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The Behavioural Immune System and Pandemic Psychology: The Evolved Psychology of Disease-Avoidance and its Implications for Attitudes, Behaviour, and Public Health during Epidemic Outbreaks

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ABSTRACT

This article provides an overview of the "behavioural immune system" – a suite of psychological mechanisms that complements immunological defences by motivating pre-emptive behavioural responses to infection threats – and summarises research documenting its implications for social attitudes and social behaviour. This summary focuses on four domains of phenomena: interpersonal interactions, stigma and prejudice, conformity, and political attitudes. Then, drawing on this conceptual and empirical background, the article discusses consequences that disease outbreaks (such as the COVID-19 pandemic) may have for individuals' attitudes and actions, and the further consequences that these attitudes and actions might plausibly have for population-level epidemiological and public health outcomes.

KEYWORDS Behavioural immune system; disease outbreaks; covid-19; health; social attitudes; social cognition; social interaction; stigma; prejudice; conformity

Infectious diseases have imposed enormous selection pressures on human, and pre-human, populations for many millions of years. One consequence is a suite of immunological defences—the immune system—that defend against infections within the body. But immunological defences are costly (and not always successful), so people are also equipped with a complementary suite of pre-emptive defences against infectious disease: Psychological mechanisms that produce behavioural responses which, through much of human history, helped to reduce the risk of infection in the first place. These psychological mechanisms comprise a motivational system that functions as a kind of *behavioural immune system*.

The behavioural immune system has many social psychological implications (Ackerman et al., 2018; Kramer & Bressan, 2021; Murray & Schaller, 2016). For example—and we will describe these effects in greater detail below—when experimental procedures lead people to feel more vulnerable to infection they are consequently more interpersonally wary, more xenophobic, and more likely to conform (e.g., Faulkner et al., 2004; Murray & Schaller, 2012; Sawada et al., 2018; Wang & Ackerman, 2019). More generally, people think and act differently when the threat posed by infectious disease is psychologically salient.

Although infectious diseases still kill millions of people per year, their threat has been mitigated by technological advances (e.g., vaccines, antibiotics, public health infrastructure); and so, for many people, the threat posed by infectious diseases may be little more than a fleeting concern. But as the worldwide COVID-19 pandemic amply illustrates, even modern societies are susceptible to devastating disease outbreaks—and, as one consequence, are also susceptible to a heightened awareness of the threat posed by diseases. Might this widespread psychological salience of disease threat have widespread consequences analogous to the attitudinal and behavioural effects observed in scientific experiments? If so, what specific effects might one expect to observe during disease outbreaks?

In order to address these questions, we provide an overview of research showing how the increased salience of disease threat influences social attitudes and behaviours. We then draw upon this background in order to identify effects that real-life disease outbreaks (such as the COVID-19 pandemic) might plausibly have on individuals' attitudes and actions, and to speculate about further implications that these attitudes and actions might have for population-level epidemiological and public health outcomes.

The Behavioural Immune System

Research on the behavioural immune system has been informed by theory and research in the biological sciences and, more specifically, by the conceptual tools of evolutionary psychology (Schaller, 2016). Within an evolutionary framework, motives are conceptualised not as deficits or desires (i.e., needs or goals) but rather as regulatory systems that evolved to regulate behavioural interactions with things in one's environment—and to do so in ways that, historically, were adaptive (Tooby et al., 2008). Different motivational systems (typically associated with different characteristic affective states; Beall & Tracy, 2017) regulate behavioural responses to functionally different phenomena. For instance, within ancestral populations, fitness benefits are likely to have accrued from interactions with friends and lovers and children, but rather different behaviours would have been adaptive depending on whether the interaction was with a friend or a lover or a child. Consequently, different motivational systems evolved to regulate affiliative behaviour, mating behaviour, and parental care-giving behaviour (Schaller, et al., 2017). Analogously, different motivational systems evolved in response to different kinds of threats. Although other dangers—such as steep cliffs and poisonous snakes—also imposed potential fitness costs, disease-causing pathogens are a functionally unique form of threat. Unlike other threats, most pathogens are so small as to be imperceptible to human sensory systems, and their presence can only be inferred indirectly on the basis of imperfect cues (e.g., a food that smells foul, a face that looks flushed). And, because pathogens impose costs through methods that differ from other threats (e.g., entering a body invisibly and attacking it from within), the behavioural means through which that threat might be mitigated are also different from behavioural means of defending against other threats. For these and other reasons, it appears that a functionally unique motivational system evolved to regulate behavioural defences against disease-causing pathogens (Aunger & Curtis, 2013; Schaller, 2016; Tybur & Lieberman, 2016).

It is this motivational system that is sometimes called the "behavioural immune system." Just as "immune system" refers broadly to the many different physiological structures and biochemical processes that provide immunological defence against pathogens that have already infected the body, "behavioural immune system" is a nickname for the entire suite of mechanisms that (a) detect potential infection threats within individuals' surroundings and (b) produce affective

and cognitive responses that (c) facilitate behavioural decisions that were adaptive—by reducing the likelihood of infection—within ancestral ecologies.[1] There is now a vast body of research on these mechanisms and their many implications for different kinds of psychological phenomena (e.g., Ackerman et al., 2009; Curtis, 2014; Fernandes et al., 2017; Hart & Hart, 2018; Kavaliers & Choleris, 2018; Kavaliers et al., 2020; Murray, Prokosch, & Airington, 2019; Nunn et al., 2015; Oaten et al., 2009; Sarolidou et al., 2020). Much of that research lies outside of the scope of this article. Our focus is on the subset of research that is most directly relevant to the key question posed above: What consequences might disease outbreaks have for people's social attitudes and behaviours?

We start by highlighting several key pieces of conceptual background, beginning with a distinction between reactive and proactive means of avoiding infection (Schaller, 2014).

Reactive and Proactive Responses

Non-human animals react aversely when they detect something infectious in their immediate vicinity (Colman, et al., 2003; Kavaliers & Choleris, 2018; Kiesecker et al., 1999). People too exhibit aversive responses of this sort, responding with disgust, dislike, and behavioural avoidance to contaminated things and to other people who are appraised as potentially infectious (Rozin & Fallon, 1987; Ryan et al., 2012; Sarolidou et al., 2020).

In addition to these *reactive* responses, many animals also engage in more *proactive* behavioural defences against infection—behaviours that reduce the likelihood that infectious things might appear in their immediate vicinity and thus require reactive avoidance (e.g., Chapuisat et al., 2007). In human societies, many behavioural rituals and norms have historically served as proactive defences against infection. Social norms governing food preparation, personal hygiene, public sanitation, and socially acceptable forms of intimate interpersonal contact can all inhibit the spread of infectious diseases. Indeed, based on ethnographic studies of pre-modern societies, Fabrega (1997, p. 36) observed that "Most conventions pertaining to subsistence and social behavior operate as prescriptions to avoid illness."

The implication is that, historically, individuals' inclinations to maintain and conform to social norms—and their reactions to people who violate norms—served as an important proactive defence against pathogens. These inclinations and reactions have been the focus of much research on the behavioural immune system.

Error Management and the Smoke Detector Principle

Lots of things can pose a potential infection risk (a sick co-worker, for instance, or someone who defecates by a source of drinking water). How do people know whether something or someone poses some potential threat of infection? They cannot know—at least not for sure. That threat must be inferred on the basis of perceptual cues (e.g., the co-worker's facial appearance, any clue that might connote someone's potential to behave in counter-normative ways). Inference errors are inevitable.

Perceivers might erroneously judge that something poses an infection risk when it actually does not (a false positive error); and perceivers might erroneously judge that something poses no risk when it actually does (a false negative error). Historically, the costs of false-positive errors were usually small, whereas false negative errors—which increased the risk of infection—could

[1] This does *not* imply that these responses are necessarily adaptive—nor beneficial in any other way—within *contemporary* societies; indeed, the opposite may sometimes be the case (Ackerman et al., 2021; Schaller et al., 2015). We discuss this point at greater length below.

be debilitating or deadly. Given these unequal costs, the cost/benefit logic of *error management theory* (Haselton et al., 2016) implies a systematic bias in people's appraisal of infection risk. An analogy is useful here, and it has its own nickname: The *smoke detector principle* (Nesse, 2005). Household smoke detectors are deliberately designed to minimise the possibility of potentially catastrophic false-negative errors by being oversensitive to smoke-like particulates in the air. Consequently, they produce lots of (less costly) false alarms. Analogously, psychological threat-appraisal mechanisms evolved to minimise the possibility of potentially catastrophic false-negative errors by being hypersensitive to perceptual cues that hint imperfectly at the possibility that something (or someone) poses that threat. Consequently, these mechanisms also produce lots of false alarms.[2]

For instance, someone might be intuitively appraised as posing an infection risk simply because their skin is blemished or their facial features are anomalous in some superficial way (an "anomalous face overgeneralization" effect; Zebrowitz & Montepare, 2008). And some threat of infection may be implied not just by norm violations that objectively increase the risk of pathogen transmission, but also by norm violations that are objectively benign. More generally: People are hypersensitive to the threat posed by infectious diseases, and often appraise other people as posing an infection threat even when they pose no real threat at all.

Trade-offs and Context-Contingency

This bias toward making false positive errors—and the consequences that it has for social inference—is more pronounced when people perceive themselves to be more vulnerable to infection (Miller & Maner, 2012). Like the smoke detector principle, this *functional flexibility principle* (Schaller & Park, 2011) follows from a logical analysis of benefits and costs. Just as immunological defences are both beneficial and costly, so too are pre-emptive behavioural defences. Energetic resources are required to engage in disease-avoidant behaviours, and there are costs also in the form of missed opportunities (e.g., avoidance of someone who might be sick—but might not be—may be a missed opportunity to acquire a mate or forge a friendship). Any actual deployment of the behavioural immune system represents a kind of trade-off between its potential benefits and its potential costs (Tybur & Lieberman, 2016).

People are sensitive to information bearing on these potential benefits and costs, and responses are modulated accordingly. Avoidant responses to potentially infectious interpersonal interactions are less likely with friends compared to foes, for instance, and with strangers who have valued traits compared to strangers who do not (Tybur, Lieberman, et al., 2020). Avoidant responses may also be inhibited under circumstances that arouse countervailing motivational systems, such as those associated with mating or affiliation (Sacco et al., 2014; Stevenson et al., 2011). In contrast, the behavioural immune system is more readily activated, and produces stronger responses, when perceivers are more vulnerable to infection. The logic is as follows: To the extent that someone is more vulnerable to infection, the potential benefit of an infection-avoiding behavioural response is greater, and thus more likely to outweigh the costs. The upshot: When individuals are (or merely perceive themselves to be) more vulnerable to infection, the behavioural immune system is likely to be more readily aroused and to produce stronger pre-emptive responses.

[2] The analogy to immunology holds here too: Immunological defenses may be mounted not only against dangerous pathogens that intrude upon the body but also against intrusive things that are objectively benign or even beneficial (e.g., organ transplants).

An illustrative example is provided by research on disgust. Disgust is the emotion most closely associated with the behavioural immune system,[3] and a person's tendency to experience disgust is one indicator of the behavioural immune system's responsiveness to perceived infection threats. Consistent with the cost/benefit analysis summarised above, people are more readily disgusted when they are more vulnerable to infection (e.g., Fessler et al., 2005).

While the behavioural immune system may produce stronger responses when people truly are more vulnerable to infection, objective reality may be less relevant than a person's subjective appraisal of their vulnerability. As a general principle, the behavioural immune system can be expected to produce stronger pre-emptive defences against infection when a person *perceives* that they are more highly vulnerable to infection (whether or not they truly are). This principle underlies two complementary research strategies that are commonly used to test hypotheses about the implications that the behavioural immune system might have for psychological phenomena. One strategy focuses on trait-like individual differences in disgust sensitivity (e.g., Tybur et al., 2009) or perceived vulnerability to disease (PVD; Duncan et al., 2009), and tests the extent to which these individual differences correlate with outcome variables of particular interest. The other strategy employs experimental methods to induce a temporarily heightened awareness of the threat posed by infectious diseases, and tests whether those experimental manipulations exert a causal influence on outcome variables of interest.[4]

Evidence of Implications for Social Attitudes and Behaviour

Given the goals of this article, we limit our focus to lines of inquiry that bear directly on attitudinal or behavioural phenomena. Additionally, we focus only on phenomena that have been empirically shown to vary depending on whether people find themselves in circumstances that make the threat of infection especially psychologically salient—i.e., evidence from experiments that actually manipulated whether participants were made aware of the threat posed by infectious diseases. We do not ignore correlational evidence. But if there is *only* correlational evidence, there is a less compelling evidentiary basis for speculations about the causal consequences of disease outbreaks, and we have chosen to limit the scope of our review accordingly.

In the following sections we summarise empirical findings pertaining to (a) interpersonal interactions, (b) stigma and prejudice, (c) conformity (and responses to non-conformity), and (d)

[3] Disgust is so closely associated with the behavioural immune system that "disgust" is sometimes used as a shorthand label for the same set of motivational mechanisms (Aunger & Curtis, 2013; Lieberman & Patrick, 2014).

[4] A different line of research applies some of these same logical principles to the study of regional differences in norms, values, and other variables that describe entire populations (rather than individuals). Studies in this line of research treat geographical regions (e.g., countries) as units of analysis, and assess the extent to which those regional differences are predicted by regional differences in the prevalence of disease-causing pathogens. Many of these studies have revealed correlations that conceptually parallel the individual-level results of the psychological studies summarised below. For example: Geographical regions characterised by greater pathogen prevalence are also characterised by lower mean levels of extraversion, less physical contact during interpersonal interactions, stronger racial prejudice, higher moral vigilance, more highly conformist attitudes and values, and more authoritarian systems of government (e.g. Bastian et al, 2019; Fincher et al., 2008; Murray et al., 2011, 2017; Murray, Schaller, & Suedfeld, 2013; O'Shea et al., 2020; Schaller & Murray, 2008; Tybur et al., 2016; Van Leeuwen et al., 2012). There are many inferential challenges associated with these kinds of data (Nettle, 2009; Pollet et al., 2014; Schaller & Murray, 2011), including the difficulty of empirically distinguishing between different causal mechanisms through which pathogen prevalence might plausibly have population-level consequences. Some of those mechanisms (e.g., ontogenesis) are conceptually distinct from the psychological processes that are our focus here, and operate on entirely different time-scales. For that reason, we do not review this body of literature here.

political attitudes. For each line of research, we provide brief overviews of relevant correlational results[5] and also—in greater detail—summarise results of experiments that actually manipulated the psychological salience of the threat posed by of infectious diseases.

Interpersonal Interactions

Because many infectious diseases are transmitted from person to person, social interactions that involve close physical proximity increase the risk of transmission. One might therefore expect that when the risk of infection is highly salient, people will be more reluctant to engage in interpersonal interactions and, when those interactions are unavoidable, to approach those interactions in a more cautious and risk-averse manner.

Evidence consistent with this expectation has been found in studies that focus specifically on sexual and/or romantic interactions. People who are more easily disgusted are less likely to seek casual sexual encounters (Sevi, 2019; Sevi et al., 2018), and people who score higher on a measure that assesses perceived vulnerability to disease (PVD) also report less interest in promiscuous sexual behaviour (Duncan et al., 2009; Murray, Jones, & Schaller, 2013). PVD also predicts reduced interest in potential romantic partners within a speed-dating context, and this effect occurred even when potential partners were highly attractive (Sawada et al., 2018).

These correlational findings are complemented by experimental evidence (Sawada et al., 2018; Tybur et al., 2011). Sawada et al. (2018, Study 3, $n = 154$) assessed Canadian participants' interest in dating potential romantic partners. Prior to obtaining information about these potential partners, participants watched a short video that, depending on experimental condition, was either designed to temporarily make the threat of infection psychologically salient ("Top Ten Revolting Hygiene Facts") or not ("Top Ten Words that Don't Translate to English"). Results revealed a statistically significant ($p = .015$) reduction in romantic interest when the threat of infection has been made temporarily salient.

Conceptually analogous results have been found in studies assessing attitudes toward affiliative behaviour more generally. Across three studies, Aarøe et al. (2016) found that participants who were more easily disgusted were also less trusting of other people—especially people with whom they lack familiarity. Higher scores on PVD are associated with lower levels of self-reported extraversion (Duncan et al., 2009); and, in a study in which participants actually engaged in a semi-structured interpersonal interaction with an experimental confederate—participants with higher PVD scores were more withdrawn and less friendly, and found the interactions less enjoyable (Sawada et al., 2018).

Complementing these correlational findings are results from two experiments conducted in the United States that manipulated the temporary salience of infectious diseases (Mortensen et al., 2010). In one study (n= 59), participants completed a personality inventory shortly after watching a slide show about either architecture (control condition) or about germs and disease transmission. Results revealed reduced levels of self-reported extraversion in the latter condition

[5] Many of the correlational studies examined correlates of disgust-sensitivity, and a subset of these studies used measures (e.g., Tybur et al., 2009) that differentiate between the extent to which people are disgusted by things that connote the immediate presence of pathogens ("pathogen disgust") and the extent to which people are disgusted by other things, such as certain kinds of sexual behaviours ("sexual disgust") and violations of moral norms ("moral disgust"). These distinctions can be informative. However, one cannot assume that only pathogen disgust is relevant to the behavioural immune system. Sexual intimacy implies increased risk of pathogen transmission, and so do behaviours that violate social norms (see the section on "Reactive and Proactive Responses," above). For the purposes of this article, we do not attend to these finer distinctions between domains of stimuli that elicit disgust.

(p = .028). In a second study (n = 139), the same experimental manipulation led participants to exhibit more avoidant motor movements in response to pictures of people (p = .034).

Also relevant here is a recent program of research on the subjective experience of crowding (Wang & Ackerman, 2019). Eight studies conducted in the United States showed that people with higher PVD scores judged crowded spaces to be more highly crowded, and evaluated those spaces more negatively. These studies also included experimental manipulations designed to make the threat of infectious diseases temporarily salient. Across these 8 experiments (total N = 1993), meta-analytic results showed that when the threat of infection was made temporarily salient, people evaluated crowded spaces more negatively (r = -.28, p = .01). It is worth noting that the majority of these experiments included control conditions in which other kinds of threats were made salient (e.g., deadly accidents, a natural disaster, a potentially dangerous gunman). Thus, the effects of the disease threat manipulations on perceptions of crowdedness cannot be attributed simply to increased anxiety or fear; these effects appear to be attributable specifically to a heightened awareness of the threat posed by infectious diseases.

In sum, there is lots of evidence indicating that when people are more acutely aware of the threat posed by infectious diseases, they exhibit more avoidant and risk-averse responses to interpersonal interactions.[6]

Stigma and Prejudice

Some people are more likely than others to actually pose a risk of infection. But according to the underlying logic of the smoke detector principle, even people who pose no real infection risk may be *perceived* to pose an infection risk if they look or act anomalous in some way. This (mis)perception of infection risk is one psychological basis for stigma and prejudice (Kurzban & Leary, 2001; Schaller & Neuberg, 2012). A further implication (based on the functional flexibility principle) is that this stigma—and the prejudicial attitudes that it produces—may be enhanced when threat of disease is more psychologically salient.

Some evidence consistent with this implication has been found in studies assessing cognitions about people whose physical appearance is might be subjectively construed to be anomalous. One study found that participants implicitly associated physical disability with the semantic concept "disease," and this implicit association was strongest among participants with higher scores on measures of disgust sensitivity and PVD (Park et al., 2003). Another study found that higher PVD scores also predict more strongly negative attitudes toward obese people (Park et al., 2007). Additionally, Park et al. (2007) reported results from an experiment conducted in Canada showing that after watching a slide show portraying germs, infections, and the prevalence of disease-causing pathogens (compared to two control conditions), participants had stronger implicit associations between obese people and "disease" (p = .078; n = 60). Another experiment on Canadian participants yielded evidence suggesting that implicit prejudice against elderly people might also be amplified under similar circumstances (Duncan & Schaller, 2009; n = 88), although that evidence was observed only among participants of European ethnic heritage, not among those of East Asian background.

Other research indicates that the perceived threat of disease also predicts prejudices against immigrants, ethnic outgroups, and other people who are perceived to be outsiders. Disease outbreaks are often blamed on foreigners and ethnic outgroups (Markel, 1999; Oldstone, 1998); and scientific experiments show that, compared to people who seem familiar and/or similar to

[6] This effect on increased cautiousness is not limited just to interpersonal interactions. Increased awareness of disease threat is associated with risk-aversion more generally (Prokosch et al., 2019).

oneself, outgroups are perceived to pose increased infection risk, and to arouse disgust (e.g., Bressan, 2020; Hodson et al., 2013). Some people are more highly disgusted by outgroups—as indicated by self-report measures of intergroup disgust—and express stronger prejudices against them, especially when outgroup behavioural practices violate ingroup norms pertaining to cleanliness or purity (Hodson & Costello, 2007; Hodson et al., 2013). Not only is intergroup prejudice predicted by intergroup disgust specifically, it is predicted by disgust sensitivity more generally and by PVD (e.g., Aarøe et al., 2017; Faulkner et al., 2004; Green et al., 2010; Navarrete et al., 2007; O'Shea et al., 2020; Zakrzewska et al., 2019).

These results are buttressed by additional results from experiments that manipulated the psychological salience of disease threat. In one experiment reported by Faulkner et al. (2004, Study 5, n = 57), Canadian participants learned about an immigrant group from either Scotland (a subjectively familiar immigrant group) or Nigeria (a more subjectively foreign group), and rated the extent to which they believed the Canadian government should allow these immigrants to settle in their local community. They made these ratings after first watching a slide show that, depending on experimental condition, either depicted means of contracting infectious diseases or (in a control condition) depicted disease-irrelevant threats to personal safety. The results revealed an interaction effect (p = .02): Participants in the control condition were approximately equally likely to support immigration of Scots and Nigerians (M's = 5.85 and 6.07, respectively); but when the threat of disease was salient, participants more strongly endorsed the immigration of Scots (M = 6.36) compared to Nigerians (M = 5.53). These results were conceptually replicated in another experiment (Faulkner et al., Study 6, n = 45) in which, following the same slide-show manipulation, Canadian participants were asked to allocate percentages of a government budget to recruit immigrants from various countries, some that were subjectively familiar (e.g., Poland, Taiwan) and some that were perceived to be more foreign (e.g., Mongolia, Nigeria). Again there was an interaction effect (p = .038): Participants in the control condition allocated approximately equal funds to attract immigrants from familiar and foreign places (M's = 52.5% and 47.5%, respectively); but when the threat of disease was salient, they allocated more funds to recruit immigrants from familiar places (M = 62.4%) compared to subjectively foreign places (M = 37.6%). More recently, O'Shea et al. (2020) reported conceptually similar results from a large-sample experiment (n = 588) showing that when disease threat is made highly salient, participants in the United States expressed more prejudicial attitudes toward racial outgroups (p = .021)—an effect that showed up most strongly among participants with higher PVD scores. It is worth noting that all three of these experiments employed control conditions in which other kinds of threats (e.g., potentially-deadly accidents; terrorist attacks) were made highly salient, indicating that the perceived threat of infectious diseases is a functionally unique, and perhaps an especially potent, amplifier of xenophobic and racist attitudes.

These studies (which are supplemented by additional results showing effects of disease threat on group categorization biases; e.g., Makhanova et al., 2015; Miller and Maner, 2012; Reid et al., 2012), provide abundant evidence that when people are more highly aware of the threat posed by infectious diseases, they are more likely to stigmatise people who seem anomalous or unfamiliar, and to express stronger prejudices against them. The effects on xenophobic attitudes are perhaps especially intriguing. It may be tempting to assume that these results simply reflect the belief that "outsiders" are carriers of exotic diseases, but results from several recent studies (Karinen et al., 2019; Zakrzewska et al., 2019) support a different explanation: Immigrants and other outgroup members are perceived to behave in ways that deviate from local norms—which

tacitly connotes a disease threat (perhaps because so many local norms have historically served as buffers against pathogen transmission; Fabrega, 1997).

Conformity

Of course it is not only outsiders who have the potential to deviate from existing traditions and norms. Anyone—including oneself—might be tempted to do things differently. Therefore, the conceptual analysis linking norm violations to disease threat has implications beyond xenophobia; it also has implications for cognitions regarding norm violations more generally. Drawing on the functional flexibility principle, one broad expectation is that when people are more highly aware of the threat posed by infectious diseases, they will be more inclined to maintain existing traditions and norms.

One way this inclination might manifest itself is by provoking "moral vigilance"—harsher moral judgments about counter-normative behaviour. Correlational studies show that both disgust sensitivity and PVD predict harsher moral judgments about norm violations, especially when those norms are relevant to moral domains such as purity (e.g., Horberg et al., 2009; Liuzza et al., 2019; Murray, Kerry, & Gervais, 2019). These correlational results are buttressed by results of an experiment reported by Murray, Kerry, and Gervais (2019; Study 3, $n = 205$). Prior to judging the moral wrongness of various norm violations, participants in the United States engaged in an autobiographical recall task. In one condition, they described a time when they felt vulnerable to infection. In two control conditions, they instead described what they had done during the previous day or described a time when they felt vulnerable to physical harm. Results showed that—even compared to the physical harm condition ($M = 2.58$)—when participants were more highly aware of the threat of infectious disease, they judged violations of moralised norms to be more morally wrong ($M = 2.83$), $p = .01$. This effect was not limited to moral domains that are transparently relevant to disease transmission; it was found across a broad range of moral domains.

An inclination to maintain existing traditions and norms may also lead people to express attitudes endorsing conformity with existing traditions and norms, and to be more conformist themselves. Multiple studies have shown that higher PVD scores are associated with more positive attitudes toward conformity behaviour (Murray & Schaller, 2012; Wu & Chang, 2012). More convincingly, conceptually analogous results have emerged from experiments. Wu and Chang (2012) reported two experiments conducted in China, both of which produced results showing that conformist responses were highest under conditions in which the threat of infectious diseases had been made temporarily salient. For instance, in one of those experiments ($n = 60$) participants completed a 10-item questionnaire assessing an attitudinal tendency toward conformity, and they did so after first watching a short excerpt from a movie. In one experimental condition, the excerpt (from *Outbreak*) depicted the dangers of a deadly disease outbreak, whereas in a control condition, the excerpt (from *The Day After Tomorrow*) depicted the deadly destruction of an earthquake. Results showed that, compared to the control condition ($M = 5.13$), self-reported conformity was higher when the threat of a disease outbreak was salient ($M = 5.72$), $p = .042$. Conceptually similar results emerged from an experiment conducted in Canada (Murray and Schaller, 2012; $n = 217$). Participants were randomly assigned to one of three experiment conditions during which they recollected either (a) their activities from the previous day, (b) a time when they feared for their physical safety, or (c) a time when they felt vulnerable to infectious disease. Afterwards, they completed four conformity-relevant dependent measures (self-reported conformist attitudes, liking for people with conformist traits, value placed on obedience, and behavioural conformity to majority opinion) that were aggregated into a single composite conformity index. Pairwise

comparisons on this index revealed that, compared to either of the other two conditions, conformist tendencies were highest when the threat of infectious disease had been made temporarily salient (both p's < .01).

It is worth noting that these experiments all included control conditions designed to make other threats salient. The implication is that, while threats of other kinds can also lead to increased conformity (e.g., Griskevicius et al., 2006), the perceived threat of infectious diseases may have an especially potent effect.

Political Attitudes

Conservative political attitudes are defined by an ideological affection for existing norms and cultural traditions, and wariness of progressive new ways of doing things. For this and other reasons, one might expect that when people are more highly aware of the threat posed by infectious diseases, they may be more likely to express conservative attitudes and to endorse conservative policies.

There is a lot of correlational evidence consistent with this expectation, most of which examines relations between disgust sensitivity and measures of political attitudes, political party affiliation, and/or voting intentions (e.g., Brenner & Inbar, 2015; Inbar et al., 2012; Liuzza et al., 2018; Shook et al., 2017; Terrizzi et al., 2013). One recent study is notable because it was conducted on eight large representative samples from Denmark and the United States (Aarøe et al., 2020). Results were consistent across samples: Disgust sensitivity and PVD correlated positively with conservative political party identification and with intentions to vote for conservative political candidates.

Complementing these correlational results is evidence from an experiment conducted in the United States (Helzer & Pizarro, 2011, Study 1; n = 52). Participants completed a measure of political conservatism/liberalism—on which higher numbers indicated more liberal attitudes—while either in immediate proximity to a hand-sanitiser dispenser (which, presumably, served as a perceptual reminder of the potential for disease transmission), or not. Compared to the control condition (M = 4.93), participants who completed the measure in the presence of the hand-sanitiser dispenser reported less liberal political attitudes (M = 4.30), p = .025. That is just one experiment, however, and it has not been replicated (Burnham, 2020). So, although there is abundant correlational evidence linking disease vulnerability to political conservatism, there is not yet fully convincing experimental evidence showing that the former actually exerts a causal influence on the latter.

Empirical Evidence on Actual Disease Outbreaks

Prior to the COVID-19 pandemic, only a few studies had examined these social psychological phenomena in the context of actual disease outbreaks. One study was conducted in Switzerland while a potential outbreak of avian influenza was in the news (Krings et al., 2012). Results showed that, among participants who already held unfavourable attitudes toward foreigners, those who expressed greater concern about avian influenza were also more likely to express the belief that avoiding contact with foreigners provided protection against infection. Another such study was conducted in the United States following an Ebola outbreak in 2014 (Kim et al., 2016). Results showed that people who perceived themselves to be more vulnerable to Ebola also expressed stronger xenophobic attitudes. (This correlation was weaker among people who held more highly collectivistic values—a finding that we return to later in this article.) Although

these results are informative, they do not test whether the onset of a disease outbreak might cause widespread attitudinal or behavioural consequences analogous to the effects observed in the experiments summarised above. To more directly address that kind of question, a longitudinal analysis is required.

One such longitudinal study tested whether the 2014 Ebola threat in North America was associated with widespread intensification of anti-gay attitudes (Inbar et al., 2016). Results were mixed—revealing no change in explicit attitudes and only a tiny change in implicit attitudes. The same Ebola outbreak was the focus of a set of studies that examined political polling results in the United States and Canada (Beall et al., 2016; Schaller et al., 2017), and found that that the onset of the Ebola outbreak coincided with temporary changes in political polling trends. For example, in the United States, during the seven days immediately preceding news of the initial outbreak, there was a rather weak trend toward increasing support for conservative candidates for the U. S. House of Representatives (b = 0.06), but this trend became substantially steeper during the seven days that immediately followed (b = 0.18). Segmented time series analyses showed this change in the temporal trend to be statistically significant (p = .002). Analogous results were observed in Canadian polling data: There was a statistically significant difference between pre- and post-outbreak polling trends (p = .037), indicating that the Ebola outbreak was associated with increasing intentions to vote for conservative candidates in the next Canadian federal election. Complementary findings emerged from a separate analysis of voting behaviour in U.S. elections that took place shortly after the Ebola outbreak, showing that heightened concern about Ebola (as measured by online activity) was associated with greater electoral support for conservative candidates (Campante et al., 2020).

These results provided some preliminary evidence that disease outbreaks might potentially produce attitudinal changes of the sort documented in the larger literature on the behavioural immune system. But these studies examined just two specific kinds of attitudinal variables; and although some alternative explanations were ruled out by additional analyses, it is impossible to rule out all possible alternative explanations. Beall et al. (2016, p. 604) urged inferential caution and the need for additional research, before concluding ruefully: "It would be inhumane to hope that future events offer opportunities to conduct conceptual replications of this investigation. Regardless, epidemiological projections (e.g., Lindgren et al., 2012) suggest that these events and opportunities are likely to occur."

The COVID-19 outbreak provided this opportunity on a heartbreakingly massive scale. Researchers in many countries have seized this opportunity and the results of their inquiries have begun to appear in the published literature. In the following paragraphs we summarise these initial findings.[7]

Some published studies have used the COVID-19 pandemic as an opportunity to test whether previously documented correlational findings (e.g. attitudinal correlates of disgust

[7] More studies of this sort are likely to be published before the words that we are typing right now appear in print, and probably many more after that. For that reason, the summary that we provide here must be viewed as merely illustrative. Given the massive scale of the COVID-19 pandemic, and the massive amount of scholarly research that continues to examine its effects, any one study testing a possible effect is unlikely to be the only study testing that possible effect. The pandemic has probably produced a large number of studies (conducted with different methods and within many different societal/cultural contexts) that are effectively conceptual replications of each other—which have many potential benefits for cumulative knowledge and scientific progress (Crandall & Sherman, 2016). Attainment of those benefits may require fully comprehensive and systematic meta-analyses of all those studies (once they all are actually completed and their results become available). We hope that intrepid meta-analysts are up to that important task!

sensitivity and PVD) actually replicate under the extraordinary psychological circumstances of an ongoing disease threat that, as a result of extensive daily media coverage and other everyday reminders, is regularly and acutely on the minds of just about everyone. Generally speaking, these effects—on variables such as social trust, interpersonal wariness, xenophobia, moral vigilance, and political ideology—have replicated during the COVID-19 pandemic, and have done so on large samples of participants in a variety of countries (e.g., Fuochi et al., 2021; Henderson & Schnall, 2021; Makhanova & Shepherd, 2020; Meleady et al., 2021; Moran, Kerry, et al., in press; Olivera-La Rosa et al., 2020; O'Shea et al., in press; Reny & Barreto, in press). For instance, across three studies conducted in the United States during the first few months of the pandemic, Henderson and Schnall (2021) found that people who were more worried about contracting COVID-19 made harsher moral judgments in response to others' norm violations. Consistent with conceptual principles that characterise the behavioural immune system (e.g., the smoke detector principle), this effect was observed for a wide range of norm violation, not just those that have obvious logical relevance to disease transmission.

The COVID-19 outbreak has also been incorporated into experimental manipulations. In an experiment reported by Moran, Kerry, et al. (in press; $n = 510$), participants in the United States were randomly assigned to one of three experimental conditions. In one condition, participants were presented with materials depicting the (then-emerging) COVID-19 outbreak. In two control conditions, participants were either presented with materials depicting the threat of accidental poisoning, or were not presented with any threat-connoting materials. Afterwards they completed a questionnaire assessing attitudinal and behavioural inclinations toward sexual promiscuity. Pairwise comparisons showed that inclinations toward sexual promiscuity were lower after the threat of COVID-19 had been made salient (M = -.14), compared to the control conditions (M's = .10 and .06; p's = .009 and .02, respectively). Another experiment (Moran, Goh et al., in press; Study 2, $n = 385$) used the same experimental manipulation and showed that when the threat of COVID-19 was made temporarily salient, participants more strongly supported bans on incoming travel from countries associated with the emerging outbreak.

A pair of additional experiments—conducted in the United States and Poland—focused on political attitudes (Karwowski et al., 2020; total N = 1237). Both experiments were conducted during the early stages of the COVID-19 pandemic, and both employed manipulations designed to make that emerging pandemic temporarily salient (or not). Following that manipulation, participants evaluated candidates for the upcoming presidential election in their country. Results from both experiments showed that when the COVID-19 pandemic was more highly salient, participants reported more negative evaluations of liberal candidates (Bernie Sanders in the United States; Robert Biedroń in Poland) and more positive evaluations of conservative candidates (Donald Trump in the United States; Andrzej Duda and Krzysztof Bosak in Poland).

What about studies using longitudinal methods to test whether the onset of the COVID-19 pandemic might have produced changes in widespread social attitudes? Studies of this kind are scarce, but are beginning to appear in the published literature. Evidence from Polish and Australian samples showed increased levels of disgust sensitivity and PVD after the onset of the pandemic (Miłkowska et al., 2021; Stevenson et al., 2020), indirectly attesting to the plausibility of broader attitude changes. Rosenfeld and Tomiyama (2021) reported results of a longitudinal study ($N = 695$) that assessed U.S. participants' self-reported gender role conformity, gender stereotypes, and political ideology at two time points: Shortly before the onset of the pandemic, and shortly after. There was no meaningful difference in political ideology ($d = 0.02$, $p = .508$) but there were differences on the other measures: After the onset of the pandemic, participants reported greater

gender role conformity (d = 0.12; p = .001), and greater endorsement of traditional gender stereotypes (d = 0.11; p = .005). A conceptually similar study, producing conceptually similar results, was conducted on a nationally representative sample of people in Poland (Golec de Zavala et al., 2021; N = 889). Analyses of data collected across three different time points (including a pre-pandemic baseline measure) linked the onset of the COVID-19 pandemic to increased authoritarianism and increased antipathy toward people who failed to conform to traditional gender and sexual norms. The results of both studies are consistent with the hypothesis that real-life disease outbreaks may dispose people toward more conformist attitudes and actions, and to endorse more traditional (i.e., conservative) social values.

Again, these are just a few studies. It remains to be seen whether these preliminary results are representative of additional results from additional studies that, surely, will appear in the near future. Still, emerging evidence suggests that real-life disease outbreaks may have psychological effects analogous to those documented in the broader scholarly literature on the behavioural immune system. There is some justification, therefore, to draw upon that literature in order to speculate further about the possible effects of disease outbreaks and their consequences.

Speculations about Implications for Health Outcomes

When speculating about implications for actual health outcomes, it is important to be mindful of what the behavioural immune system can and cannot do. Just as immunological defences provide only limited and imperfect protection against diseases, pre-emptive behavioural defences are also imperfect. The behavioural immune system is most effective at inhibiting contact with pathogens that are associated with readily detectable stimuli (e.g., visible and distinctive features of people who pose an infection risk). Not all infections are so conveniently detectable. (Indeed, many viral and bacterial infections are readily spread precisely because infected individuals are often asymptomatic.) In the absence of meaningful perceptual inputs, the behavioural immune system cannot do much to prevent disease outbreaks from occurring, and spreading (Ackerman et al., 2021). There are also logical limits to the kinds of behaviours that might be regulated by this motivational system. The underlying mechanisms evolved to regulate behaviours that were adaptive in *ancestral* ecologies (e.g., avoidance of close physical contact, wariness of strangers, conformity to social norms). These mechanisms cannot be expected to necessarily regulate behavioural decision-making in regard to more modern means of mitigating the risk of infection, such as vaccination or facemask-wearing.[8] There may be implications for those decisions, but those implications are likely to be indirect and non-straightforward. (E.g., if facemask-wearing is perceived to be the social norm within one's cultural ingroup, activation of the behavioural immune system might be expected to increase an individual's inclination to also wear a facemask; but if not, then it would not.)

A key point here is that many contemporary human societies are profoundly different from the ancestral ecologies within which the behavioural immune system evolved. Given this

[8] This point is worth bearing in mind when reflecting on evidence showing that, in the United States, people who identified as politically conservative—an attitude associated with chronic activation of the behavioural immune system—were more reluctant than liberals to engage in certain kinds of epidemiologically beneficial behaviours during the COVID-19 pandemic (e.g., facemask-wearing; Mallinas et al., 2021). These correlations are readily attributable to political partisanship and to other explanatory processes that are conceptually independent of the specific psychological phenomena that are the focus of this article (e.g., Boykin et al., 2021; Grossman et al., 2020; Samore et al., 2021).

mismatch, attitudes and actions that were adaptive throughout much of human history may *not* be adaptive, or even healthy, in modern societies (Li et al., 2018). The upshot: The behavioural immune system may provide rather limited protection against modern disease outbreaks, such as the COVID-19 pandemic; and while some of its attitudinal and behavioural effects may be beneficial, these effects can also be potentially problematic (Schaller et al., 2015).

With this perspective in mind, we revisit key psychological phenomena reviewed above and discuss possible consequences—some beneficial and some not—for health outcomes.

Interpersonal Interactions

When activated, the behavioural immune system leads to increased wariness of crowds and of close interpersonal contact—especially with strangers. This wariness has potential benefits within the context of an outbreak of a disease that actually is transmitted from person to person. Wary individuals are less likely to become infected and, to the extent that large numbers of people exhibit this wariness, it can slow the spread of infection within a population (Fazio et al., 2021; McGrail et al., 2020). Wariness of crowds, strangers, and unfamiliar peoples may also lead people to avoid airports and international travel (Hamamura & Park, 2010), which can help limit the potential for a local outbreak to become a global pandemic.

Interpersonal wariness is not without potential costs, however, as it may make people more vulnerable to social isolation and loneliness—experiences that are stressful and have long-term negative health consequences (Hawkley & Capitanio, 2015; Holt-Lunstad et al., 2015). Even short-term isolation and loneliness can be problematic. Data collected during the COVID-19 pandemic indicate that the onset of the pandemic was associated with increased loneliness, and also show that increased isolation and loneliness were associated with increased incidence of depression, suicidal ideation and other problematic mental health outcomes (e.g. Killgore et al., 2020; Zheng et al., 2021). Wariness of crowds and strangers might also reduce inclinations to engage in certain kinds of behaviours that offer immediate disease-mitigating benefits—if those behaviours (e.g., receiving a vaccination) require interactions with strangers in public spaces.

Stigma and Prejudice

Activation of the behavioural immune system leads perceivers to respond more aversely to certain people—including people whose appearance or behaviour is perceived to be counter-normative in some way. This form of discrimination can limit the potential for disease transmission if it inhibits contact with individuals who actually are displaying symptoms of infection. But these same mechanisms can also lead to prejudice and discrimination against people who are disfigured or disabled, against immigrants, and against members of ethnic outgroups. Being discriminated against—or even being aware of the potential be discriminated against—is associated with a broad range of negative health consequences for the large numbers of people who are targets of discrimination (Johnston & Lordan, 2012; Schmitt et al., 2014; Williams et al., 2019). These negative health consequences might plausibly be amplified during disease outbreaks.

Additionally, if disease outbreaks lead to increased "othering" of immigrants and ethnic minority groups, it is possible that people who are vulnerable to being perceived as outsiders might be motivated to counteract that perception by strategically doing things to fit in, which might sometimes lead to unhealthy behavioural choices. For example, research conducted in the United States shows that when Asian-Americans' American-ness was questioned, they consequently showed an increased preference for prototypically American cuisine rather than prototypically Asian cuisine—with the consequence that they actually consumed more highly caloric, less

healthful food (Guendelman et al., 2011). This kind of phenomenon too might plausibly be exaggerated during disease outbreaks.

Xenophobic attitudes are also associated with a tendency to blame outgroups for disease outbreaks (e.g., Eichelberger, 2007; Perry et al., 2021), which may blind people to actual sources of infection risk and thus inhibit the uptake of behavioural strategies that might actually limit the risk of infection. Xenophobia may lead people to be distrustful of vaccines or other medical assistance offered by foreign nations and transnational organizations. For example, in 2003, distrust of Western governments led three Nigerian states to boycott a World Health Organization vaccination program (Jegede, 2007). More generally, whereas xenophobic attitudes may have been associated with reduced incidence of infection in ancestral populations (that lacked modern solutions to the problems posed by infectious diseases), things are different now—and xenophobic attitudes may potentially undermine effective responses to disease outbreaks.

Conformity

Activation of the behavioural immune system also leads to increased conformity with social norms, and this too can have positive epidemiological consequences—if those norms actually do serve as barriers against disease transmission. If, in the midst of a disease outbreak, there is normative pressure to wear facemasks, widespread activation of the behavioural immune system implies widespread compliance with that norm; and if the disease does actually spread via aerosol transmission, that widespread compliance can reduce the transmission and produce public health benefits. Similarly, the behavioural immune system is associated with authoritarian attitudes, which implies increased likelihood of obeying advice offered by an authority figure. This increased obedience to authority can also have public health benefits—if that authority figure's advice (e.g., wear facemasks in public settings) is epidemiologically sound.

But these same psychological tendencies can have rather different consequences when a social norm does *not* pose a barrier to disease transmission or when an authority figure offers advice that is epidemiologically *un*sound. For instance, in 2003, South African government officials resisted antiretroviral treatments for AIDS, while advocating instead for traditional dietary remedies such as beetroot and beer (Kalichman, 2009). And in 2020, the United States president openly opposed effective means of curbing COVID-19 transmission, and instead promoted idiosyncratic interventions that were of dubious utility and potentially dangerous (Yamey & Gonsalves, 2020). Under these circumstances, widespread increases in conformist and/or authoritarian attitudes are likely to be epidemiologically counterproductive.

Speculations About Variability Across Individuals, Cultures, and Circumstances

Even if disease outbreaks do activate the behavioural immune system, producing effects on attitudes and behaviour, those effects are unlikely to be the same for everybody. These effects may vary across individuals, across cultures, and across different circumstances that people might find themselves in during disease outbreaks.

Individual Differences

Experiments testing the psychological effects of disease-threat manipulations have sometimes shown that these effects are moderated by individual differences in perceived vulnerability to disease (PVD). Although at least one experiment showed a stronger effect among low-PVD participants (Sawada et al., 2018), the opposite effect is more typical: Disease-threat

manipulations often have stronger effects on the attitudes and behaviour of participants with high PVD scores (e.g., Mortensen et al., 2010; O'Shea et al., 2020; Wang & Ackerman, 2019). This interaction of chronic concerns and context-specific cues is consistent with the following interpretation: People who feel more vulnerable to infection are more sensitive to information connoting a potential disease threat, and respond more dramatically to that information.[9] The implication is that, if disease outbreaks do cause people to be more interpersonally cautious or xenophobic or inclined to conform to traditional social norms, these effects may be especially pronounced among people who generally feel most vulnerable to disease.

If there is any merit to this implication, then it suggests additional nuances to some of the speculations about health consequences identified above. For example: All else being equal, individuals who are chronically worried about infectious diseases (e.g., people who score highly on measures of PVD or disgust sensitivity) may be especially likely to strategically avoid interpersonal contact when outbreaks occur—and thus may be less likely to become infected (and less likely to transmit an infection to others), but may be more vulnerable to health problems associated with isolation and loneliness.

Just as individual differences in PVD may make people more susceptible to the effects that disease outbreaks have on attitudes and behaviour, other individual differences may buffer against those effects. Experimental evidence shows that the typical effects associated with the behavioural immune system—on xenophobia for instance—may be reduced when people are made aware of means to mitigate the threat posed by infectious diseases (Aarøe et al., 2017; Huang et al., 2011). Even if an individual feels vulnerable to infection, the psychological consequences of that vulnerability may be diminished if that individual also perceives that they have some sort of safety net or buffer against that threat. That protective function might be provided by a subjective sense of social support or attachment security (Mikulincer & Shaver, 2007). Obliquely consistent with this perspective are results showing that, during the 2014 Ebola scare in the United States, the positive correlation between fear of Ebola and xenophobia was weaker among individuals who expressed more collectivistic values (Kim et al., 2016). Also consistent with this perspective are results of a study that examined the moderating effects of interdependent self-construal—the perception that oneself is embedded within a network of meaningful social relationships (Salvador, Kraus, et al., 2020). Following an experimental manipulation designed to make the threat of disease psychologically salient (or not), participants were presented with depictions of norm violations, and neural responses were assessed as indictors of participants' reactions to those violations. Results showed that in the disease-threat condition (but not the control condition), a more highly interdependent self-construal predicted a weaker response to norm violations. The broader implication is that individuals who have some subjective sense of "social capital" may be more resistant to the psychological impact of disease outbreaks.

Research on the behavioural immune system might help to provide a deeper understanding of previously-documented findings linking other individual differences to disease-prevention

[9] The perceived threat of disease may also serve as a tacit justification to express attitudes that people might otherwise be reluctant to express—such as prejudicial attitudes (Crandall & Eshleman, 2003). For example, during the COVID-19 pandemic, data collected in the United Kingdom and Ireland showed that right-wing authoritarianism more strongly predicted anti-immigrant attitudes among people who expressed greater anxiety about the pandemic (Hartman et al., 2021). Just as authoritarianism disposes people to certain kinds of prejudices, so too does PVD; experimental procedures that make the threat of disease salient may facilitate expression of those latent prejudices. This process might help to explain some interactive effects of PVD and disease threat manipulations (e.g., effects on racial prejudice; O'Shea et al., 2020)—although it cannot explain all such effects (e.g., effects on extraversion and on perceptions of crowding; Mortensen et al., 2010; Wang & Ackerman, 2019).

behaviours. One straightforward predictor of preventative behaviour is a belief that the behaviour will actually reduce the rate of disease transmission (e.g., Miao & Huang, 2012). What role might the behavioural immune system play in this relationship? People with a chronically active behavioural immune system may be more highly motivated to believe in the efficacy of protective behaviours. One study found that PVD scores positively predicted the perceived efficacy of recommended preventative behaviours—such as hand washing—during an H1N1 influenza outbreak in Switzerland (Gilles et al., 2011), implying that disease outbreaks may be more readily contained in populations that that have higher mean levels of PVD. It is worth noting that there is at least one form of preventative behaviour to which this bit of speculation does not readily apply: Vaccination. Vaccinations can elicit concerns pertaining to impurity and contamination, and people who score more highly on measures of PVD and disgust sensitivity tend to have more negative attitudes toward vaccines (Clay, 2016; Luz et al., 2019). Consequently, for reasons distinct from perceptions of efficacy, higher levels of PVD may actually hinder widespread uptake of non-compulsory vaccines.

Adoption of preventative behaviours may also be influenced by gender: Compared to men, women tend to be more willing to adopt non-pharmaceutical preventative behaviours such as hand-washing and social distancing (Moran & Del Valle, 2016). Women also have higher mean scores on measures of disgust sensitivity and PVD (e.g., Duncan et al., 2009); and people with higher disgust sensitivity and PVD are more likely to engage in a wide range of preventative behaviours, including hand-washing, social distancing, and facemask wearing (Makhanova & Shepherd, 2020; Shook et al., 2020). It is therefore plausible that women's higher uptake of disease-prevention behaviours may be explained, in part, by women's generally higher chronic activation of the behavioural immune system.

Cultural Differences

Individual differences in chronic activation of the behavioural immune system are unlikely to be randomly distributed. There is likely to be some heritable basis for these individual differences (Sherlock et al., 2016; Tybur, Wesseldijk, & Jern, 2020), and these individual differences may also be partially the product of social learning processes (Stevenson et al., 2010). Consequently, these individual differences may be clumpy—with variation between families, friendship networks, and cultural populations. (For example, data collected in Canada revealed relatively higher PVD scores among participants with East Asian backgrounds; Duncan et al., 2009). Considered in isolation from other cultural differences, this might imply that attitudinal responses to disease outbreaks may be more pronounced in cultures with higher mean levels of perceived vulnerability to disease. But one must also consider cultural differences in other variables that might moderate these responses, such as collectivistic values and interdependent self-construal (Kim et al., 2016; Salvador, Kraus, et al., 2020). (These variables, like PVD, tend to be higher in East Asian cultures.) A more nuanced prediction is that the attitudinal consequences of disease outbreaks may be greatest in cultural populations characterised jointly by relatively *high* levels of perceived vulnerability and *low* levels of variables that provide a subjective sense of social interconnection.

On a thematically related note, the behavioural immune system may be indirectly implicated by different countries' different levels of success in combatting the COVID-19 pandemic. While much of the variation across countries is surely accounted for by idiosyncratic governmental (non)responses (Yamey & Gonsalves, 2020), and by differences in societal norms that are conceptually unconnected to the behavioural immune system (e.g. norms pertaining to

entering and exiting social relationships; Salvador, Berg, et al., 2020), there is evidence that countries that managed the emerging COVID-19 outbreak most successfully—as indicated by relatively lower caseloads and death rates—were countries characterised by cultural values that more strongly emphasise behavioural conformity and intolerance for nonconformists (Gelfand et al., 2021). Why are some cultures more conformist and authoritarian in the first place? One line of argument is that these cultural difference may owe their origins, in part, to historical differences in the prevalence of infectious diseases in local ecologies (Schaller & Murray, 2011). Indeed, just as experimental manipulations of disease threat lead individuals to be more conformist and morally vigilant, the prevalence of infectious diseases in a geographical region predicts higher levels of conformity and authoritarianism within entire regional populations (Murray et al., 2011; Murray, Schaller, & Suedfeld, 2013). Disease prevalence is also linked to cross-national differences in personality traits: Historically higher levels of disease prevalence predicts lower mean levels of extraversion and openness to experience within countries (Schaller & Murray, 2008). Findings such as these suggest the possibility that regional differences in epidemiological outcomes may be explained, in part, by differences in cultural norms that are themselves the indirect cultural products of many generations of differences in activation of the behavioural immune system. This is pure speculation, of course, and it is the kind of speculation that is extraordinarily difficult to put to rigorous empirical test.[10]

Circumstances that May Activate Other Motivational Systems

The behavioural immune system is one of many motivational systems that regulate human behaviour (Schaller et al., 2017), and other motivational systems too might be more readily activated in the wake of disease outbreaks—not directly by the disease threat itself, but indirectly by individual and/or societal responses to that threat. Behavioural responses facilitated by the behavioural immune system may not be compatible with behavioural responses facilitated by these additional motivational systems (Tybur et al., 2020). This kind of "psychological tug-of-war" (Beall & Schaller, 2019) may be resolved differently depending on an individual's personal characteristics or circumstances.

For example, disease threat can lead to social withdrawal, an individual-level response that may be compounded by formal policies that constrain opportunities for interpersonal interactions with friends. The resulting circumstance (especially if it is accompanied by feelings of isolation or loneliness) is likely to activate the motivational system that regulates affiliative behaviour, producing a stronger desire for social interaction. This conflict—between avoidance- and approach-oriented responses to interpersonal interactions—has consequences. Experimental evidence has shown that when affiliation motives are activated by a social exclusion manipulation, people are consequently less concerned about infection (Sacco et al., 2014). Analogously, a study conducted in Poland during the COVID-19 pandemic found that loneliness predicted decreased concern about personal health (Okruszek et al., 2020). Thus, even during disease outbreaks, the behavioural immune system may sometimes lose the psychological tug-of-war against the subjective need for affiliation—which can have nontrivial consequences for individual-level behavioural decision-making (e.g., failure to comply with social distancing guidelines) and population-level public health outcomes (failure to contain a disease outbreak). This dynamic may play out especially among adolescents and young adults—whose affiliation motives tend to be strongly prioritised (Neel et al., 2016) and thus prone to be thwarted by restrictions on social gatherings (Folk et al., 2020). This might help to explain why younger adults are less compliant

[10] See Footnote 1 for references to reasons to be cautious about interpreting those kinds of correlational findings.

with social distancing measures during disease outbreaks (Makhanova & Shepherd, 2020; Singh et al., 2019).

A different dynamic between multiple motivational systems might potentially play out among people who are parents to small children and who are compelled (e.g., by workplace restrictions or daycare closures) to spend more time at home with those children. Increased proximity to children may activate motivational mechanisms regulating parental care-giving behaviour (Schaller, 2018). As with the behavioural immune system, activation of the parental care motivational system disposes people toward risk aversion, inter-group prejudice, moral vigilance, and conservative social attitudes (Eibach et al., 2009; Eibach & Mock, 2011; Gilead & Liberman, 2014; Hofer et al., 2018; Kerry & Murray, 2018, 2020). There is no psychological tug-of-war here; these two motivational systems are mutually reinforcing. The implication is that, during disease outbreaks, parents of small children may be especially likely to experience the attitudinal and behavioural effects associated with the behavioural immune system.

Envoi

The COVID-19 pandemic has directly or indirectly touched every life around the globe, and has offered a stark reminder that—no matter our level of technological sophistication—opportunistic infectious diseases are an enduring presence within human social ecologies. Outbreaks are inevitable. Research on the behavioural immune system provides a basis for predicting consequences that these disease outbreaks might have on people's attitudes, actions, and health outcomes—and for understanding how those consequences may indirectly reflect our species' long history of coexistence with, and adaptation to, the threat of infection.

Funding

This work was supported by the Social Sciences and Humanities Research Council of Canada (Insight Development Grant 430-2018-00218).

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