COGNITION AND EMOTION
2022, VOL. 36, NO. 4, 568–580
https://doi.org/10.1080/02699931.2022.2031905

Routledge
Taylor & Francis Group

Control over pathogen exposure and basal immunological activity influence disgust and pathogen-avoidance motivation*

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ABSTRACT

Disgust is reasoned to operate in conjunction with the immune system to help protect the body from illness. However, less is known about the factors that impact the degree to which individuals invest in pathogen avoidance (disgust) versus pathogen management (prophylactic immunological activity). Here, we examine the role that one's control over pathogen contact plays in resolving such investment trade-offs, predicting that (a) those from low control environments will invest less in pathogen-avoidance strategies and (b) investment in each of these two strategies will occur in a compensatory fashion (i.e. they will be traded off with one other). Across four studies, we found support for these predictions, using a variety of manipulations and measures. By providing novel insights into how one's control over pathogen exposure influences disgust sensitivity and immune system activity, the current research poses an important contribution to the literature on disgust, pathogen avoidance, and the immune system.

ARTICLE HISTORY
Received 21 April 2020
Revised 3 January 2022
Accepted 15 January 2022

KEYWORDS
disgust; control; pathogen avoidance; immune system; functional flexibility

Humans have evolved numerous defences to combat the threat of infectious diseases. One set of defences includes pathogen-management strategies, such as the body's immune system, which serves to protect the body and facilitate recovery after an individual comes into contact with pathogens. More recently, researchers have identified a second set of defences that humans possess that function to mitigate the threat of pathogens *before* they contact the body. These are pathogen-avoidance strategies, sometimes collectively referred to as the "behavioural immune system" (Schaller & Park, 2011), which are thought to be motivated by the emotion of disgust (Curtis et al., 2011).

Although pathogen-avoidance strategies are superior to pathogen-management strategies when it comes to minimizing the physiological costs and infection risks posed by pathogens, such strategies cannot be effectively used by by those whose living and occupational conditions do not allow for a high degree of control over pathogen exposure (Tybur et al., 2018). Pathogen-avoidance strategies rely on one's ability to minimize one's contact with pathogens without compromising their ability to solve the myriad challenges inherent in survival and reproduction. The degree to which one's environment or personal circumstances offer the possibility for avoiding pathogen exposure is therefore hypothesized to represent an important source of input into psychological mechanisms calibrating disgust sensitivity (Tybur et al., 2018). In particular, individuals should be more likely to invest in pathogen-avoidance strategies (characterized by high disgust sensitivity and decreased investment in immunological activity) when in conditions that offer the ability to avoid pathogen contact without incurring substantial costs. We refer to this latter construct as *control over*

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Supplemental data for this article can be accessed https://doi.org/10.1080/02699931.2022.2031905.
*The contributions of the first and second authors were equal to one another.

pathogen contact, which will necessarily vary based on numerous interpersonal and situational factors (e.g. status, socioeconomic position, occupation, parenthood, etc.). Conversely, conditions in which one does not have high control over pathogen exposure should favour investment in pathogen-management strategies, characterized by low disgust sensitivity and increased investment in prophylactic immunological activity. Recent field research supports this reasoning, showing that individuals exhibit higher disgust sensitivity and lower inflammation in contexts where the costs of pathogen avoidance are lower (Cepon-Robins et al., 2021).

Here, we test these possibilities by examining the relationship between one's ability to control pathogen exposure, disgust sensitivity, and the activities of the immune system. Because the degree to which individuals invest in pathogen-avoidance versus pathogen-management is expected to differ based on the expected costs and benefits of each (Ackerman et al., 2018; Tybur et al., 2018), we predicted that disgust sensitivity would vary as a function of one's ability to control exposure to pathogens. Additionally, because the body must find alternative means of mitigating disease risk when control over pathogen exposure is low, we predicted that decreases in disgust sensitivity would be associated with increased immune system activity. Lastly, because our hypothesis implies a trade-off between pathogen-avoidance (characterized by relatively higher levels of disgust sensitivity) and pathogen-management (characterized by relatively higher levels of basal immunological activity) strategies, we predicted that experimentally suppressing the activities of the immune system would increase disgust sensitivity. Together, this research offers novel insights into the bidirectional relationship between humans' pathogen-management psychology and the activities of the immune system.

Pathogen management and avoidance mechanisms

Many consider pathogens one of the most potent and ubiquitous selection pressures shaping human evolution (Fumagalli et al., 2011). Accordingly, considerable research has been dedicated to understanding the various means by which humans protect themselves from these threats. Broadly speaking, this research suggests that humans have evolved two categories of responses to the recurrent threat posed by infectious agents: those aimed at pathogen management and those aimed at pathogen avoidance. Pathogen-management strategies serve to deal with potential contaminants internally, once they have entered the body. Among these is the body's immune system, which mobilizes cellular and molecular defences in the body to detect, remove, and remember encountered infectious agents (Travis, 2009). Although remarkably effective, the immune system is costly to operate (Lochmiller & Deerenberg, 2000), and its responses are imperfect. For example, the immune system is not always equipped to combat rapidly evolving microorganisms (Siddle & Quintana-Murci, 2014), generates collateral tissue damage (Dröge, 2002), and contributes to diseases of aging (Franceschi & Campisi, 2014).

Given the costs and limitations of managing the risk of infection and disease internally, many animals–including humans–possess a set of defences that function to mitigate the threat of disease before it comes into contact with the body (i.e. a pathogen-avoidance strategy). These defences, often referred to as the behavioural immune system (Schaller & Park, 2011), describe a complex array of mechanisms that serve to detect pathogen cues in the environment and avoid them, thereby mitigating infection risk by prevention. These mechanisms play important roles in a range of human psychological processes, including attention (Ackerman et al., 2009) and moral reasoning (Van Leeuwen et al., 2017).

Although pathogen-avoidance behaviours are motivated by a variety of cognitive processes, the emotion of disgust is among the most important (Curtis et al., 2011; Oaten et al., 2009). Typically evoked by sensory cues indicating pathogen presence (Curtis et al., 2004), disgust prompts avoidance behaviours (Krings et al., 2012; Mortensen et al., 2010; Porzig-Drummond et al., 2009). For instance, disgust increases discomfort around–and motivation to avoid–potentially contaminated objects/others (Park et al., 2013; Reynolds et al., 2014; Ryan et al., 2012). Such avoidance, however, can be costly, as disgust is prone to false positive errors, thereby imposing costs on one's ability to survive and reproduce. As such, disgust is theorized to functionally shift in response to various costs and benefits of contact with potentially contaminated objects/others (Ackerman et al., 2018). For example, parenting and sexual intercourse both involve interacting with bodily products, which are cross-culturally nominated as elicitors of disgust (Curtis & Biran, 2001). Research finds that mothers report less disgust when smelling the

soiled diaper of their child (vs. an unrelated child) (Case et al., 2006). Moreover, individuals who are sexually aroused report finding sex-related stimuli less disgusting (Borg & De Jong, 2012; Stevenson et al., 2012). Other research finds that cadets exposed to harsh training camps exhibit decreased disgust sensitivity once entering the training camp (Batres & Perrett, 2020). Together, this research suggests that disgust both serves an important pathogen-avoidance function and is tuned to the various costs and benefits of avoidance behaviour.

Given the pathogen protection functions served by disgust, researchers have proposed this emotion may work in conjunction with the activities of the immune system to protect the body from pathogens. That is, these two systems are reasoned to work in coordinated fashion to prevent illness. Consistent with this hypothesis, research finds that exposure to disgust-eliciting stimuli induces physiological changes consistent with upregulation of immunological activity (Gassen, Makhanova, et al., 2019a; Schaller et al., 2010; Stevenson et al., 2012). For example, exposure to cues of infection risk lead individuals to experience increases in core body temperature (Stevenson et al., 2012) and increases the release of proinflammatory cytokines (Gassen, Makhanova, et al., 2019a; Schaller et al., 2010), which both play an important role in the immunological response to infection. Although most of this research used small sample sizes and all used a limited number of measures, results support possible linkages between immunological parameters and pathogen-avoidance processes.

In addition to working alongside the activities of the immune system in a complementary manner (with both systems increasing alongside each other in response to pathogen cues), research suggests that disgust sensitivity may also complement the activities of the immune system, with decreased activation of one system being counterbalanced by increased activation of the other. For example, disgust increases during the first trimester of pregnancy, when the activities of the immune system are suppressed to allow for implantation of the embryo (Fessler et al., 2005). Others find that those higher in pathogen-avoidance motivation have lower levels of basal inflammatory activity (Cepon-Robins et al., 2021), as well as lower levels of oxidative stress (Gassen et al., 2018). Although others have failed to find a relationship between progesterone, an immunomodulatory hormone, and disgust sensitivity (Jones et al., 2018), these lines of research nonetheless suggest that aspects of humans' pathogen-avoidance (i.e. disgust sensitivity) and pathogen-management (i.e. the immune system) strategies may work together in concert, with each serving an important role in managing pathogen threats.

The current research

Here, we sought to examine the relationship between one's ability to control exposure to pathogens, the activities of the immune system, and pathogen-avoidance motivation. We hypothesized that an individual's investment in pathogen-avoidance versus pathogen-management strategies would be modulated by one's ability to control contact with potential sources of infection. Specifically, we predicted that individuals in low-control environments would demonstrate lower pathogen-avoidance motivation than those in high-control environments (Studies 1-3). Moreover, we predicted that differences in pathogen-avoidance motivation would be associated with compensatory shifts in the activities of the immune system (Studies 3-4). See supplemental materials (SM) for power analyses and data analytic plans.

Study 1

Study 1 was designed to test the hypothesis that lacking control over pathogen contact would predict less negativity toward stimuli containing pathogen cues. Here, we assessed control over pathogen contact using a self-report measure which examined the extent to which one was generally able to avoid interactions with disgust-eliciting things.

Method

Participants. Participants were 263 undergraduates (145 female; $M_{age} = 19.20$, $SD_{age} = 2.05$; age range: 18-41). All were recruited from a psychology undergraduate participant pool and received partial course credit for participation. Prior to analysis, participants were excluded for: failing attention checks ($n = 18$), self-reporting careless responding (i.e. below the midpoint on a 7-point scale; $n = 6$), patterned responding across all measures with reverse-coded items (i.e. selecting the same answer across all items; $n = 2$), and reporting extensive prior participation in academic studies (i.e. having completed thirty or more; $n = 20$), as extensive past experience with studies using deception increases suspicion and may influence participants' responses (Ortmann & Hertwig, 2002).

Materials and procedure. Participants completed all measures online. After providing informed consent, participants completed a measure that assessed their ability to control their exposure to pathogens and then evaluated stimuli containing pathogenic cues. See SM for results and discussion of other measures collected.

Control over pathogen contact. Ability to avoid contact with pathogens was assessed using a 5-item measure that was developed for the current research. An example item is: "I have the ability to avoid disgusting things." See SM for all items.

Negativity toward pathogen cues. Participants viewed five images featuring pathogen cues (e.g. sores on an armpit). See SM for pre-test regarding disgust evaluations of the stimuli. To assess participants' negativity towards the pathogenic stimuli, participants responded to the following three items: "How disgusting is this image?" (1: *not at all disgusting*, 7: *very disgusting*); "How pleasant is this image?" (reverse coded; 1: *very unpleasant*; 7: *very pleasant*); and "How do you feel about this image?" (reverse coded; 1: *very negative*; 7: *very positive*). These items were used to capture both evaluative and affective responses to the stimuli (Ajzen, 1991; Breckler & Wiggins, 1989), which each play an important role in guiding behaviours.

Results and Discussion

Mean composites were created each for (a) control over pathogen contact (α = .74) and (b) negativity towards the pathogenic stimuli (α = .87). Higher values indicate (a) more control over pathogen contact and (b) more negativity toward the pathogenic stimuli, respectively.

We examined zero-order correlations between participants' control over pathogen contact and their judgments of pathogenic stimuli. Results revealed a positive correlation between control over pathogen contact and stimulus judgments, $r(261) = .15$, $p = .014$, 95% CI [.03, .27]. Consistent with the hypothesis that one's ability to behaviourally manage pathogen threats plays a role in modulating disgust sensitivity, lower control over pathogen contact predicted less negativity toward potential pathogen-harbouring stimuli (i.e. less disgust sensitivity)

Study 2

Study 1 provided initial support for the hypothesis that one's ability to behaviourally manage pathogen exposure plays a role in modulating disgust sensitivity. Study 2 was designed to test our hypothesis experimentally, examining whether being in an environment offering low control over pathogen contact (i.e. a dirty laboratory room) would impact participants' negativity toward stimuli containing pathogen cues. In the context of the dirty laboratory room, participants could not control their exposure to pathogen cues by leaving the room without violating a number of social contracts and incurring social costs (e.g. going against social norms: Lin et al., 2013), making this a context in which the costs of pathogen avoidance were reasoned to outweigh the benefits. We predicted that participants who completed the study in the dirty room, where they had low control over pathogen contact, would exhibit less negativity toward pathogenic stimuli than those who completed the study in a clean room.

Method

Participants. Participants were 203 undergraduates (105 female; $M_{age} = 19.59$, $SD_{age} = 2.78$; age range: 17-43). All students were recruited from a psychology undergraduate participant pool and received partial course credit for participation. Prior to analysis, participants were excluded for: self-reporting careless responding ($n = 5$), patterned responding across the dependent measure ($n = 1$), or reporting extensive prior participation in academic studies (i.e. having completed thirty or more studies; $n = 30$).

Materials and Procedure. Participants came into the laboratory and were told that they would be participating in a study on body state perception and responses toward visual stimuli. Approximately half of the participants completed the study in a dirty experimental room ($n = 108$); the remaining participants completed the study in the same experimental room when it was clean ($n = 95$). Similar experimental manipulations have been used in previous research to elicit state-level changes in pathogen-avoidance motivation (e.g. Reynolds et al., 2014; Tybur et al., 2011). If participants inquired about the state of the room, the research assistant replied that the room had been filled with taste-testing research all day, and they had not had time to clean it. Participants were instructed that they could not take steps to try to clean their testing area or the room, as the study had to begin on time. As in Study 1, participants viewed the pathogenic stimuli and responded to items assessing their negativity toward them. Participants also completed a manipulation check of room

cleanliness, the Positive and Negative Affect Schedule (PANAS; Watson et al., 1988), responded to standard demographic items, and were then debriefed and dismissed. See SM for results of the manipulation check, PANAS, and results and discussion of other measures collected.

Room manipulation. The researcher created a foul smell in the experimental room by microwaving one cup of frozen broccoli florets for 5 min in a small amount of water 10 min before each session. Keyboards and mice were coated with rubber cement, popcorn pieces, and one strand of human hair each. Food wrappers and water bottles (containing a small amount of water with floating pieces of food) were also left at each computer terminal. The two trash cans in the room were overflowing with discarded water bottles, various food wrappers, and other debris. The research assistant running these sessions was dressed in a stained, wrinkled lab coat. See SM for photographs. We created a clean environment by removing all trash from the experimental room. Prior to each study session, the key boards and mice at each computer terminal were wiped down with Lysol wipes. A large bottle of hand sanitizer was placed near the sign-in sheet. The research assistant running these sessions was dressed in a clean lab coat.

Results and Discussion

As in Study 1, we created a composite variable of negativity towards the pathogenic stimuli (α = .83). We then conducted an independent samples *t*-test on judgments of pathogenic stimuli, which revealed a significant effect of room condition, $t(201) = -2.64$, $p = .009$, $d = .37$, 95% CI [-.37, -.05]. That is, participants in the dirty room (who were less able to control their exposure to pathogens) reported less negativity toward the images ($M_{dirty} = 5.73$, $SD_{dirty} = .59$) than participants in the clean room that offered greater control ($M_{clean} = 5.94$, $SD_{clean} = .54$). As such, the current results demonstrate that experimentally manipulating control over pathogen contact influences disgust sensitivity, lending support for the hypothesis that a causal relationship exists between one's ability to avoid pathogen contact and disgust sensitivity, with lower control predicting less disgust.

Study 3

The current study was designed with two goals in mind. First, we sought to conceptually replicate the pattern of results observed in Studies 1 and 2 using a behavioural measure of pathogen avoidance–an approach-avoidance task. We predicted that individuals reporting an inability to avoid pathogen contact would be slower to push away pathogen-connoting–but not neutral–stimuli. Second, we sought to examine whether the relationship between one's ability to avoid pathogen contact and diminished efforts to avoid them (i.e. how quickly they push away the disgusting stimuli) co-occur alongside compensatory shifts in the activities of the immune system. Given that individuals in low-control contexts need to invest in an alternative means of pathogen management, we predicted that (a) individuals reporting an inability to avoid pathogen contact would have higher basal immune system activity and (b) high basal immune system activity would, in turn, be associated with a reduction in behavioural pathogen avoidance.

Method

Participants. Data were collected as part of a larger study on immunological parameters and decision-making; see Gassen, Prokosch, et al. (2019b) for eligibility requirements. The sample consisted of 136 participants with complete biobehavioral data (67 female; $M_{age} = 20.17$, $SD_{age} = 2.68$; age range: 17-30) recruited from the community and a psychology undergraduate participant pool. Prior to analysis, participants who lacked behavioural ($n = 3$) or biological ($n = 20$) data due to technical issues were excluded.

Materials and Procedure. See Gassen, Prokosch, et al. (2019b) for detailed description of the procedure. All participants arrived at the lab between 7:00-7:30 AM on the day of their testing session. Participants first answered additional survey questions–including the 5-item measure used in Study 1 assessing control over pathogen contact (α = .74)–followed by an approach-avoid task that served as our key dependent measure. After completing the questionnaires and behavioural task, 85mL of blood was drawn from each participant via venepuncture into EDTA-containing Vacutainer® tubes (Becton-Dickinson, Franklin Lakes, NJ). Participants were then compensated and dismissed.

Approach-avoid task. For the approach-avoid task (AAT) we used a modified version of the task described by Wiers et al. (2009) using Inquisit software. A joystick was centered between the computer and the participant so that the participant could push the joystick

forward toward the computer and also pull the joystick towards him or herself. Pushing the joystick forward resulted in the presented image shrinking (i.e. as if it were being pushed away) and pulling the joystick toward oneself resulted in the presented image growing larger (i.e. as if it were being pulled towards the participant). Initial reaction time (RT) to either push or pull was recorded for participants' responses to each image. See SM for full description of the AAT task. After completing practice trials to familiarize them with the task, participants were shown two categories of images: pathogenic items (e.g. an open sore, a dead mouse) and non-pathogenic, neutral items (e.g. a road). Per the original authors' methodology, AAT difference scores were computed as the median RT for pushing images minus the median RT for pulling images within each category (Wiers et al., 2009). Higher values indicated greater approach motivation (i.e. longer delay in pushing compared to pulling images within each category), which indicates decreased negativity toward the stimuli.

White blood cell count. After blood collection, total white blood cell count was quantified using a 5mL sample of whole blood through electrical impedance using a haematology analyser (AC•T™ *5diff CP,* Beckman Coulter, Indianapolis, IN). Total white blood cell count represents a reliable measure of basal immunological activity, and has been used as such in fields as diverse as behavioural ecology (Cizauskas et al., 2015) to clinical research (Brown et al., 2001; Shankar et al., 2006). In the fields of public health and disease epidemiology, white blood cell count is often used as a marker of systemic inflammation, which is a key facet of the body's general response to pathogen exposure and injury (Brown et al., 2001; Medzhitov, 2008; Shankar et al., 2006).

Results and Discussion

We used a multivariate mediation model and bootstrapping procedure (Mplus, Version 8; Muthén & Muthén, 2012) to examine whether there is an indirect relationship between one's control over pathogen contact and their pathogen avoidance motivation via the activities of the immune system (see Figure 1 for graphical depiction of model). This model was chosen because it adjusts for covariance between performance on trials using pathogenic stimuli and performance on trials using non-pathogenic stimuli (i.e. due to individual differences in reaction time, attention, etc.). Five thousand bootstrap resamples were performed to generate a 95% bias corrected confidence interval for the indirect effect.

Results revealed a significant indirect effect of control over pathogen contact on behavioural efforts to avoid pathogenic stimuli via immune system activity, $b = -9.69$ ($SE = 6.06$), 95% CI [−26.16, −0.89]. Specifically, they revealed that control over pathogen contact predicted higher white blood cell count (*a* path), $b = -.52$ ($SE = .25$), $t = -2.11$, $p = .035$, 95% CI [−1.07, -.10]. Higher white blood cell count predicted less avoidance motivation toward the disgusting stimuli (*b* path), $b = 18.55$ ($SE = 7.09$), $t = 2.62$, $p = .009$, 95% CI [2.38, 31.66] (i.e. slower reaction times in pushing away the pathogen-connoting images). The coefficient representing the direct effect of control over pathogen contact on pathogen avoidance motivation was not significant (*c* path), $b = -2.78$ ($SE = 12.78$), $t = -.22$, $p = .83$, 95% CI [−27.48, 23.97], nor was the coefficient representing the direct effect of control over pathogen contact on pathogen avoidance motivation after controlling for the mediating influence of white blood cell count (*c*′ path), $b = 6.85$ ($SE = 13.21$), $t = .52$, $p = .60$, 95% CI [−18.49, 32.29]. As predicted, control over pathogen contact did not impact behavioural avoidance of non-pathogenic stimuli ([*c*′ path], $b = 4.56$ [$SE = 10.84$], $t = .42$, $p = .67$, 95% CI [−16.08, 26.44]), nor did immunological activity mediate the relationship between control over pathogen contact and nonpathogen avoidance motivation (95% CI of indirect effect [−6.22, 7.17]).

Results provided evidence of an indirect relationship between control over pathogen contact and pathogen-avoidance motivation via the activities of the immune system. Further, the results of an alternative model testing the indirect effect of control over pathogen exposure on immune system activity via behavioural efforts to avoid pathogenic stimuli (see SM for results) support the proposed of directionality of this relationship. However, contrary to expectations, there was no direct effect of control over pathogen contact on pathogen avoidance motivation.

The results of Study 3 revealed that the activities of the immune system may play a mechanistic role in mediating the relationship between one's ability to control exposure to pathogens in one's environment and efforts to behaviourally avoid disgusting stimuli. Specifically, results revealed that individuals who perceived that they had less control over exposure to pathogens in their environments had higher white blood cell counts. Those with higher white blood cell counts, in turn, were slower to push away stimuli

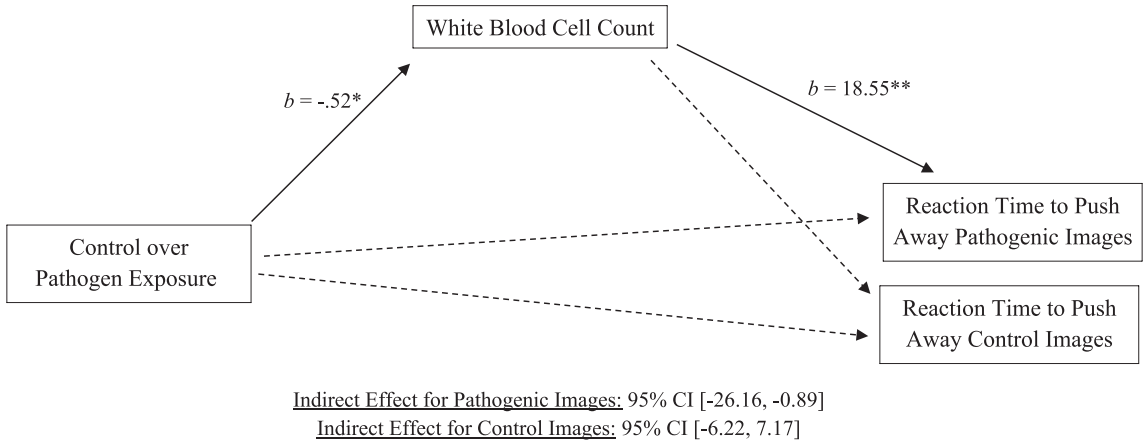

Figure 1. Unstandardized regression coefficients for the relationship between control over exposure to disgusting environment and reaction time to push away disgusting and control images as mediated by white blood cell count in Study 3. Dotted lines denote non-significant paths. *$p \leq .05$; **$p \leq .01$.

connoting pathogen presence (but not neutral stimuli). This finding is consistent both with the findings in Studies 1 and 2, providing support for the overall hypothesis that when pathogen exposure is uncontrollable, immunological activity increases to compensate for reduced behavioural disease avoidance efforts.

Although we anticipated both a direct and indirect effect of control over pathogen exposure on AAT performance, only an indirect effect mediated through white blood cell count was found. This pattern was not anticipated in advance; however, it is not necessarily inconsistent with the patterns observed in the first two studies. Unlike the subjective evaluations reported in Studies 1 and 2, the AAT largely reflects implicit attitudes (Krieglmeyer & Deutsch, 2010) and is sensitive to differences in impulsivity (Kakoschke et al., 2017). Accordingly, it is possible that a direct effect of control over pathogen contact on AAT scores failed to emerge as a by-product of these differences. Importantly, as predicted, the results of Study 3 found evidence of an indirect relationship between environmental controllability and pathogen avoidance behaviours through the activities of the immune system. These results are consistent with the hypothesis that the activities of the immune system may play a critical role in influencing disgust sensitivity and its relationship with one's environment, which we further explored in Study 4.

Study 4

In Study 4, we sought to further explore the relationship between immunological activity and pathogen-avoidance motivation, testing whether experimentally suppressing basal inflammatory activity–which plays a key role in the immune system's defence against pathogens (Medzhitov, 2008)–would lead to increased pathogen-avoidance motivation. We experimentally manipulated basal inflammatory activity by giving participants a dose of aspirin (acetylsalicylic acid)–an over-the-counter non-steroidal anti-inflammatory drug (NSAID)–or a placebo. We chose aspirin because this medication has been shown in previous research to inhibit basal inflammatory activity (Liu et al., 2017; Morris et al., 2009; Yin et al., 1998), including, but certainly not limited to, the activities of myeloid cells (i.e. as was measured in Study 3; Abramson et al., 1985; Ortiz-Muñoz et al., 2014). Next, participants indicated their negativity toward the same pathogenic stimuli used in the first two studies. We predicted that, compared to participants given a placebo, those given aspirin–for whom basal inflammatory activity was suppressed–would exhibit more negative evaluations of the potential contaminants (indicating heightened disgust sensitivity) compared to those in the placebo condition. If found, these results will lend further support for the hypothesis that the activities of the immune system play an important role in calibrating contextually-mediated changes in disgust sensitivity.

Method

Participants. Data were collected as part of a larger study on immunological parameters and decision-making. Participants were 179 undergraduates recruited from a psychology undergraduate

participant pool, 169 of whom completed the target measures (100 female; $M_{age} = 19.97$, $SD_{age} = 2.44$; age range: 18-42). All participants indicated that they could safely take the experimental and placebo medications prior to participation. All received partial course credit for participation. Prior to conducting the analyses, 20 participants were excluded for reporting that they had either taken an anti-inflammatory medication or recreational drugs in the 48 h leading up to the session, which was in violation of their participation instructions. We chose these exclusion criteria because prior administration of anti-inflammatory medications and recreational drug use impact inflammatory signalling, which could interfere with our experimental manipulation (Kesteloot, 2004; Liu et al., 2017; O'Connor et al., 2009). After this exclusion, 149 participants remained in the final sample.

Materials and Procedure. Participants arrived to the research laboratory in the morning between 8:00-9:30 AM. Upon arrival, participants filled out the informed consent and read additional safety information about the medications used in the study. Using a double-blind procedure, participants were then randomly assigned to receive either a placebo medication ($n = 73$; Vitamin B-6; pyridoxine hydrochloride; 50 mg given as two 25 mg pills), or the same dose of the placebo (50 mg of Vitamin B-6; given as a single pill) plus a standard 325 mg dose of aspirin ($n = 76$). In both conditions, the medications were presented as two unmarked, white tablets.

A 30-minute intermission followed administration of the medications, during which participants filled out demographic information and watched a neutral video. This intermission was consistent with the length of time necessary for aspirin levels to reach peak plasma concentration in healthy subjects (Benedek et al., 1995). As in Studies 1 and 2, participants then viewed the five disgusting images and rated their negativity toward them. At the conclusion of the session, participants were debriefed and dismissed.

Results and Discussion

After creating a composite variable measuring participants' negativity toward the pathogenic stimuli (a = .73), we conducted an independent samples *t*-test on perceptions of the disgusting stimuli, which revealed a significant effect of condition, $t(149) = 2.03$, $p = .044$, $d = .33$, 95% CI [.01, .71]. Specifically, participants in the aspirin condition reported more negativity toward the pathogenic stimuli ($M_{aspirin} = 5.37$, $SD_{aspirin} = .97$) than those in the placebo condition ($M_{placebo} = 5.02$, $SD_{placebo} = 1.17$).

These results provide some of the first evidence establishing a causal relationship between the activities of the immune system and disgust sensitivity, suggesting that the two may work together in a compensatory fashion (see also compensatory prophylaxis hypothesis; Fessler et al., 2005; Oaten et al., 2017). Specifically, these results found that when individuals were given an NSAID (compared to placebo), which reduces cellular-inflammatory signalling (Liu et al., 2017; Yin et al., 1998), they exhibited an increase in disgust sensitivity. Such a shift would help keep the body safe from pathogens when immunological defences are down, as an increase in disgust sensitivity would promote behavioural avoidance from potentially infectious substances. These results lend additional support for the hypothesis that the activities of the immune system may play an important mediating role in the relationship between one's ability to avoid pathogens in one's environment and disgust sensitivity, as found in Study 3.

General discussion

Pathogens have posed a substantial threat to survival throughout human history. Accordingly, humans have evolved various physiological, cognitive, and behavioural adaptations that function to counter these threats. Such adaptations can be parsed into two broad categories: pathogen-management strategies (characterized by higher levels of basal immunological activity and lower disgust sensitivity) and pathogen-avoidance strategies (characterized by high disgust sensitivity and strong motivation to avoid pathogen cues). The degree to which individuals invest in pathogen avoidance versus pathogen management vary depending on the costs and benefits of pathogen-avoidant behaviours relative to the costs and benefits of activating an immune response (Tybur et al., 2018). Accordingly, we predicted that individuals would be more likely to invest in a pathogen-avoidance strategy when in conditions that offer high control over pathogen exposure, thus allowing for the downregulation of basal immunological activity (Cepon-Robins et al., 2021; Gassen et al., 2018). Conversely, when one cannot control exposure to pathogens in the environment, the benefits associated with a pathogen-avoidance strategy are low, and thus disgust sensitivity should be reduced in favour of a pathogen-

management strategy. That is, immunological activity should be heightened when control over pathogen exposure is low to compensate for increased infection risk when contact with pathogens is inevitable, and a pathogen-avoidance strategy is ineffective.

Support for these hypotheses was found across four studies. Specifically, the results of the current research found that when individuals' perceived ability to control pathogen exposure was low (Study 1)–or when individuals were placed in an environment where they could not control pathogen exposure (Study 2)–they reported less negativity toward pathogenic stimuli. Additionally, low perceived control over pathogen exposure predicted higher basal immune system activity (i.e. a higher white blood cell count), which, in turn predicted decreased behavioural reactions to avoid pathogenic visual stimuli (Study 3). Finally, Study 4 demonstrated that when activities of the immune system were experimentally downregulated (via NSAID administration) disgust sensitivity subsequently increased, providing evidence for a causal relationship between the activities of the immune system and disgust sensitivity. See SM for an internal meta-analysis examining the reliability of results across all studies. Together, these results lend support to the idea that humans' pathogen avoidance psychology changes in dynamic, contextually-contingent, functionally flexible ways (Ackerman et al., 2018; Ceponˆ-Robins et al., 2021; Tybur et al., 2018).

The findings of the current research make an important contribution to the literature examining the complex relationships between biological and behavioural pathogen defence mechanisms (Ackerman et al., 2018; Gassen et al., 2018; Schaller et al., 2010). For instance, the results of Study 3 provided support for the hypothesis that the activities of the immune system are associated with psychological outcomes, revealing that those with higher white blood cell counts were slower to push away disgusting stimuli. These results suggest that the relationship between immunological activity and pathogen-avoidance psychology may be compensatory in nature, in which one increases to counter decrements in the other. For example, individuals with lower perceived control over pathogen exposure had higher white blood cell counts, presumably to compensate for heightened infection risk when pathogen contact is inevitable. In Study 4, we found that the administration of aspirin (vs. placebo) increased participants' sensitivity to pathogenic stimuli, representing some of the first evidence that experimentally inhibiting inflammatory activity–or any facet of immune function–leads to a compensatory increase in psychological pathogen-avoidance processes (Fessler et al., 2005; Oaten et al., 2017).

While the current results are valuable in providing an initial framework to understand the relationship between the immune system and pathogen avoidance psychology, future research is needed to identify the specific physiological and neurological mechanisms underpinning such bidirectional communication between each. The current research was only able to measure a snapshot of the relationship between a single marker of immunological activity and disgust sensitivity. Because the immune system is complex and comprised of multiple sub-systems (e.g. innate and adaptive immunity, cellular and humoral immunity, etc.), additional research is necessary to delineate the intricate role of the immune system in human psychology. Moreover, additional research and a more comprehensive theoretical framework is needed to address which facets of our psychological pathogen-management system are redundant (i.e. with pathogen avoidance increasing alongside immunological activation) versus those that are compensatory (i.e. with pathogen-avoidance behaviours decreasing as immunological activity increases). Although there is a tendency in the literature to assume that these hypotheses are mutually exclusive, they are not. It is likely that there are elements of our pathogen management psychology that are redundant, and others compensatory.

Further, although we experimentally manipulated basal immunological activity using a well-validated anti-inflammatory medication in Study 4 (i.e. aspirin; Hayasaka et al., 2013; Liu et al., 2017; Morris et al., 2009; Yin et al., 1998), we did not directly measure the magnitude of changes in immune activity in response to the manipulation. This is an important objective for future research, as there are likely individual differences in the extent to which one's basal immunological activity is impacted by aspirin and similar anti-inflammatory medications (see e.g. Mannini et al., 2006). Accordingly, it is possible that those who experience greater post-manipulation changes in immunological activity may also experience greater post-manipulation changes in disgust sensitivity.

Inherent in the current research are several other limitations that must be considered. First off, our current study designs examining the relationship

between control and disgust sensitivity (Studies 1-3) do not allow us to rule out the alternative explanation that the relationship between low control and lowered disgust sensitivity is driven by habituation. However, habituation is not necessarily an alternative explanation and could likely be the mechanistic pathway through which lowered disgust sensitivity occurs in low control environments. That is, one function of habituation may be to diminish investment in costly, emotionally-mediated behavioural responses for which the costs no longer outweigh the benefits. Future research would benefit from further explicating this reasoning and by examining the time course across which these effects (i.e. shifts in disgust sensitivity and immune system activity) occur.

Further, disgust sensitivity is not always uniform across domains (e.g. pathogen, sexual, and moral disgust; Tybur et al., 2013). Although we found that evaluations of visual pathogenic stimuli were impacted by one's perceived/manipulated controllability over pathogen exposure (Studies 1-2) and the activities of the immune system (Studies 3-4), the same pattern may not apply to evaluations of sexually or morally disgusting objects or situations. Moreover, it is likely that this relationship, especially when experimentally manipulated, may emerge for certain measures of pathogen disgust and not others. That is, as suggested by additional measures reported in the SM, experimentally manipulating control over pathogen exposure (Study 2) did not influence self-report trait measures of disgust, but did influence subjective evaluations of pathogenic stimuli, which is arguably a more naturalistic measure of state disgust. Future research on this and related topics would benefit from explicating the difference between various measures of disgust sensitivity, particularly the factors that influence shifts in each.

Next, the relationship between control over pathogen exposure, activities of the immune system, and pathogen-avoidance behaviours in Study 3 was found using a cross-sectional design. Although these results were consistent with our hypothesis, such designs cannot determine causality or directionality; future research is needed to determine the directionality of this relationship. Additionally, we only examined disgust sensitivity across dependent measures easily collected in the lab (i.e. self-reported negativity towards stimuli and an approach-avoid task). Future research should investigate whether perceived controllability over pathogen exposure also influences more naturalistic behavioural displays of disgust or aversion, such as one's willingness to interact with objects connoting disease risk (Ryan et al., 2012).

Importantly, these data were collected prior to the COVID-19 pandemic. Future work should examine how the current hypotheses and findings apply to a world where infection risk has become more omnipresent and how this may impact COVID-19-relevant behaviors. For example, disgust is associated with increased likelihood of engaging in recommended COVID-19 preventative behaviors (e.g. mask use, social distancing, etc.; Shook et al., 2020). The current findings, however, identify perceived control over exposure as a potential individual difference variable. That is, it is possible that those who perceive high likelihood of exposure to COVID-19, regardless of their personal actions, might downregulate disgust and adherence to prophylactic behaviors. Relatedly, these findings may help explain phenomena like pandemic fatigue (i.e. decreased adherence to preventative behaviors over time; Haktanir et al., 2021). As COVID-19 remains pervasive, perceived control over pandemic outcomes may decrease, prompting a shift towards investment in pathogen management rather than avoidance strategies. Further, this work may be relevant for future research examining health outcomes for those whose occupations place them in close proximity to others and therefore face greater infection risk during the pandemic (e.g. health-care and essential workers; Hawkins, 2020; Nguyen et al., 2020).

The present research poses as an important contribution to the literature on disgust, pathogen avoidance, and the immune system by providing novel insights into previously unstudied factors that might influence disgust sensitivity. As such, this research helps provide a clearer picture regarding how context can impact the cognitive and emotional motivators of pathogen avoidance. Identifying control over pathogen exposure as a variable that impacts both behavioural and biological pathogen defences may lead to more nuanced predictions about relationships between the environment, pathogen avoidance behaviours, and the activities of the immune system. Together, these results demonstrate how control over environmental exposure to pathogens impacts disgust sensitivity and provides some of the first empirical evidence regarding the complementary nature of the physiological immune system and the cognitive and behavioural mechanisms associated with pathogen avoidance.

Disclosure statement

No potential conflict of interest was reported by the author(s).

Funding

This research was supported in part by a grant from the National Science Foundation awarded to S.E.H (BCS# 1551201).

Data availability statement

The data that support the findings of this study are available upon request from the corresponding author [HKB]. The data are not publicly available due to containing information that could compromise the privacy of research participants.

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