05	0.17**
Sexual Disgust	2.44	0.26**	0.06
Moral Disgust	1.76	−0.03	−0.02
Trait Anger (STAXI)	1.21	0.15**	0.16**
Trait Anxiety (STAI)	1.21	0.35**	0.24**
Religion	1.11	0.19**	0.34**
Gender	1.43	−0.21**	−0.12*
F-Test (7, 512)		24.93**	24.49**
R^2		0.25	0.25
Adj. R^2		0.24	0.24

*$p < 0.05$; **$p < 0.01$.

Results

Fear of Sin

Save for moral disgust, all zero-order correlations with fear of sin were in the expected direction (positive) and statistically significant (**Table 1**). The fear of sin regression equation was significant and explained 25% of the overall variance ($F(2,7) = 20.13$, $p < 0.01$). All parameters, except pathogen and moral disgust (n/s), reached statistical significance at an alpha level of 5%. With the exception of moral disgust, all parameters functioned in the expected direction. Although moral disgust was associated with lower levels of fear of sin, the zero-order correlation between these two was positive, which suggests the negative beta likely resulted from suppression. When the relative influence of all variables is considered, sexual disgust ($\beta = 0.26$, $p < 0.01$), and trait anxiety ($\beta = 0.35$, $p < 0.01$) are the most powerful predictors. Higher levels of sexual disgust and trait anxiety are also associated with greater fear of sin. These variables are followed in power by participant gender ($\beta = 0.21$, $p < 0.01$),

TABLE 1 | Means, standard deviations, alphas and correlations for all measures used in the study.

		M	*SD*	α	2	3	4	5	6	7
1.	Fear of Sin – Revised	10.44	7.85	0.93	0.77**	0.17**	0.17**	0.07	0.24**	0.35**
2.	Fear of God – Revised	6.63	4.72	0.90		0.23**	0.13**	0.09*	0.23**	0.23**
3.	Pathogen Disgust	24.74	8.93	0.86			0.60**	0.56**	0.04	0.03
4.	Sexual Disgust	22.94	10.84	0.88				0.56**	−0.17**	0.13
5.	Moral Disgust	25.11	9.19	0.89					−0.09	0.17**
6.	Trait Anger (STAXI)	18.16	4.39	0.79						0.35*
7.	Trait Anxiety (STAI)	46.55	5.63	0.89						

*$p < 0.05$; **$p < 0.01$.

whether the participant identifies as a Christian ($\beta = 0.19$, $p < 0.01$), and finally, trait anger ($\beta = 0.15$, $p < 0.01$). Males and Christians are more likely to fear sin and higher trait anxiety is related to greater fear of sin.

Fear of God

All zero-order correlations with fear of God were in the expected direction (positive) and statistically significant (**Table 1**). The fear of God regression equation was significant and explained 17% of the variance ($F(2,7) = 24.49$, $p < 0.01$). The resulting model shows that whether or not the respondent identifies as a Christian is the most powerful predictor, with Christians endorsing greater fear of God than non-Christians ($\beta = 0.34$, $p < 0.01$). Trait anxiety ($\beta = 0.24$, $p < 0.01$) and pathogen disgust ($\beta = 0.17$, $p < 0.01$) are significantly and positively related to fear of God as well. Finally, participant gender plays a significant role with males reporting greater fear God than females ($\beta = 0.12$, $p < 0.05$).

Discussion

Results of the first study provide initial evidence that highlights the relationship between specific types of disgust sensitivity and religious fear. In particular, results suggest a positive relationship between two domains of religious scrupulosity and specific domains of disgust sensitivity with sexual disgust predicting a fear of sin and pathogen disgust predicting a fear of God. In the regression model, moral disgust negatively predicts fear of sin. However, as the zero-order correlation between moral disgust and fear of sin was positive and not significant, this effect was likely a statistical artifact. Further work should consider the possible mechanistic role that anger and anxiety play in scrupulosity as trait anger strongly and positively predicted both the fear of sin and the fear of God while trait anxiety positively predicted fear of sin. Taken as a whole, regression models suggest that negative affect likely plays a substantial role in scrupulosity but that specific manifestations of negative affect (e.g., trait anger and disgust sensitivity) are also implicated.

The present study advances the understanding of the relations between individual differences in emotional processing of religion in two ways. First, it provides evidence for specific emotional traits correlating with religious scrupulosity. Second, domain-specific relationships were found between disgust sensitivity and religious scrupulosity. The findings here provide preliminary evidence for the disease avoidance role of specific religious doctrine; sexual disgust predicted fear of sin and pathogen disgust predicted fear of God. It may be that scrupulosity increases due to disgust sensitivity, that disgust sensitivity is elevated because of scrupulous beliefs, or that some as-yet evaluated variables concomitantly influence both. For example, the observed relationships between disgust sensitivity and scrupulosity may be the result of the mostly Christian sample used, given that Christian participants endorsed greater scrupulosity and religious orientation was the most robust predictor of fear of God. This may reflect the fact that many Judeo-Christian-based religions tend to emphasize cleanliness in doctrine and rituals.

This first study highlights the possible relationship between individual differences in specific domains of disgust sensitivity and religious attitudes. If such propensities to disgust are relevant to the manifestation of specific religious attitudes and behaviors, as would be accounted for with the HBIS model, then the acute experience of disgust should also modulate specific religious activity. The second experiment was therefore carried out to assess whether the acute induction of disgust can influence attitudes about religious scrupulosity. Here it was hypothesized that the induction of disgust through pathogen-based pictorial stimuli will have the effect of increasing scrupulosity. More specifically, it was hypothesized that the induction of disgust would increase fear of God based upon the positive associations between this component of religious scrupulosity and pathogen disgust sensitivity. While pathogen disgust sensitivity was not significantly associated with fear of sin when controlling for the effects of other predictors in the regression equation, there remains a significant zero-order correlation between pathogen disgust sensitivity and fear of sin, suggesting that the induction of disgust may also increase fear of sin. This latter prediction is more speculative and is therefore treated as exploratory.

THE EXPERIENCE OF DISGUST AND RELIGION

Participants

Previous work from our group suggests that the experimental induction of disgust can exert large effects on self-reported religious attitudes. For example, an olfactory disgust induction increased self-reported belief in "biblical truth" to a large degree ($\eta_p^2 = 0.10$ to 0.18; Adams et al., 2014). The pictorial disgust induction used in the present study was not expected to be as powerful as in-person disgusting odors (see section "Discussion" below). As such, a medium effect size ($d = 0.50$) was used for power analyses, which suggested that, for the proposed mixed ANOVA and moderate power (0.80), a sample of 52 subjects would be required to detect a significant ($a = 0.05$) interaction effect and a sample of 112 subjects would be required to detect a significant between-subjects effect. Two hundred and four individuals entered the experiment's website, with 175 successfully completing the study. Of this number, 165 accurately identified one of the treatment images as a manipulation check, with 95 participants in the control condition and 70 in the treatment condition. The average age of participants was 25 years old ($SD = 8.38$), with the majority of participants female (78.8%), and identifying as Christian (87.9%).

Procedures

The entire experimental protocol was delivered online and consisted of the experimental condition in which participants viewed three disgust-inducing images (dog feces, vomit, a cold sore) and a control condition in which three neutral images were presented to participants (a chair, a tree, a mushroom). These stimuli were collected from the public domain and were matched for picture attributes (e.g., complexity etc.) These six images were selected from a total corpus of 14 images, which were first shown to a group of independent raters who were blind to the experimental hypothesis (11 female, with a mean age

19 years within the range 18–21 years). They were asked to rate each image on a 10-point scale for the dimensions of disgust[2], image complexity and also each the sexual content of each specific images. Of these the disgust images were matched for disgust content (Cold Sore MN = 7.3, *SD* = 1.7, Dog Feces MN = 7.5, *SD* = 2.8, Vomit MN = 7.3, *SD* = 2.4) and image complexity (Cold Sore 1.8, *SD* = 2.3, Dog Feces MN = 1.7, *SD* = 3.0 and Vomit MN = 2.4, *SD* = 1.9). These were distinct from the scores for the control imagery (Chair, Mushroom and Tree) which received an average rating of 1 for image complexity and were considered as having no disgust content at all by the raters. No image was considered to contain any sexual content.

Participants were asked to drag an indicator on a 0–100-point scale with the endpoints 'Not at all' and 'extremely to indicate the degree to which they felt disgusted by each of the experimental stimuli. The procedures were based upon that used by Smith et al. (2011) with participants viewing each image for 10 s apiece, with 5 s between each image. To verify participants were complying with the task they were asked to submit a description of one of the images they saw. Participants were also asked to complete the PIOS-R and TDDS items as described above. As with study 1 all possible orders of presentation were randomized throughout.

Data Analysis

Independent samples *t*-tests were performed to examine the effect of the image-based disgust induction on subjective disgust ratings. Mixed-factor ANOVA was then used to test the effects of the treatment (control vs. disgust induction) on scrupulosity (main effect of treatment) and the effects of the treatment on specific domains of scrupulosity (treatment by PIOS factor interaction). Independent samples *t*-tests were performed to probe significant interaction effects.

Results

After adjusting for the violation of homogeneity, there were significant differences in subjective disgust ratings, $t(163) = 11.68$, $p < 0.001$, between the treatment ($M = 68.03$, $SD = 38.51$) and control ($M = 8.50$, $SD = 21.35$) conditions. Here the experimental stimuli that were used in this study powerfully induced the experience of disgust with a Cohen's d of 1.91.

There was a significant main effect of the treatment on scrupulosity, $F(1,163) = 7.20$, $p < 0.01$, partial-$\eta^2 = 0.04$, suggesting that the disgust induction increased scrupulosity (control $M = 10.84$, $SE = 0.73$ and disgust $M = 13.83$, $SE = 0.85$). There was also a significant interaction between the treatment and PIOS dimension factor, $F(1,163) = 5.17$, $p < 0.05$, partial-$\eta^2 = 0.03$ (see **Figure 1**). *Post hoc* contrasts revealed that fear of God, which due to the findings of Study 1 was hypothesized to be increased by pathogen disgust induction, was not significantly different between participants in the disgust and control groups; though results were trending in the hypothesized direction, $t = 1.53$, $p = 0.13$, $d = 0.24$ (disgust group $M = 8.89$, $SD = 5.55$; control $M = 7.64$, $SD = 4.85$). On the other hand, participants in the pathogen disgust induction group did report significantly greater *fear of sin* than participants in the control group, $t = 2.73$, $p < 0.01$, $d = 0.42$ (treatment $M = 18.77$, $SD = 13.17$; control $M = 14.03$, $SD = 9.11$). There were no significant between group differences in sex, age, religion, moral disgust, sexual disgust, or pathogen disgust (all $p > 0.10$).

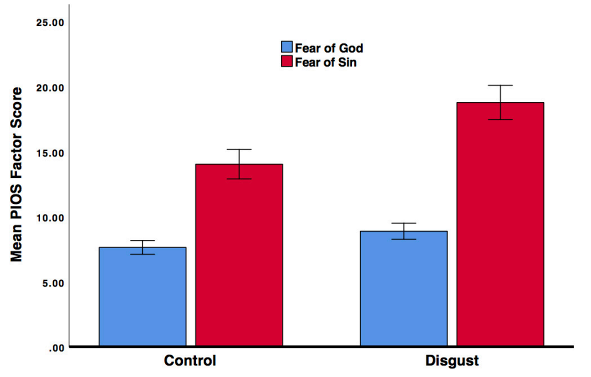

FIGURE 1 | The treatment effects on fear of God and fear of sin scrupulosity domains for the experience of disgust.

Discussion

The major findings are that the acute induction of disgust had a significant effect on scrupulosity and this effect was significantly pronounced for the fear of sin, but not the fear of God. These latter findings are somewhat unexpected given the findings from Study 1; regression analyses revealed a significant relationship between individual differences in pathogen disgust sensitivity and fear of God but not fear of sin. However, significant zero-order correlations were observed between individual differences in pathogen disgust and fear of sin and fear of God. One of the three images used to induce disgust in the second study showed an open sore under the lips of the model, which could be linked to sexual activity, and may have activated sexual disgust; however, this is unlikely given that all independent raters rated all three disgust induction pictures as having zero sexual content. The stronger effect of the disgust induction may be explained by the nature of the threats posed by the images in the disgust treatment condition. Specifically, feces, vomit, and open sores are addressed on a regular basis within social groups. Thus the connection with fear of sin may be expected due to that dimension's focus on the self-monitoring of everyday behavior.

GENERAL DISCUSSION

Researchers are increasingly appreciating the role played by disgust in religiosity, especially given the central role religion plays in informing social and political attitudes (Olatunji et al., 2007c; Olatunji, 2008; Thornhill and Fincher, 2014b). This study adds to and elaborates on the role played by disgust sensitivity and its induction on religious scrupulosity at the individual level, finding that not only do different types of disgust sensitivities

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[2] Raters were asked to look at each picture and decide how disgusting, complex or sexual each scene was and disgust images retained were those that scored within 1 SD of each other. We would like to thank the reviewer for prompting us to include this here.

play a role in specific types of religious scrupulosity, with fear of sin most strongly related to with sexual disgust sensitivity and fear of God with pathogen disgust sensitivity, but also that experimentally induced disgust influences religious scrupulosity, albeit at different levels for fear of sin and fear of God.

The implications of our findings are that higher levels of pathogen and sexual disgust sensitivity may play an important role in religious attitudes related to scrupulosity. With regard to the relation between sexual disgust sensitivity and fear of sin, both studies provide preliminary evidence for the disease avoidance role of proscribed behavior within religions. Results from these studies may be due, at least in part, to the mostly Christian sample used in this study. As many of the prohibited or sinful practices within Judeo-Christianity are sexual in nature, it may also be that sexual practices in general come to be associated with disgust through evaluative or other verbal forms of conditioning (Olatunji et al., 2007b). This alternative explanation may be even more viable, given that some items on the sexual subscale of the TDDS pose relatively little disease risk.

Although the current study provides strong evidence for the relation between trait and state disgust and religious scrupulosity, findings should be interpreted with caution due to several limitations. The relatively young and demographically homogenous sample limits the generalizability of both studies. Furthermore, the overwhelming majority of participants in both studies identified as Christian. As such, findings may not generalize to individuals of other religious backgrounds. Similarly, the measure for religious scrupulosity is largely based on a monotheistic perspective. It remains to be seen whether a more diverse religious perspectives both in sampling and measurement would result in a different outcome. While the findings from both correlational and experimental designs underscore the role of disgust both as a trait and an induced state, effect sizes were small to medium. Moreover, replication is necessary to more strongly support and accurately delineate the relationships between disgust and religious scrupulosity.

Geography may have also influenced the present results. Specifically, participants were drawn from a population tending to be raised and currently living in the states comprising the American South. This region is noted for being highly conservative, which according to Thornhill and Fincher (Thornhill and Fincher, 2014a) has beliefs that may be seen as partly driven by an "ideological defense against infectious diseases" (p. 6). In other words, many participants in both studies, in addition to being exposed to religious and cultural teachings that focus on in-group favoritism and out-group avoidance, as well as concomitant strategies of favoring tradition while avoiding new ideas and practices, may also have an accentuated response to pathogenic threat.

Further studies should consider the possible implications of the relatively large sample size for the first study, which was determined on the basis of previous work that had employed relatively large cohorts to examine disgust sensitivity and its predictive power for a variety of complex social processes that are similar to religious scrupulosity (Inbar and Gilovich, 2011). Such an approach is valid yet needs to be replicated with large and demographically representative samples to exclude the possibility of a false positive result (Forstmeier et al., 2017).

One further note for future work to consider is based on the theoretical and empirical premise of the work of Thornhill and colleagues (e.g., Fincher and Thornhill, 2008), which employed group wide analyses with countries or regions as units of analysis to elucidate the role of pathogen stress in the facilitation of in-group behaviors. It is worth noting that some scholars have argued that such a "Nation-unit analyses always suffer(s) from Galton's problem, in which units of analysis fail to ensure statistical independence" (Horita and Takezawa, 2018, p. 2). Such an issue can be addressed by grouping the units of analysis along shared demography (Murray, 2014). Indeed, future studies that integrate geographic factors into their exploration of the relationship between pathogen stress and religious scrupulosity should be mindful of these types of artifacts.

Taken together the findings from both studies inform our understanding of the Human Behavioral Immune System model and highlight the means by which this theoretical model can account for idiosyncratic religious attitudes. Results from these studies highlight the nuanced ways that individual differences in specific domains of disgust sensitivity and the acute induction of a disgusted state can influence distinct manifestations of scrupulosity.

DATA AVAILABILITY STATEMENT

The datasets generated for this study are available on request to any of the corresponding authors.

ETHICS STATEMENT

The study was reviewed and approved by the University of Arkansas IRB (Ref 12-02-494). All participants provided written informed consent.

AUTHOR CONTRIBUTIONS

All authors listed have made a substantial, direct and intellectual contribution to the work, and approved it for publication.

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ORIGINAL RESEARCH
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Visual Perception of Moisture Is a Pathogen Detection Mechanism of the Behavioral Immune System

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The behavioral immune system (BIS) includes perceptual mechanisms for detecting cues of contamination. Former studies have indicated that moisture has a disgusting property. Therefore, moisture could be a target for detecting contamination cues by the BIS. We conducted two experiments to examine the psychophysical basis of moisture perception and clarify the relationship between the perception of moisture and the BIS. We assumed that the number of high luminance areas in a visual image provided optical information that would enable the visual perception of moisture. In two experiments, we presented eight images of dough that contained different amounts of moisture as experimental stimuli. The amount of moisture shown in the images was increased in eight steps, from 28.6 to 42.9% of the total weight of the dough. In Experiment 1, the images were randomly presented on a computer display, and the participants (n = 22) were asked to rank the images in the order of the visually perceived moisture content. In Experiment 2, the participants (n = 15) completed pairwise comparisons based on the perceived moistness of the images. Furthermore, to examine the BIS responses, the participants rated the strength of disgust evoked by the stimuli, their motivation to avoid touching the stimuli, and the estimated magnitude of the risk of contamination by physical contact with the stimuli. The results indicated that the moisture content and the numbers of high luminance areas in the images accurately predicted the perception of moisture, suggesting that the detection of visual moisture was highly accurate, and the optical information served as an essential perceptual cue for detecting moisture. On the other hand, the BIS responses peaked in response to stimuli having approximately 33 to 39% moisture content. These results show that objects containing a moderate amount of moisture could be the target of visually detecting pathogens by the BIS.

Keywords: behavioral immune system, disease avoidance, pathogen detection, visual moisture perception, psychophysics

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INTRODUCTION

Infectious diseases are significant threats to our survival. The physiological immune system (PIS) protects us from these threats by resisting and eliminating pathogens in our body. One cost of this adaptive function is the sustained physiological burden on the body (Sheldon and Verhulst, 1996). The PIS is activated by the invasion of the body by pathogens. Therefore, humans are already at risk for infection by the time that the PIS starts to function. The behavioral immune system (BIS) is a motivational system that is oriented to the goal of avoiding diseases (Schaller and Park, 2011) and compensates for the limitations of the PIS by preventing physical contact with pathogens. The BIS is a psychological process consisting of several components, including a perceptual system for detecting pathogens, evaluating the threat of disease, and initiating avoidance behavior. An essential component of this motivational system is disgust, which has been considered to be an emotion for disease-avoidance (Matchett and Davey, 1991; Oaten et al., 2009; Tybur and Lieberman, 2016).

The concept of BIS is widely accepted today; however, the underlying psychological basis of the BIS has not been sufficiently clarified to date. Specifically, research focusing on the pathogen detecting process is relatively rare (Murray and Schaller, 2016). The perceptual detection of pathogens is positioned in the first phase of the psychological model of the BIS (Tybur and Lieberman, 2016). This suggests that the perceptual detection of pathogens plays a role in triggering the drive for later processing. There is evidence that perceptible cues suggesting the need to protect the self from disease can activate the BIS (Faulkner et al., 2004; Ackerman et al., 2009). It is also pointed out that emotional conditions and cognitive contexts might influence the detection process (Miller and Maner, 2012; Chan et al., 2016; Hunt et al., 2017), suggesting that this process works interactively with other components of the BIS. Therefore, it is necessary to clarify the psychological basis of the perceptual system for detecting pathogens to understand these interactions.

Specific studies have investigated the nature of the perceptual aspect of the BIS. Hunt et al. (2017) used psychophysical methods and reported that the induction of disgust enhanced tactile sensitivity such that it lowered the threshold for detecting tactile stimuli. Our skin is an anatomical barrier against pathogens. Therefore, skin lesions facilitate the intrusion of pathogens into the body and increase the risk of infections, suggesting that increased skin sensitivity might serve as a precursor to self-grooming behavior, which can decrease the risk of infection. Chan et al. (2016) found similar effects of disgust on the olfactory threshold. Odors can provide information about potential environmental hazards like food decay. Moreover, body products, which are regarded as disgust elicitors, are malodorous. In general, oral or tactile contact with such products that might contain pathogens is a risk to our health. Enhanced olfactory perceptual sensitivity facilitates pathogen detection and risk avoidance. The abovementioned studies have successfully investigated the perceptual aspect of BIS by using psychophysical methods. The purpose of psychophysics is to describe relationships between stimuli and psychological phenomena and identify mechanisms underlying these relationships, which was also the purpose of the current study. Therefore, we used psychophysical methods in this study.

The detection of pathogens by the BIS is not always accurate. Pathogens are microscopic, and they cannot be directly perceived by human beings. The detection process of the BIS consists of likelihood estimation using perceptible cues (Tybur and Lieberman, 2016). According to Schaller and Park (2011), this estimation is biased in favor of making false-positive judgments. This could be because although false-positive judgments in estimating pathogenicity can lead to subjective suffering and social dysfunctions due to excessive avoidance behavior and disgust, false-negative judgments might directly lead to a life crisis, and the false-positive bias is more advantageous for survival. Therefore, pathogenicity estimation by the BIS is tuned to a state of high sensitivity. As a result, the risk of infection can be overestimated when there are perceptual cues suggestive of pathogenicity, even in the absence of an actual risk of infection. This bias in the detection process is called *the smoke detector principle* (Nesse, 2005; Schaller and Park, 2011). The studies mentioned above (Chan et al., 2016; Hunt et al., 2017) also show that pathogen detection sensitivity fluctuates according to the state of activation of the BIS, which helps our survival, although it may cause psychosocial problems. For example, the fear of contamination is characterized by overestimating the pathogenicity of stimuli in the environment. Previous studies have indicated that the fear of contamination is one of the commonest themes in obsessive-compulsive disorder (McKay, 2006; Deacon and Olatunji, 2007), suggesting that the overestimating pathogenicity might be related to severe emotional and behavioral problems. Therefore, elucidating the process of detecting pathogens could potentially develop our understanding of psychopathologies, including obsessive-compulsive disorder.

Current Study

This study investigated the psychophysical basis of visual moisture perception. Generally, warm water containing nutrients is known to promote the propagation of miscellaneous bacteria. Therefore, physical contact with this type of water might carry the risk of contracting infectious diseases. As a result, there could be survival value in the ability to visually detect moisture without using touch. Previous studies have demonstrated that moisture can cause reactions of disgust (Oum et al., 2011; Thibodeau, 2016). These findings indicate that the sense of wetness might be a phenomenological cue used by the BIS to estimate pathogenicity. However, we cannot directly calculate the moisture content of an object from visual information. Therefore, it is reasonable to assume that humans use perceptible optical information to estimate the moisture content of an object.

We focused on perceived moistness as a visible cue used for the detection of pathogens by the BIS. Organic materials containing abundant nutrients that absorb water, such as feces or food paste, easily acquire pathogenicity through bacterial growth. These materials tend to change their surface shape based on the amount of water they contain. For example, the surface of dough containing a small amount of water is rough and relatively matt. However, when the amount of water in the dough increases, the dough becomes smoother and gelatinous, which further increases the water content until it becomes flat and liquid (**Figure 1**).

The law of reflection states that the surface condition of an object defines the angle of reflection (Bennett and Porteus, 1961). **Figure 1** shows the nature of reflection under different surface conditions. If the surface of the dough is rough, the incidental rays of light will strike areas that are inclined at different angles to each other, and therefore the reflected light rays would be diffused in irregular directions. However, if the

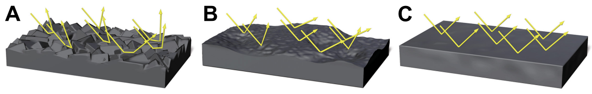

FIGURE 1 | Images representing the difference in surface shape of the dough and light direction due to changes in moisture content. Arrays represent light direction. A rough surface reflects light in irregular directions **(A)**. A relatively smooth and wet surface reflects light at angles that are closer to the incident rays **(B)**. A smooth and liquid-state surface reflects light at angles that are nearly identical to incident rays **(C)**.

surface is smooth and wet, the angle of the reflected light would be closer to the incidental rays. If the surface shape of liquid-like dough is flat, the angles of reflected light are nearly identical to the incidental rays. These characteristics change the perceived images of a light source when observed from a given angle to the object. Perceived images arising from a rougher surface might be segmented, whereas perceived images arising from a liquid-state surface might be more intact. Therefore, we predicted that the moisture content of an object could be estimated by the number of areas with high luminance. Based on this prediction, we focused on the number of high luminance areas contained in a stimulus image as a perceptible optical cue for the visual perception of moisture.

We conducted two experiments to clarify the process of visually detecting pathogenicity by the BIS. In Experiment 1, we used a simple ranking task consisting of sorting multiple images by quantifying the water content in the descending order of perceived moistness to evaluate the accuracy of visually estimating moisture. We also tested whether perceived moistness could be predicted by the number of high luminance areas in a stimulus image. Moreover, we investigated the BIS responses, including disgust, estimation of contamination risk, and the motive for avoidance behavior of stimuli, to clarify the amount of moisture that is used as a cue of pathogens. In Experiment 2, the replicability of the result of Experiment 1 was tested by using a pairwise comparison focusing on perceived moistness. Moreover, in both experiments, we used self-reports to assess the BIS responses directed toward the stimuli.

EXPERIMENT 1

We investigated the psychophysical basis of visual moisture perception and its relationship with the BIS responses in Experiment 1.

Methods

Participants

Female undergraduate students (*n* = 22, Mean age 20.46 years, *SD* = 1.97) participated in Experiment 1. The participants were recruited via an email invitation that explained the aims of the study and provided a brief description of the experimental procedure, the ethics of the study, and described the reward given to participants after completing the experiment (500 Japanese Yen, or approximately US$ 4.5).

Apparatus

Participants individually completed the experiment in a laboratory. Stimulus images were randomly placed in a 4 × 2 array and presented on a color-calibrated IPS-TFT LCD monitor (ColorEdge CG247, Eizo Nanao Corp., Tokyo, Japan). All responses were written and recorded on paper by the participants themselves. Participants sat in a chair that was placed approximately 60 cm from the display. However, no physical restrictions were placed on the distance between participants and the stimuli. Moreover, participants were able to observe the stimuli freely without being constrained by a time limit. The participants pressed the right key of the keyboard to move to the next ranking and rating task after completing each ranking and rating task. The entire experiment was controlled by the Microsoft PowerPoint program (Microsoft Corp., Redmond, WA, United States).

Materials

We presented pictures of dough (flour mixed with water) as the experiment stimuli such that the dough shown in each picture had a different moisture content. The moisture content was controlled using the following procedure. First, we mixed 90 g of flour with 10 g of black cocoa powder on a paper plate to color the dough for the easy identification of high luminance regions. Then, we added 2.5cc of water and mixed the dough using a plastic spatula. We made images of the stimuli by photographing the dough after adding 40cc or more water because the dough did not mix well with less than 40cc of water. The background of the photographs was kept constant, and the light source was set at a 45° angle of incident. A digital camera with a macro lens (20 mega-pixels; Canon, Tokyo, Japan) was set at the reflection angle of 135°, such that the area of specular reflection fitted in the center of the image and the distance from the light source to the dough was 60 cm. We placed the camera 20 cm away from the dough to capture the texture of the surface of the dough at a high resolution. The acquisition of all the pictures was completed in approximately 1.5 h.

We photographed the dough with the identical degree of moisture on three occasions, each time changing the surface of the dough with a spatula. We also photographed the identical dough after blocking the light source, although these photographs were not used in the study. There was no significant change in the appearance of the dough when the water exceeded 75cc. Therefore, we selected the experimental stimuli from images having a water content of 40 to 75cc with the width of water content set at 5cc. One image that included the identical amount of water was randomly chosen as a stimulus. The moisture content of stimuli was quantified using the ratio of the amount of water added to the total weight of the dough. Therefore, the moisture content was not measured directly but estimated. Eight images having a moisture content ranging from 28.57 to 42.86% were selected as stimuli (**Figure 2**). We used these images after converting them to a grayscale. All images were trimmed to 512 × 512 pixels, centered on the specular reflection area of the light source.

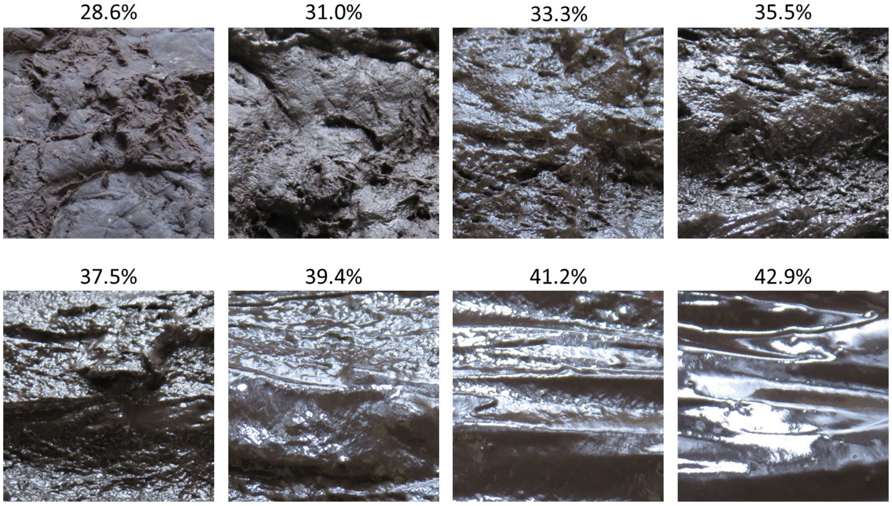

FIGURE 2 | Images of dough used as experimental stimuli in this study. The percentages shown above each image indicate the ratio of water added to the total weight of dough. This ratio represents the estimated water content in each stimulus.

Procedure

We examined the perceived moisture content of the stimuli by using a ranking task. The participants were asked to rank eight simultaneously displayed images in the order of increasing sense of moisture, to identify relative differences in appearance caused by changes in moisture content. The order of the stimuli on the display was randomized for each participant. The size of the presented images was 6 cm × 6 cm. Then, the participants rated the degree of disgust ("How disgusted do you feel about this object?"), motivation for avoiding physical contact ("How much do you want to avoid physical contact with this object?"), and perceived risk of contamination ("How much do you feel that you are likely to be contaminated by physical contact with this object?") for each image. The stimuli were presented consecutively in the rating phase. The rating was conducted by using a 10-point Likert scale ranging from 1 (*extremely weak*) to 10 (*extremely strong*), with higher scores indicating stronger feelings, which were used to assess the BIS responses.

Data Analysis

We conducted image analyses to count the number of high luminance areas included in the images by using the *particle analysis* function of an image analysis software (ImageJ 1.50: Schneider et al., 2012). **Figure 3** depicts the sequence of analysis. First, we set the threshold of luminance values to extract areas of high luminance. The average values and the variance of luminance in each image were different. Therefore, a threshold value was set as the luminance value closest to the upper 20% of each image, instead of determining a threshold. Next, we converted all images into a binary form based on this threshold to extract high luminance areas. We converted all pixels in the images that had a luminance value under the threshold to white (luminance value = 255) and all pixels that had a luminance value above the threshold to black (luminance = 0). Finally, we counted the number of independent black particles (not pixels) contained in these images. Pearson product-moment correlation coefficient was calculated between the amount of water contained in the dough and the number of particles to identify the relationship between these variables. The result indicated a nearly linear correlation ($r = -0.969$), suggesting that the number of particles accurately reflected the amount of water in the stimuli.

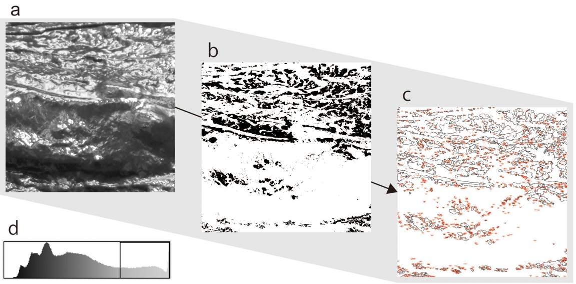

FIGURE 3 | Sequence of particle analysis of this study. All pictures were gray scaled **(a)**, and then binarized according to thresholds of luminance values **(b)**. Each threshold of pictures was set at a value that is closest to the upper 20% in the luminance histogram **(d)**. Finally, the independent black particles in the binary image were counted **(c)**.

We performed a series of regression analyses to clarify relationships between the variables examined in this study. First, we regressed the sense of moisture by the moisture content and the number of high luminance particles to clarify the psychophysical basis of visual moisture perception. Next, we regressed each BIS response by the amount of water to clarify the amount of moisture that is used as a cue of pathogens. We first applied linear regression analyses in these analyses. If the fitness of the linear model was insufficient, then we explored other methods such as polynomial regression analysis for curve fitting.

TABLE 1 | The water content, number of high luminance particles, and descriptive statistics of self-reported variables of each image used in used in Experiment 1.

Images	Water content	Number of particles	Sense of moisture		Disgust		Avoidance		Contamination	
			Mean	*SD*	Mean	*SD*	Mean	*SD*	Mean	*SD*
No.1	0.286	3986	1.09	0.43	2.95	1.81	4.50	2.18	5.05	2.19
No.2	0.310	2593	2.05	0.49	4.50	2.04	5.77	2.33	6.73	2.21
No.3	0.333	2170	3.50	0.80	5.55	3.19	6.64	3.17	7.95	2.52
No.4	0.355	1759	4.00	0.76	5.91	2.86	6.77	2.91	7.73	2.68
No.5	0.375	1522	4.64	1.22	5.27	2.43	6.77	2.43	8.09	2.37
No.6	0.394	1194	6.05	0.38	5.18	3.29	6.82	3.05	8.27	2.29
No.7	0.412	851	6.68	0.78	4.50	3.04	6.14	2.87	7.55	2.76
No.8	0.429	436	8.00	0.00	4.09	3.13	5.59	3.20	7.14	2.83

Moreover, we adopted identical analyses in Experiment 1 and 2 to confirm the replicability of the results.

Results and Discussion

Table 1 shows the descriptive statistics of all variables used in Experiment 1. We used the following scaling procedure for the sense of moisture. First, we inverted the rank values judged by the participants such that larger the value, the stronger was the sense of moisture. Next, we averaged these values for each stimulus and used these averaged values as scale values of the sense of moisture. Furthermore, we computed the standard errors for each stimulus. The procedure for calculating standard errors of scale values has not been established in Guilford's (1954) normalized-rank method, which is a well-known scaling method of ranked values. In the present study, we applied the above procedure by giving priority to reporting interval estimates.

We conducted a series of regression analyses to examine the psychophysical basis of sense of moisture (**Figure 4**). Results indicated that the water content accurately predicted the subjective sense of moisture (R^2 = 0.99, $F(1,6)$ = 227.30, $p < 0.001$), suggesting that the visual perception of moisture accurately reflected the relative amount of water contained in the stimuli. Furthermore, particles with high luminance in the images accurately predicted the sense of moisture (R^2 = 0.91, $F(1,6)$ = 69.49, $p < 0.001$), indicating that the distribution of high luminance particles on the object surface could be used as a perceptual cue for visually evaluating moisture.

We conducted another series of regression analysis to examine the BIS response to the stimuli (i.e., disgust, motivation for avoidance, and the estimation of the risk of contamination). Results showed that linear models did not fit well (R^2 = 0.09, 0.03, 0.25, respectively). We inferred from the shape of the distribution that the relationship between each BIS response and water content approximated a quadratic curve (**Figure 5**). Therefore, we conducted quadratic multinomial regression analyses and compared the fitness of the quadratic models with linear models by using the Bayesian Information Criterion (*BIC*). The results indicated that the quadratic curve model provided a better fit for all the variables (**Table 2**). The quadratic curve showed an upward convex shape, indicating that moderate amounts of water (i.e., from 33.3 to 39.4%) tended to result in peak BIS responses. The omnibus effect size of water content was larger for contamination risk estimation and moderate for disgust and the motivation for avoidance (**Table 2**). These results suggested that optical information reflecting a moderate amount of water could be used as a perceptual cue for the detection of pathogens by the BIS.

EXPERIMENT 2

Experiment 1 indicated that the moisture content and the number of particles accurately predicted the sensation of moisture. Furthermore, the ratings of disgust, avoidance, and the perceived risk of contamination peaked for a moderate amount of moisture. We conducted a second experiment using a different methodology to test the replicability of the findings of Experiment 1.

Methods

Participants

Female undergraduate students (n = 15, Mean age 20.93 years, SD = 2.34) participated in Experiment 2. We recruited all participants via an emailed invitation that explained our research aims and provided a brief description of the experimental procedure, ethics, and reward for participation. No participants in Experiment 2 had taken part in Experiment 1. The participants received 500 Japanese Yen as a reward for taking part in the experiment.

Material and Procedure

The stimuli used in Experimental 2 were the identical eight pictures of dough used in Experiment 1. In Experiment 2, we used the paired comparison method (Thurstone, 1927), which is one of the most common methods used in psychophysics experiments. The nature of a stimulus can be quantified by using this method and on a specific axis of evaluation. The purpose of this study was to quantify the perceived moistness of stimuli, and the paired comparison method was ideal for this purpose. We used the Bradley-Terry (BT) model (Bradley and Terry, 1952; Bradley, 1984; Turner and Firth, 2012) to convert the paired comparison data to a psychophysical rating scale, because the BT model can estimate confidence intervals more robustly than the Thurstone's Case V model (Tsushima et al., 2016). We developed

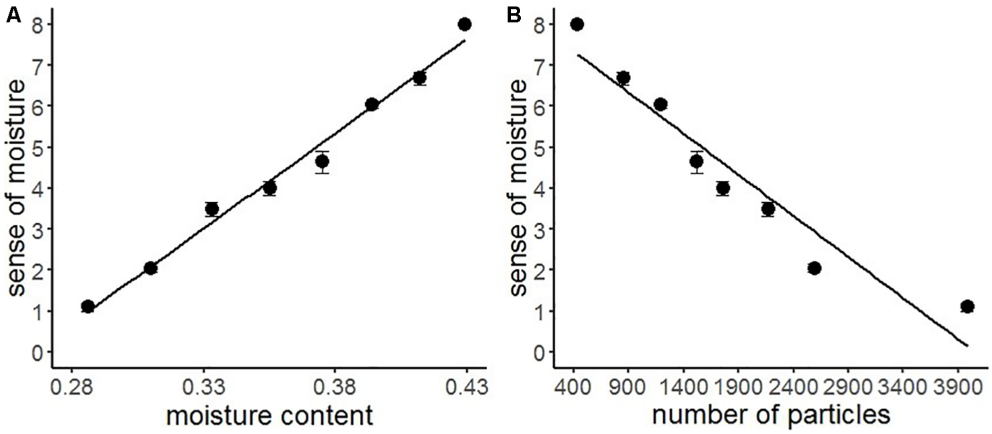

FIGURE 4 | Regression analyses of sense of moisture by moisture content **(A)** and number of high luminance particles **(B)** with the regression line of Experiment 1. Bars represent standard errors.

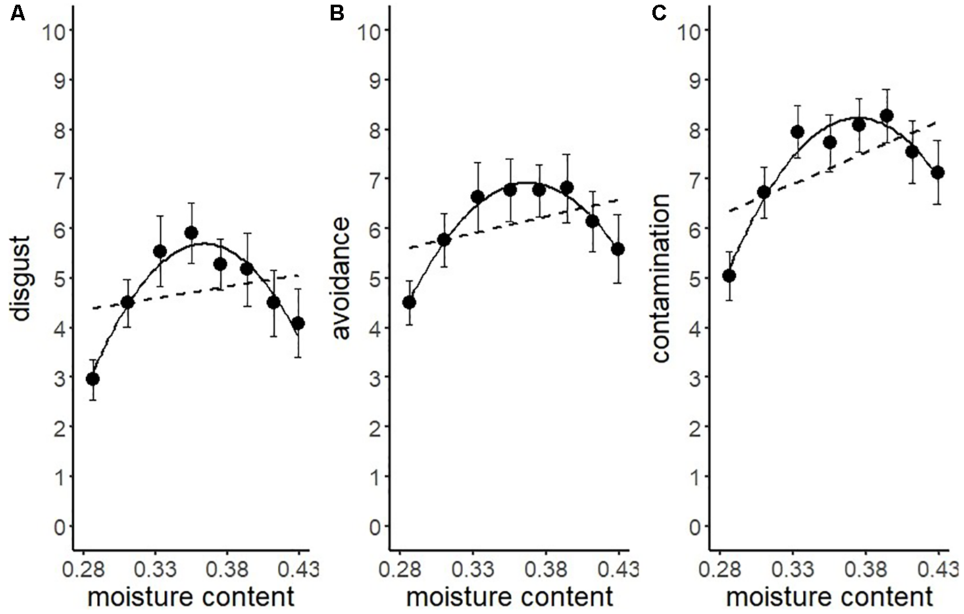

FIGURE 5 | Linear versus quadratic regression of disgust **(A)**, motivation for avoiding physical contact **(B)**, and perceived risk of contamination **(C)** in Experiment 1. Broken lines represent the linear equation, and the solid line represents the quadratic equation. Bars represent standard errors.

the paired comparison task in this study as follows: The eight images of the dough were combined to construct 28 stimulus pairs. These stimulus pairs were presented one at a time, such that the images were placed on the left and right sides. The size of the presented images was 16.14 cm × 16.14 cm. Each pair of stimuli was presented twice by interchanging left and right images to control for the influence of the presentation position. As a result, 56 paired comparisons were presented in one block in four blocks, resulting in 224 trials. Therefore, the participants performed the paired comparison judgment eight times for each stimulus pair. Since there were 15 participants in the experiment, the total number of comparison judgment for each pair was 120 judgments. The presentation order of the stimulus pairs was randomized for each block. The participants were requested to choose the image that gave them the strongest feeling of moistness. Eight practice trials were conducted before the experiment, in which the participants chose the more beautiful image from two images of landscapes.

The participants completed the task using nearly identical apparatus as in Experiment 1. We used a chinrest for all participants during Experiment 2 to fix the distance from the display and the participant's face with the distance set at 60 cm. The task presentation was controlled by PsychoPy version 1.90.3 (Peirce et al., 2019). Responses were obtained by using a keyboard, such that the left image was selected by pressing the F key, and the right image was selected by pressing the J key.

TABLE 2 | Summary of the regression analyses conducted in Experiment 1.

Variables	*BIC*		Quadratic coefficient of quadratic equation	Effect size of water content	
	Linear	Quadratic		η^2	95% CI
Disgust	26.41	6.78	−431.546	0.091	0.001–0.146
Avoidance	23.07	−6.19	−358.717	0.062	0.000–0.105
Contamination	24.98	6.89	−395.479	0.139	0.029–0.205

BIC is Bayesian Information Criterion of linear and quadratic equations for each variable. The quadratic coefficient of quadratic equations and η^2 *are shown for summarizing the shapes of the quadratic curve.*

When the key was pressed, it automatically shifted to the next stimulus pair. As in Experiment 1, we asked the participants to rate the strength of disgust, motivation for avoiding physical contact, and the perceived risk of contamination for each image using a 10-point Likert scale.

The eight images for each item were presented in random order. This rating procedure was repeated four times to obtain a stable rating for these items. The mean ratings for each image were used in the analysis.

Results and Discussion

Table 3 shows the descriptive statistics of all the variables used in Experiment 2. According to the above-mentioned data analysis plan, we conducted a series of regression analyses of psychophysical data of visual moisture perception (**Figure 6**). The result of regressing the sense of moisture by water content indicated that the water content accurately predicted the sense of moisture ($R^2 = 0.93$, $F(1,6) = 77.17$, $p < 0.001$). Furthermore, we regressed the sense of moisture by the number of high luminance particles ($R^2 = 0.97$, $F(1,6) = 179.00$, $p < 0.001$). The result indicated that the number of particles also accurately predicted the sense of moisture, which replicated the results of Experiment 1.

Another series of regression analysis indicated that the relationships between the BIS responses (disgust, motivation for avoidance, and the estimation of the risk of contamination) and water content, fitted a quadratic curve (**Figure 7** and **Table 4**). The quadratic coefficients indicated that the curves were relatively gentle, and all omnibus effect sizes of water content were smaller than in Experiment 1 (**Tables 2**, **4**). Similar to Experiment 1, these results supported the description of the BIS responses as a quadratic function of water content. However, it also suggested that factors other than the water content affected the magnitude of the BIS responses. The participants were exposed to the stimuli more frequently in Experiment 2 than in Experiment 1, which might have resulted in the habituation of emotional elements in the BIS response. From a different perspective, contrast adaptation might have influenced the results of Experiment 2. Contrast adaptation refers to the phenomenon in which prolonged viewing of a stimulus with a specific contrast reduces the perceptual and neural sensitivity to a subsequent stimulus with a similar contrast (Blakemore and Campbell, 1969; Smirnakis et al., 1997; Solomon et al., 2004). The stimuli used in this study were stained black, and therefore, the contrast with the reflective area was generally high. We can speculate that continuous exposure to high contrast stimuli caused contrast adaptation to the corresponding contrast band. Recent study revealed that temporal contrast adaptation can alter the visual discomfort of flicker stimuli (Yoshimoto et al., 2019). The relationship between spatial contrast adaptation and visual discomfort has not been clarified to date. Nevertheless, we cannot rule out that such a perceptual change might have affected the strength of the BIS responses. Another explanation of the difference between the results of the two experiments might be related to individual variations in the intensity of the BIS responses including disgust emotion (Haidt et al., 1994; Van Overveld et al., 2006; Duncan et al., 2009). We did not control for individual differences in these experiments, which might have been a confounding factor. In future research, it would be necessary to consider possible individual differences in BIS responses.

In sum, the results of Experiment 2 generally replicated the findings of Experiment 1. However, the effect sizes of water content on the BIS responses were smaller than in Experiment 1.

GENERAL DISCUSSION

In this study, we examined the psychophysical basis of visual moisture perception to elucidate the process of perceptually detecting pathogens by the BIS. Two experiments indicated that the visual perception of moisture could accurately estimate the

TABLE 3 | The water content, number of high luminance particles and descriptive statistics of self-reported variables of each image used Experiment 2.

Images	Water content	Number of particles	Sense of moisture		Disgust		Avoidance		Contamination	
			BT score	*SE*	mean	*SD*	mean	*SD*	mean	*SD*
No.1	0.286	3986	0.00	0.00	5.17	3.26	5.80	3.35	4.93	3.27
No.2	0.310	2593	2.11	0.13	5.10	2.83	6.10	2.88	5.68	2.78
No.3	0.333	2170	4.42	0.15	5.65	2.41	6.45	2.78	6.12	2.30
No.4	0.355	1759	4.61	0.15	5.73	2.43	6.75	2.42	6.27	2.19
No.5	0.375	1522	4.77	0.15	5.58	2.25	6.63	2.58	6.35	2.16
No.6	0.394	1194	6.31	0.15	5.42	2.88	6.28	3.07	5.98	2.59
No.7	0.412	851	6.48	0.15	4.80	2.55	6.18	3.12	5.82	2.65
No.8	0.429	436	7.50	0.16	4.32	2.84	5.42	3.22	5.48	2.81

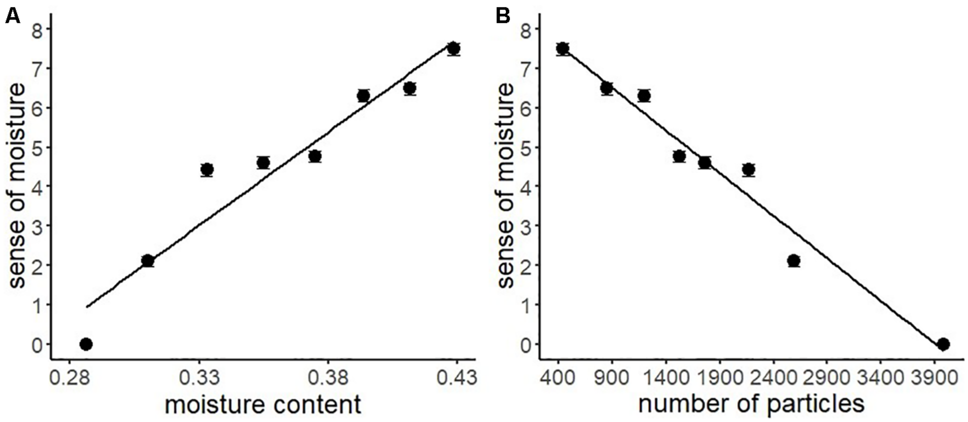

FIGURE 6 | Regression analyses of the sense of moisture by moisture content **(A)** and the number of high luminance particles **(B)** with the regression line of Experiment 2. Bars represent standard errors.

TABLE 4 | Summary of the regression analyses conducted in Experiment 2.

Variables	***BIC***		**Quadratic coefficient of quadratic equation**	**Effect size of water content**	
	Linear	**Quadratic**		**η^2**	**95% CI**
Disgust	14.36	1.77	−195.140	0.027	0.000–0.047
Avoidance	14.33	−1.57	−203.167	0.019	0.000–0.034
Contamination	15.01	−5.21	−212.980	0.027	0.000–0.047

BIC is Bayesian Information Criterion of linear and quadratic equations for each variable. The quadratic coefficient of quadratic equations and η^2 are shown for summarizing the shapes of the quadratic curve.

relative amount of water contained in perceived objects. Also, it was shown that the number of high luminance particles distributed on the surface of a stimulus image could be used as a perceptual cue for visually evaluating the moisture content. The BIS responses consistently approximated the quadratic function of water content, although the omnibus effect sizes of water content on the BIS responses varied in the two experiments. Moreover, the BIS responses peaked for stimuli with intermediate amounts of moisture. These findings suggest that humans can evaluate environmental stimuli by using their surface textures and identify stimuli that might be contaminated because such stimuli would seem disgusting, and possibly pathogenic. This study identified the characteristics of the BIS when visually detecting the possible existence of pathogens in an object.

Nevertheless, the evaluation of pathogenicity demonstrated in this study does not correctly reflect actual risks. According to the literature (Troller and Christian, 1978; Barbosa-Cánovas et al., 2007), bacterial growth depends on the *water activity*, which is defined by the ratio of vapor pressures of the solution and solvent. This definition suggests that higher amounts of water contained in an object results in higher water activity. Bacteria and germs are known to breed well when water activity is higher than their indigenous threshold. In other words, there would be sufficient free water available to bacteria and germs for breeding in an environment with high water activity. Such microbial breeding is directly linked to spoilage and the risk of infections. This suggests that an increase in water content would not reduce the risk of contamination at least within the middle to the higher range of water content, as was the case in the present study. However, our results showed that the BIS responses fluctuated in an inverted U-shape with the increase in water content, suggesting that the participants in this study underestimated the risk of stimuli containing too much moisture. As mentioned above, the estimation of pathogenicity by the BIS tends to be biased in favor of false-positive results. Nevertheless, the results of this study were not consistent with this notion because underestimating the risk of contamination for very moist stimuli would have resulted in false negative-results.

There are some possible explanations for the discrepancy between the actual and the estimated risk observed in this study. Firstly, it is known that the cognitive context plays a crucial role in determining the emotional responses toward moist objects (Iwasa and Komatsu, 2015). For example, the moistness of vegetables or fruits is sometimes recognized as a sign of freshness, whereas moistness was evaluated as disgusting in the present study. This could be because the appearance of stimuli with an intermediate amount of moisture that was used in this study shared similarities with disgust elicitors such as feces, while stimuli with low and high moisture might be seen as other objects such as certain types of food. The perception of this similarity might have acted as the cognitive context for strengthening negative responses. Therefore, it is possible that moistness is interpreted in combination with properties of perceived objects, rather than by itself. It is suggested that the influence of such top-down processing should be examined in future research. Especially, asking what the stimulus looked like might also help to examine this possibility. Secondly, the results of this study can be explained by the variability of the spatial frequency of stimuli. Many studies have suggested that high amplitude images in a specific spatial frequency range cause aversive response (e.g., Conlon et al., 2001; Fernandez and Wilkins, 2008; O'Hare and Hibbard, 2011; Cole and Wilkins, 2013; Sasaki et al., 2017). This effect is robust and could be a potential factor in explaining the results of this study. However, investigating these possibilities

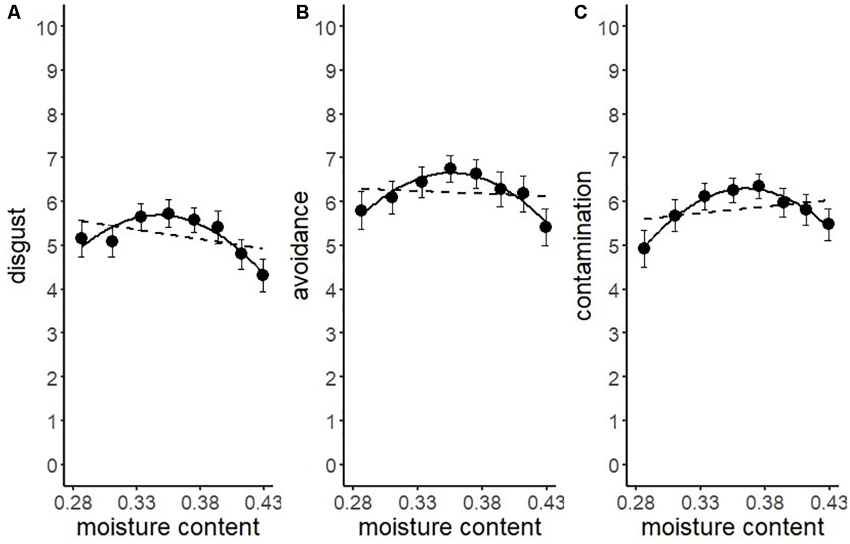

FIGURE 7 | Linear versus quadratic regression of disgust **(A)**, motivation for avoiding physical contact **(B)**, and perceived risk of contamination **(C)** in Experiment 2. Broken lines represent the linear the equation, and solid lines represent the quadratic equation. Bars represent standard errors.

was not within the scope of this study, and they remain to be investigated in future studies.

There are several limitations to this study. Firstly, we used only eight mixtures of dough as experimental stimuli, which limits the generalizability of our findings, because it is unclear whether the findings can be applied to materials other than dough. Sawayama et al. (2017) demonstrated that the surface color of wet objects looks more saturated, which suggests that perceptible cues of moisture might depend on the type of material. Furthermore, the number of stimuli used in these two experiments was small, which makes it difficult to conclude if the results reflect the general characteristics of dough or characteristics specific to the stimuli. This limitation can be solved by expanding the types of materials and the number of stimuli that are used in future experiments. Secondly, we applied only one image statistic, which is the number of high luminance areas based on the simple principle of reflection. Our results showed that this simple image statistic worked well for predicting the participant's perception of visual moisture. However, it is possible that the prediction could have been made more robust by adding other image statistics, such as components of spatial frequency, the number of low and medium luminance areas, and the skew of the luminance histogram (Motoyoshi et al., 2007), among others, which is a possibility that should be addressed in the future. More simply, the pictures used in this research differed in their surface shape and streaks. These differences could not be controlled because we photographed the actual dough. Manipulating the luminance distribution of a 3D rendered image of the same object could be a solution for controlling these potential confounding effects. Thirdly, we suggested in the introduction that visual moisture perception might represent a process for detecting pathogens that have implications for psychopathology, which is potentially a productive possibility. However, this study did not provide any empirical findings on this topic. It is suggested that the relationship between individual differences in visual moisture perception and the BIS responses should be addressed in future studies. Moreover, examining the influences of psychopathology, such as obsessive-compulsive disorder, on visual moisture perception could be an exciting possibility, which could provide clinical benefits in for assessment and treatment of psychological disorders. Finally, we did not determine the sample sizes of each experiment in advance. The present research was based mainly on model fitting for psychophysical variables. The evaluation of the fitness of regression models can be more accurate when the sample sizes and the number of trials are optimally designed prior to the experiments. There are some suggestions about optimal design for paired comparison model (Graßhoff et al., 2004; Graßhoff and Schwabe, 2008). Designing experiments based on such suggestions is crucial for future studies.

CONCLUSION

The results of this study showed that visual perception of moistness was accurate, and predicted by simple optical information. The BIS responses fluctuated in an inverted U-shape with the increasing water content in stimuli. These findings provided the first empirical support to the assumption that visual moisture perception serves as a part of the pathogen detection process of the BIS. On the other hand, this study raised new questions about underestimating the risk of contamination in stimuli showing a high content of water. The cognitive misestimation indicated by this finding, which is inconsistent with the smoke detection principle of the BIS, suggests the need for further research.

To the best of our knowledge, this is the first study to focus on the pathogen detection function related to visually perceiving moisture. Future research is needed to investigate detailed features of this function and its underlying mechanisms, including top-down processing. Progress in such research is expected to answer questions such as: What visual cues do people use for detecting the risk of infection? What psychological mechanisms enable the visual detection of cues suggestive of pathogens? What cognitive processes facilitate estimating the risk of infections and the biases in this process? Moreover, how do these cognitive processes affect our behavior and health? Exploring these questions will increase the sophistication of the BIS theory and its practical implications.

DATA AVAILABILITY STATEMENT

The datasets and stimuli used in this study are available in the Open Science Framework: https://osf.io/5quj9/.

ETHICS STATEMENT

This study was reviewed and approved by the IRB of the Shujitsu University, in Japan. Written informed consent was obtained from all the participants before participation in the study. Participation was voluntary, and participants were informed that they could withdraw from the study at any time without providing a reason.

AUTHOR CONTRIBUTIONS

KI and TK conceived and designed the study and interpreted the results. KI, AK, and YS developed the experimental stimuli and collected the data. KI analyzed the data. KI, AK, YS, and TK reviewed and edited the manuscript, approved the final manuscript in the current form, and agreed to submit the manuscript for publication in the frontiers in Psychology.

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Influence of Stress and Depression on the Immune System in Patients Evaluated in an Anti-aging Unit

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Background: There is compelling evidence pointing out that stress and depression produce a dramatic impact on human well-being mainly through impairing the regular function of the immune system and producing a low-chronic inflammation status that favors the occurrence of infections, metabolic diseases, and even cancer. The present work aims to evaluate the stress/depression levels of some patients treated in an antiaging unit and detect any potential relationship with their immune system status prior of the implementation of a physical/psychological program designed to prevent health deterioration.

Methods: We evaluated 48 patients (16 men and 32 women with a mean age of 55.11 ± 10.71 years) from middle-upper class from psychological and immunological points of view. In particular, we analyzed neutrophil chemotaxis and phagocytosis; lymphocyte chemotaxis and proliferation, and natural killer (NK) cell activity.

Results: Women showed more depressive symptoms than men. Chemotaxis levels of lymphocytes and neutrophils in women showed a significant reduction compared with those in men. We also found a strong negative correlation between depression and NK cell function. This correlation was also significant independently of gender.

Conclusion: We conclude that NK activity is affected at least by depression state, and we propose that a combined treatment consisting of cognitive behavioral therapy and physical activity programs might improve patient health deterioration.

Keywords: stress, depression, biological markers, exercise, cognition

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INTRODUCTION

Psychoneuroimmunology (PNI) is a multidisciplinary science that is focused on the interaction between the brain and the immune system and the possible clinical outcomes (Solomon et al., 1997). Clinically, PNI includes the knowledge of biological mechanisms subordinated to underlying psychosocial events that start and/or develop the immunological disease and the understanding of

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Abbreviations: C.p.m., counts per minute; LCI, Lymphocyte Chemotaxis Index; LP, lymphocyte proliferation; NCI, Neutrophil Chemotaxis Index; NK, natural killer; NPI, Neutrophil Phagocytic Index; PAN, phagocytic activity of neutrophils; PHA, phytohemaglutinin; PNI, psychoneuroimmunology; PSQ, Perceived Stress Questionnaire.

the immunological responses generated in psychiatric diseases. In the last part of the 1950s and at the beginning the 1960s, Rasmussen et al. (1957) elegantly demonstrated in laboratory rats the connection between aversive learning and the susceptibility to the infection produced by herpes virus. Independently in the 1970s, Solomon and de Vessye reported the first correlation between suffering long stress periods and the decreased antibody reactivity in animal models (Solomon, 1969; Solomon et al., 1974). Thus, PNI might represent a link among different disciplines such us psychiatry, psychology, neurology, endocrinology, immunology, neurosciences, internal medicine, and even surgery (wound healing).

Evidence supports the interaction between neuronal and immune systems. Thus, preliminary studies reported that psychosomatic observations were related to some autoimmune disease such as lupus erythematosus, Grave's disease, and rheumatoid arthritis (Solomon, 1969). Then, in the 1980s, it was demonstrated that lymphocytes were able to synthesize adeno corticosterone and β-endorphin molecules and not only produced exclusively by neuronal cells (Blalock et al., 1985). Guillemin et al. (1985) reported that hypothalamic response is increased after antigen administration and that the hypothalamic–pituitary–adrenal (HPA) axis is also activated by antigen presence and pro-inflammatory cytokines resembling stress conditions. The influence of stress, anxiety, and depression in allergies, dermatitis, and asthma has also been reported. These studies point to a delayed response of T and B cells which are activated in these situations (Gil et al., 1987; Pariante et al., 1994; Djurić et al., 1995). There is ample evidence supporting that depression and stress are related to cancer development (Burnet, 1971; Nakaya, 2014). Thus, in stress animal model, it has been reported a diminution of lymphocyte proliferation, natural killer (NK) cell activity, cytokine production, and an increase in the tumor size, angiogenic process, and metastasis (Monjan and Collector, 1977; Visintainer et al., 1982; Glaser et al., 1985; Ben-Eliyahu et al., 1991; Wu et al., 2000). Nowadays, there are compelling evidences demonstrating that pro-inflammatory status influences neurological function leading to changes in serotonin production which in turn induces depression (Leonard, 2010).

In humans, several studies have reported that depression or stress situations such as bereavement, a divorce, demanding work environment, or students in exam periods produce a decrease in NK, neutrophil, and lymphocyte activities such as lysis, proliferation, and chemotaxis, making the activities of these immune cells good markers of immune status in patients (Irwin et al., 1988; Schleifer et al., 1996; Andersen et al., 1998; Benschop et al., 1998; Byrnes et al., 1998; Bosch et al., 2005; Arranz et al., 2009; Boscolo, 2009). Stress and depression also modulate the production of hormones such as adrenaline, corticoids, and catecholamine that in turn influence the immune system (Leonard, 2010). It has been reported that stress, depression, and inflammation can activate and modify cytokine homeostasis (Kiecolt-Glaser et al., 2003). Cytokines might have a depressive effect well directly through releasing corticotrophin or indirectly increasing the resistance to activation of glucocorticoid receptors. This will cause a system hyper-activation due to the suppression of the normal feedback mechanism of the HPA axis.

Lymphocytes, neutrophils, and NK cells play an important role in the immune response against pathogens and tumor cells. Currently, it is easy to evaluate in a sample of blood oxidative activity and phagocytosis of neutrophils and its chemotaxis, which is to quantify the movement of the mentioned cells in a gradient of chemotactic agents (Matzner, 1987; Lord, 1989). In particular, Lymphocyte Chemotaxis Index (LCI), Neutrophil Chemotaxis Index (NCI), Neutrophil Phagocytic Index (NPI), lymphocyte proliferation (LP), and NK activity (NK lysis %) are markers routinely used for immune function evaluation. Immune biomarkers have been found altered in relation to stress or depression in previous studies (Khanfer et al., 2010; Vitlic et al., 2014; Duggal et al., 2015, 2016). Thus, chronic stress reduces chemotaxis of peripheral blood of mononuclear cells (Merry et al., 1996; Redwine et al., 2004), and phagocytic activity of neutrophils (PAN) has been reported downregulated in clinically depressed patients (McAdams and Leonard, 1993) as well as LP and NK activity have also been reported decreased (Esterling et al., 1996; Andersen et al., 1998; Scanlan et al., 2001; Gan et al., 2002; McGuire et al., 2002).

Nowadays, and given the aging population, more people want to receive a specific treatment focused on alleviating or delaying the effects of aging to get a better quality of life. We also believe that a psychological/physical program designed to prevent physical and physiological deterioration might achieve this goal. However, before implantation of this program, it would be necessary to know the depression and stress levels of each patient and his or her immunological status. Thus, we aimed to characterize the immune status in an middle-upper class population that is often under stressful conditions. We also wanted to explore if the patient's gender, given the differences between men and women from a psychological and physiological point of view, might affect these evaluations. Thus, in this study, we aimed to evaluate if there was any association between stress and depression status in patients who are under study in an antiaging unit and the levels of immune response markers in these patients prior to the implementation of a physical activity program to prevent physical and psychological deterioration.

MATERIALS AND METHODS

Study Design and Psychological Evaluation

We analyzed the immune system status of 48 patients (32 women and 16 men) who are classified under middle-upper class population according to Spanish settings who developed their professional life under stressful conditions. The patients were evaluated in an antiaging unit following a psyche–clinical evaluation to determine its basal status regarding biological age from a physical and psychological point of view.

We evaluated psychologically the patients through Beck Depression Inventory (BDI) (Beck et al., 1988) and Perceived

Stress Questionnaire (PSQ) (Sanz-Carrillo et al., 2002). Briefly, the BDI is a questionnaire that includes 21 items, each including four alternative statements ranging in order of severity from 0 to 3. Conventional cutoffs are 0–9 for normal range, 10–18 for mild to moderate depression, 19–29 for moderate to severe depression, and 30–63 for severe depression. Regarding the PSQ, this questionnaire evaluates with 30 items the stress levels of the patient. The questions have 4 degrees ranging from 1 equaling almost never to 4 meaning almost always. Then, an index is obtained that can range from 0 (low level of perceived stress) to 1 (high level of perceived stress).

This study was carried out following the guidelines of the Helsinki Declaration on human studies. The scientific-ethical board of the center approved this study. All patients were previously informed and signed the corresponding informed consent.

This study was carried out in our antiaging unit of our institution. Briefly, the antiaging unit focused on providing psychological and medical attention to patients who wanted to prevent their physical and cognitive deterioration. The patients were evaluated from a medical and psychological point of view, and the patients received a report in which the medical–psychological team decided the treatment that included pharmacological and psychological therapy together with physical exercise and nutritional recommendations.

Blood Sample Collection

Patients' blood samples were taken by venipuncture from an inner fold arm vein with Vacutainer® tubes between 8 and 10 a.m. and under starvation conditions. For serum hormone levels, one tube of 5 ml (containing separating gel and clot activator) was collected per patient. For immune cell functional assays, including lymphocyte proliferation, neutrophil phagocytic, lymphocyte/neutrophil migration, and NK activity assays, two tubes of 10 ml (sodium heparin) were collected per patient.

We evaluated the hormonal levels in the patients' blood samples, sexual hormones (progesterone, testosterone, estradiol 17β, prolactin), thyroids hormones [thyroid-stimulating hormone (TSH) and thyroxine (T4)], insulin, and insulin-like growth factor I (IGF-I).

Immune System Status

Specifically, regarding the immune system, we performed neutrophil function analysis chemotaxis index (NCI) and phagocytosis index (NPI); lymphocyte function analyses, chemotaxis index (LCI), and proliferation (LP); and NK activity (lysis %).

Neutrophil and Lymphocyte Isolation, Lymphocyte Proliferation Assay

Neutrophils were separated from peripheral blood using a Miltenyi magnetic column. Briefly, blood from a heparinized tube was labeled with antibodies against lymphocytes, monocytes, and leukocytes [antibodies against CD2, CD5, CD45R, and F4/80 and intercellular adhesion molecule (ICAM)-I]. Blood was added to a MACS column, and then passed through fraction was collected as neutrophil fraction (Cotter et al., 2001).

Lymphocyte Isolation and Proliferation Assay

We isolated the lymphocytes from Ficoll-Hypaque peripheral blood mononuclear cells of heparinized samples of patient's blood. After that, we adjusted lymphocyte concentration to 5×10^6 cells/ml and added mitogen stimulus phytohemaglutinin (PHA); no PHA was added to controls. We culture the cells for 68 h and then incubate the cells with 0.5 mCi of ^{3}H-thymidine for 4–6 h. We filtered the cultures with Whatman paper, and the filters were dried and counted in a γ-counter. Proliferation index was calculated as (cpm PHA stimulated cultures)/(cpm non-PHA stimulated cultures).

Neutrophil Phagocytic Assay

We evaluated PAN using Phagotest kits (Orpegen Pharma GmbH, Heidelberg, Germany) within 2 h of blood extraction. This kit evaluates neutrophil phagocytosis of fluorescein isothiocyanate-labeled opsonized *Escherichia coli*. Whole blood (100 μl) was incubated with 20 μl of fluorescent bacteria (2×10^7) at 37°C for 10 min, whereas a negative control sample remained on ice. Using a flow cytometer using a blue-green excitation light 488 nm argon-ion laser, we measure the mean fluorescent intensity corresponding to the number of bacteria phagocytosed by neutrophils.

Migration Assays for Neutrophil (Neutrophil Chemotaxis Index) and Lymphocytes (Lymphocyte Chemotaxis Index)

After isolation of mononuclear white cells from peripheral blood, we proceeded to migration assays. Chemotaxis assays were performed on Transwell chambers with 5.0 mm pore size inserts (Corning, Corning, NY, United States) as previously described (Figueroa-Vega et al., 2010). Lower chambers were filled up with RPMI-1640 culture media supplemented with 0.2% human serum albumin with or without recombinant human angiopoietin (Ang)-1 or Ang-2 at 100 ng/ml (R&D Systems). Monocytes (5×10^5 in 100 ml) were seeded into the upper chamber. After 2 h of incubation at 37°C, filters were removed, fixed, and stained with 4′,6-diamidino-2-phenylindole. Cells that had migrated and were attached to the lower side of the membrane were counted per field with an epifluorescence microscope. Results were expressed as the average number of migrated cells.

Natural Killer Cell Activity (Lysis %)

We have assayed NK cell activity as previously described (Davis et al., 2011). First, we isolated peripheral mononuclear cell from the blood of the patient that we have previously collected in heparinized tubes. Then, the NK cells were isolated using an NK Cell Isolation Kit (Miltenyi Biotec) according to the manufacturer's instructions. We stimulated NK activity by incubating the cells with interleukin (IL)-2 (100 U/ml), IL-18 (20 ng/ml), and IL-12 (5 ng/ml) overnight at 37°C. Then, we characterized NK cell cultured population using a fluorescence-activated cell sorting (FACS) analysis with a sample of cells that were added to 200 μl of PBE buffer: phosphate buffered saline (PBS), pH 7.2 0.5% bovine serum albumin (BSA), and 2 mM ethylenediaminetetraacetic acid (EDTA), with 5 μl of phycoerythrin (PE)-conjugated anti-CD56 and 5 μl PE/Cy5-conjugated anti-CD3 (Abcam). We labeled target cells K562 (5×10^5 cells) with 100 μCi of ^{51}Cr for 1 h at 37°C in 5% carbon dioxide (CO$_2$). Then NK cells were added to K562 cells in an effector–target ratio of 1:1 and incubated for 4 h a 37°C in 5% CO$_2$. After that, the supernatant was aspirated, and ^{51}Cr was measured in a γ-counter. We calculate lysis % following the formula [experimental release – spontaneous release]/[maximum release – spontaneous release] × 100.

Statistics

We use Mann–Whitney *U*-test to find out the differences in age between men and women. Spearman correlation (R) test was used to find the possible associations. SPSS v21 software ran the statistical tests. A $p < 0.05$ was considered significant.

RESULTS

Patient Description

This study included 48 patients who were visiting our antiaging unit in 2017. The average age was 55.11 ± 10.71 years with a variation coefficient of 19%. Data by gender are presented in **Table 1**. There were no significant differences in age between men and women. The hormone levels were within normal ranges for their respective ages (**Table 1**).

TABLE 1 | Patient's data and hormonal values.

Patients	Men	Women	Reference values
Number	16 (%, 33.3)	32 (%, 66.7)	n.a.
Age	52.56 ± 11.11	55.41 ± 10.16	n.a.
Sexual hormones			
FSH (mUI/ml)	7.2 ± 3.9	84.6 ± 24.6	Men: 1.4–18.1 Women: 0.5–76*
LH (mUI/ml)	5.3 ± 2.5	41.3 ± 17.8	Men: 1.5–9.3 Women: 0.5–76*
Estradiol 17-β (pg/ml)	n.d.	107.6 ± 53.9	Women 11–196*
Progesterone (ng/ml)	n.d.	11.8 ± 4.9	Women: 1–20
Prolactin (ng/ml)	n.d	14.7 ± 7.0	Women: 1.8–29.2
Testosterone (ng/ml)	3.6 ± 2.0	n.d.	0.86–7.88
Thyroid hormones			
TSH (μUI/ml)	3.4 ± 1.4	2.9 ± 1.6	0.35–5.5
T4 (ng/dl)	1.4 ± 0.4	1.3 ± 0.5	0.78–1.8
Insulin (mg/dl)	84.5 ± 11.2	78 ± 11.6	60–100
IGF-I (ng/ml)	131.4 ± 55	111.2 ± 48.1	43–220

*Data are mean ± standard deviation. n, number of patients. *Depends on menstrual cycle and postmenopausal status. n.a., not applicable; n.d., not determined. Estradiol 17β, progesterone, and prolactin levels were evaluated only in women, whereas testosterone was evaluated only in men. FSH, follicle-stimulating hormone; TSH, thyroid-stimulating hormone; LH, luteinizing hormone; IGF-I, insulin-like growth factor I.*

Depression and Stress Levels

One of our first tasks was to analyze depression and stress levels in our population. When we analyzed the levels of depression and stress in both men and women, we found that depression levels were significantly higher in women than in men ($p < 0.05$), mean difference 5.06; IC$_{95\%}$ = -0.062–10.19 (**Table 2** and **Figure 1A**). Then, we wanted to find out the stress levels in our patients. In this case, we did not find any differences in the stress levels between both genders (**Table 2** and **Figure 1B**).

Immune Status by Gender

Our next step was to figure out if there were differences in immune system response regarding gender. Thus, we found that men showed significantly ($p < 0.05$) higher values in the NCI and LCI values than women (**Table 3** and **Figures 2A,B**). However, regarding PAN, LP, and NK activity, we did not find any significant differences (**Table 3** and **Figures 2C–E**).

Correlations Between Stress, Depression, and the Immune System

Then, we analyzed the possible correlation between stress and the different immunological markers under evaluation. We found a trend ($p = 0.053$) between NCI and this stress (**Table 4** and **Figure 3**). However, we did not find any correlation between PAN, LP, NK activity, and stress. When we carried out this correlation analysis with depression, we found a strong correlation between NK activity and depression (**Table 5**; $p = 0.001$; $R = -0.604$, **Figure 4**), pointing out that when depression level is higher, the NK activity decreases.

Correlation of Immune Markers With Age

We also evaluated the possible correlation between quantified studied immune markers and patients' age. In this regard, we found a significant negative correlation between age and NCI ($p = 0.004$) and PAN ($p = 0.035$), meaning that immune system activation is impaired with age (**Table 6** and **Figures 5**, **6**). However, we did not find any correlation between LCI, LP, or NK activity with age.

Differences in Correlations by Gender

We analyzed separately the correlations by gender, and we found that the trend between stress and NCI was not significant for men but it was significant for women (**Table 7**). However, the correlation between depression and NK activity was also significant for each gender (**Table 8**).

TABLE 2 | Depression and stress levels.

	Men	Women	p
Stress	0.41 ± 0.10	0.38 ± 0.18	0.501
Depression	8.75 ± 5.92	13.81 ± 9.25	**0.027**

Data are mean ± standard deviation. p is the associated value to the corresponding statistical test.

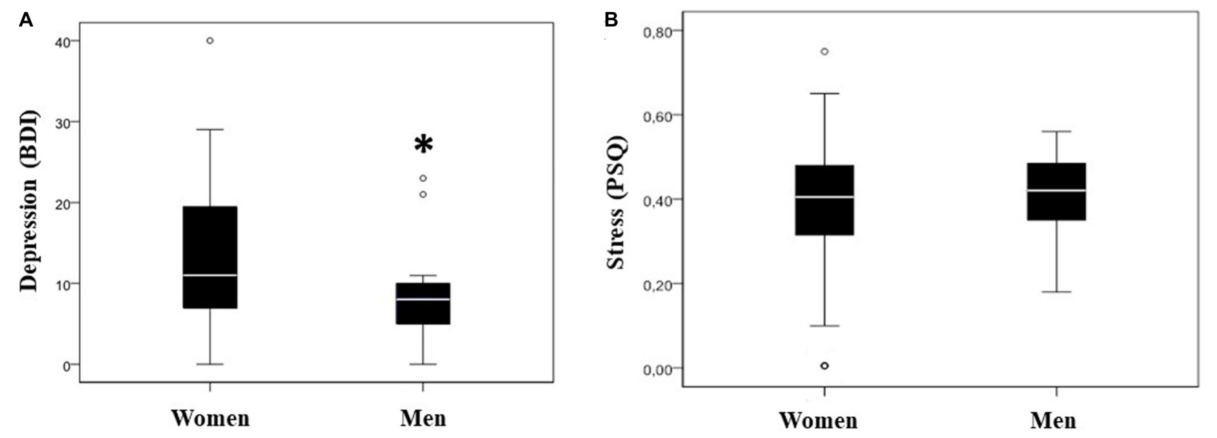

FIGURE 1 | Stress and depression levels. Box and whisker plots of stress and depression levels of the population under study (median is represented with a white bar). Depression levels evaluated by Beck Depression Inventory (BDI) **(A)**. BDI levels 0–9 for normal range, 10–18 for mild to moderate depression, 19–29 for moderate to severe depression, and 30–63 for severe depression. $^*p < 0.05$ vs. women depression levels. Stress levels evaluated by Perceived Stress Questionnaire (PSQ) **(B)**. PSQ level 0 means a low level of perceived stress, whereas a value of 1 is a high level of perceived stress.

DISCUSSION

It is well accepted that a good psychological status favors a better immune response against disease (Solomon, 1969; Solomon et al., 1974; Connor and Leonard, 1998; Bauer et al., 2009; Dragoş and Tănăsescu, 2010; Leonard, 2010; Stojanovich, 2010; Robson et al., 2017). Thus, several reports demonstrate that improving the psychological status through the use of social support techniques is related to an increase in survival in women with metastatic breast cancer or melanoma (Spiegel et al., 1989; Fawzy et al., 1993; Mustafa et al., 2013; National Collaborating Centre for Cancer [UK], 2015). Also, neuropsychological interventions using physical exercise of different tools related to cognitive improvement appear to slow cognitive decline (Levin et al., 2017). However, the effectiveness of psychological interventions in improving patient's biological status is under debate. Thus, a recent meta-analysis analyzing this relationship reported little evidence between the benefits of psychological treatments for depression and positive biological outcomes. This lack of effect might be due to methodological inconsistencies in the revised studies (Cristea et al., 2019).

TABLE 3 | Immune status by sex.

Marker	Men	Women	*p*
NCI	468 ± 29.27	350 ± 21.15	**0.032**
PAN (a.u.)	237 (144–329)	184 (147–393)	0.965
LCI	291 ± 22.46	185 ± 10.14	**0.002**
LP (cpm)	18,493 ± 1,481	15,202 ± 1,440	0.279
NK (lysis %)	42 ± 2.75	42 ± 7.24	0.955

NCI, Neutrophil Chemotaxis Index (number of cells); PAN, phagocytic activity of neutrophils (a.u., arbitrary units; range in brackets minimum and maximum); LCI, Lymphocyte Chemotaxis Index (number of cells); LP, lymphocyte proliferation (cpm); NK, natural killer. Data are mean ± SEM. p is the associated value to the corresponding statistical test.

Here, our aim was to characterize the status of immune response and its correlation with stress and depression in a group of patients before their participation in a psychological/physical program that designed to prevent physical and physiological deterioration. We treated more women (66.7%) than men (33.3%) in our antiaging unit in 2017. Of note, there were no significant differences in age between men (52.56 ± 11.11 years old) and women (55.41 ± 10.16 years old).

Women showed a basal level of depression of 13.81 in BDI related to a low-level depression. However, men only reach 8.75 points in this test, which is associated with no depression at all in BDI. It has been reported that women are twice likely to suffer depression during their life than men, and this might be caused by multiple reasons such as hormonal differences, cultural backgrounds, gender differences in social activities, and response to stressful situations (Wharton et al., 2012; Altemus et al., 2014; Kuehner, 2017). In our study, one of the causes of this ostensible increase might be explained because they are close to perimenopause period. Huge life changes in this period might be related to endocrine metabolic, sexual activity, and even family conflicts that lead to anxiety and depression (Gyllstrom et al., 2007; Maki et al., 2018; Willi and Ehlert, 2019). Regarding basal stress levels evaluated through the PSQ questionnaire, both genders showed medium scores that means that men and women are inside the range of moderate stress (men 0.41 and women 0.38), although there were no significant differences. This moderate stress levels might be related to a high working demanding environment (senior executives), aging related to a perception of cognitive and physical outputs, and even with the social commitments belonging to their high economic level.

In our study, we have found significant differences between genders in NCI and LCI parameters being both significantly greater in men than in women. We have to underline that our patients are stressed but not depressed or in the lower phase of depression and probably they are not yet immunologically

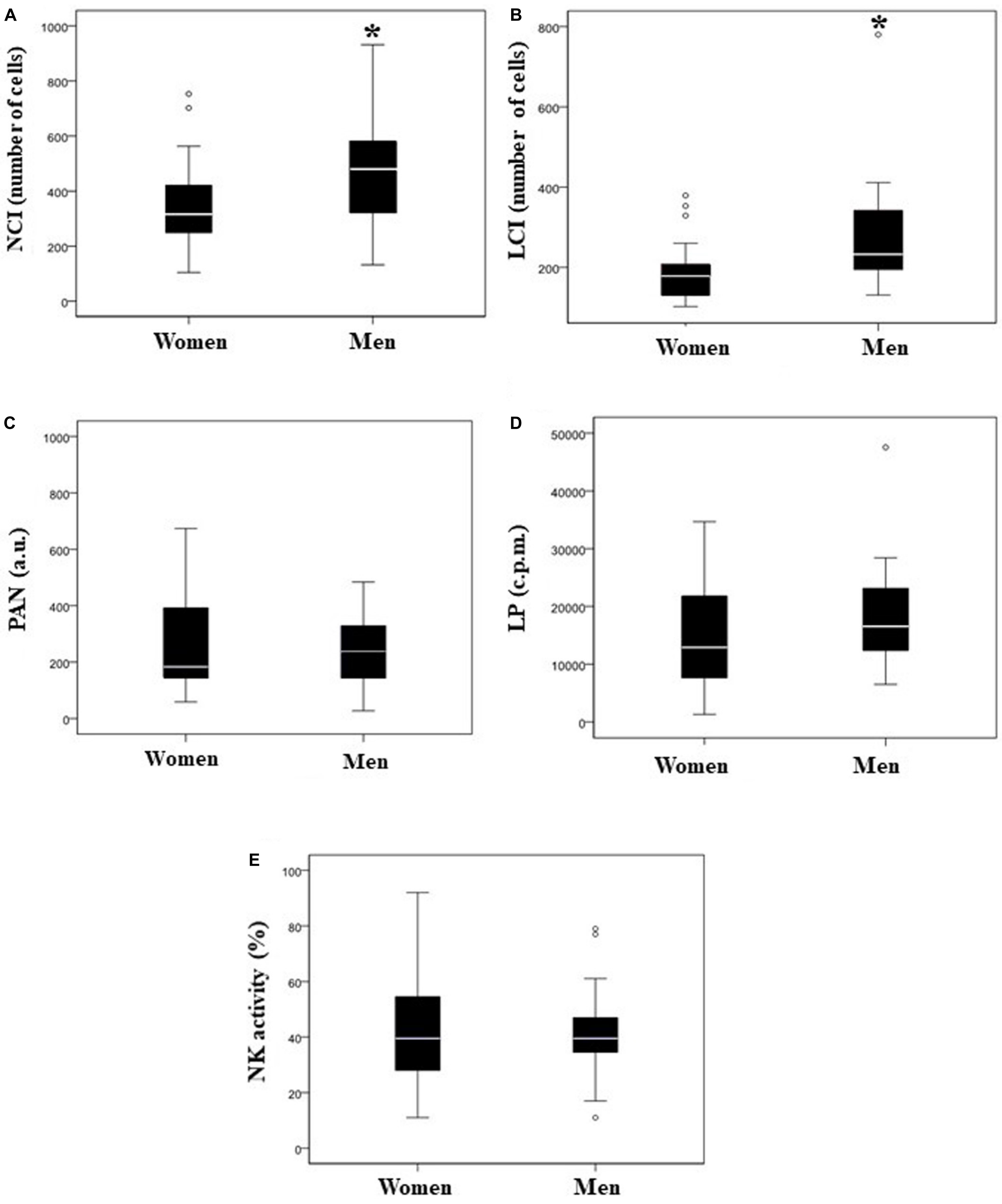

FIGURE 2 | Comparison of immune response in both sexes; box and whisker plots. Neutrophil Chemotaxis Index (NCI; number of cells) **(A)**, Lymphocyte Chemotaxis Index (LCI; number of cells) **(B)**, phagocytic activity of neutrophils (PAN; a.u., arbitrary units) **(C)**, lymphocyte proliferation (LP; c.p.m.) **(D)**, and natural killer (NK) activity **(E)**. White bar denotes the median. $^*p < 0.05$ vs. women.

TABLE 4 | Stress and immune marker correlations.

Marker	R Spearman	*p*
NCI	−0.281	0.053
PAN	−0.083	0.575
LCI	−0.062	0.677
LP (cpm)	−0.095	0.503
NK (lysis %)	−0.017	0.908

NCI, Neutrophil Chemotaxis Index; PAN, phagocytic activity of neutrophils; LCI, Lymphocyte Chemotaxis Index; LP, lymphocyte proliferation; NK, natural killer.

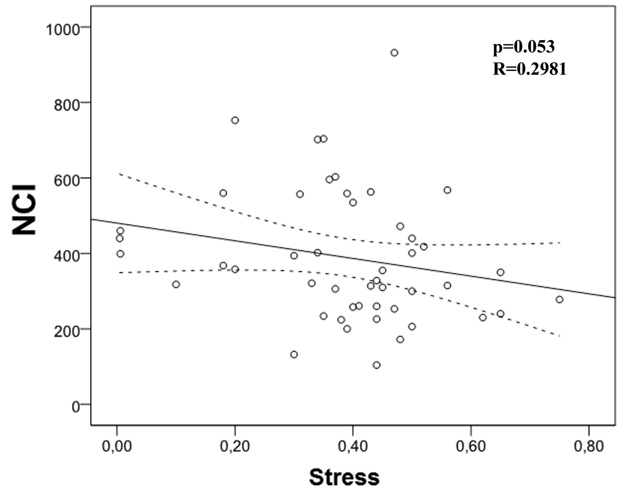

FIGURE 3 | Correlation between Neutrophil Chemotaxis Index (NCI) and stress. There is a strong trend correlation between NCI and stress (*p* = 0.053, *r* = -0.281).

TABLE 5 | Depression and immune marker correlations.

Marker	R Spearman	*p*
NCI	0.001	0.994
PAN	−0.116	0.433
LCI	−0.015	0.919
LP	−0.096	0.514
NK activity (lysis %)	−0.604	0.001

NCI, Neutrophil Chemotaxis Index; PAN, phagocytic activity of neutrophils; LCI, Lymphocyte Chemotaxis Index; LP, lymphocyte proliferation; NK, natural killer.

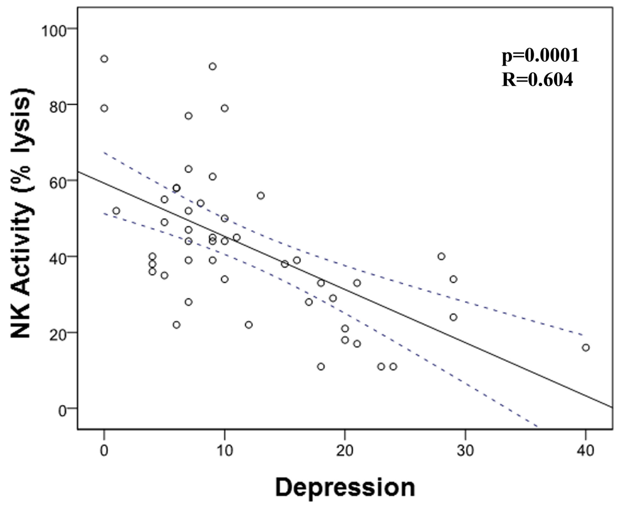

FIGURE 4 | Correlation between natural killer (NK) cell activity and depression. There is a significant correlation between NK activity and depression (*p* = 0.001; *R* = -0.604).

TABLE 6 | Correlation between immune markers and age.

Marker	R Spearman	*p*
NCI	−0.406	**0.004**
PAN	−0.305	**0.035**
LCI	−0.239	0.101
LP	−0.204	0.165
NK activity (lysis %)	−0.016	0.913

NCI, Neutrophil Chemotaxis Index; PAN, phagocytic activity of neutrophils; LCI, Lymphocyte Chemotaxis Index; LP, lymphocyte proliferation; NK, natural killer. p is the associated value to the corresponding statistical test.

affected, which makes them good candidates for a prevention program. In fact, our hypothesis was that we might find some signs of immune function deterioration in our patients. Indeed, we have found a negative correlation between depression and NK activity, meaning that higher depression level is associated with a lower cytotoxic NK activity, which concurs with previous reports (Zorrilla et al., 2001) where the authors reported in a meta-analysis review an overall leukocytosis, a reduced NK cell activity, and a poor proliferative response to mitogen of lymphocytes in patients with depression. However, when we analyzed if there were any correlation between stress with NCI and gender, we only found a significant association for women (**Table 7**). This might point out that women will have a worse neutrophil chemotaxis response, i.e., a reduced response against infection. On the other hand, the negative correlation found between depression and NK activity was found to be independent of patient gender.

One study limitation is that our patients are quite homogeneous regarding age (we have a variation coefficient of 19%), so we cannot separate them into different groups by this factor. However, we have found a negative correlation between age and NCI or PAN in our group of patients. This result agrees with the widely accepted fact that aging deteriorates immunological response (Khanfer et al., 2010; Fülöp et al., 2016). Another limitation of our study is that women are almost double than men. We recognize that this is not the ideal situation, and the gender groups should be more homogeneous to get stronger conclusions. Finally, we realize that the best way to analyze gender impact in our study is when there has been a regression model (moderation analysis) that would clarify whether or not gender is an independent factor that produces changes in stress, depression, and immunity. We could not perform this analysis because the only demographic variable is "age," and we did not find any differences regarding this variable between men and women. However, it is also true that at least in our

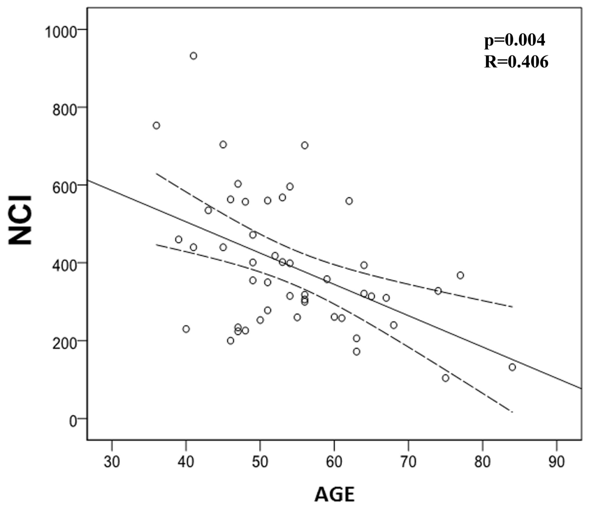

FIGURE 5 | Correlation between Neutrophil Chemotaxis Index (NCI) and age. There is a significant negative correlation between NCI and age (*p* = 0.004; *R* = -0.406).

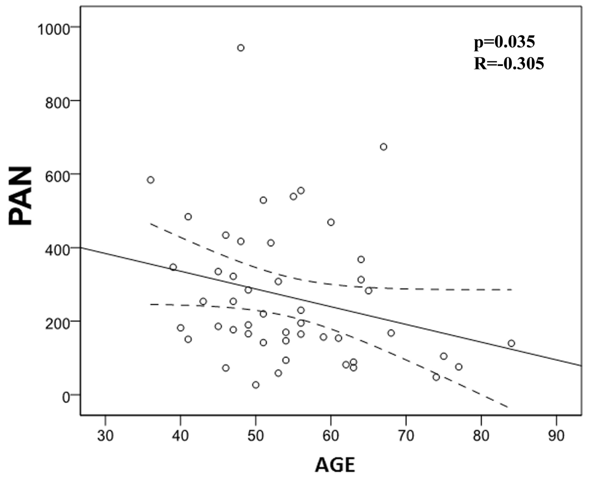

FIGURE 6 | Correlation between phagocytic activity of neutrophils (PAN) and age (*p* = 0.035; *R* = -0.305). There is a significant negative correlation between PAN and age.

TABLE 7 | Correlation between stress and NCI in both sexes.

Correlation	R Spearman	*p*
NCI and men	−0.060	0.824
NCI and women	−0.372	**0.036**

NCI, Neutrophil Chemotaxis Index. p is the associated value to the corresponding statistical test.

social context, more women come to our antiaging unit than men for undetermined reasons. Thus, our results might be also important for similar situations where more women than men were under evaluation.

TABLE 8 | Correlation between stress and NK activity in both genders.

Correlation	R Spearman	*p*
NK activity (lysis %) and men	−0.625	0.010
NK activity (lysis %) and women	−0.648	0.001

NK, natural killer.

CONCLUSION

Our study confirms reported data, which demonstrated that stress and depression affect the nonspecific immune system underlining the alteration of NK cytotoxic response. Another goal of this intervention would be to preserve and improve physical and cognitive capacities, which would make that the biological age of the patient will be far from chronologic age and thus keep them away from disease. In this regard, interventions such as meditation exercise program should be tested as new tools to alleviate or prevent stress and depression effects. Careful monitoring of patient status will help to a better evaluation of the results of psychological programs regarding stress, depression, and immune system status. Thus, we could improve physical and psychological capacities, disease resistance, and improve patient life quality.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation, to any qualified researcher.

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by the Scientific-Ethical Board of the center (Fundación Tejerina, Madrid) approved this study. The patients/participants provided their written informed consent to participate in this study.

AUTHOR CONTRIBUTIONS

BC-G recruited the patients, performed the experiments, analyzed the data, and wrote the manuscript. AF-N performed the statistical analysis. JR reviewed the manuscript. VM-F carried out the design and direction of the study and reviewed the statistical analysis and manuscript. All authors approved the final version of the manuscript.

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.