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Human pathogen avoidance adaptations

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Over the past few decades, researchers have become increasingly interested in the adaptations guiding the avoidance of disease-causing organisms. Here we discuss the latest developments in this area, including a recently developed information-processing model of the adaptations underlying pathogen avoidance. We argue that information-processing models like the one presented here can both increase our understanding of how individuals trade-off pathogen avoidance against other fitness relevant goals and elucidate the nature of individual differences in pathogen avoidance. With respect to pathogen disgust in particular, we show how contact avoidance can be traded-off against other tasks, including food choice, cooperation, and mate choice.

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Pathogens pose problems to all humans, all primates, all mammals, and all vertebrates (and the list could go on, all the way to bacteria that are infected by viruses [1]). Not surprisingly, natural selection has shaped elaborate defenses against pathogens (e.g., the innate and adaptive immune systems) that exist in species across taxa. Many of these defenses are behavioral, and many behavioral defenses function to reduce the probability of contact with — and hence infection by — pathogens [1,2]. What behavioral defenses do humans have?

This question was scarcely considered two decades ago. Since being posed, though, it has generated an avalanche of hypotheses and empirical tests [3••]. Research in this area has outlined the contours of human pathogen avoidance adaptations, showing how such adaptations mold mate preferences [4,5•,6], dietary behaviors [7,8], xenophobia [9], ideological liberalism versus conservatism [10,11,12•], and antipathy toward homosexuals [13], the obese [14,15], the elderly [16] and the disabled [17].

Here we discuss how considerations of the information processing mechanisms underlying pathogen avoidance adaptations can inform when pathogen-neutralizing behaviors are relaxed versus engaged. Work on the emotion disgust — perhaps the most intuitive aspect of our pathogen avoidance psychology — provides an illustrative example.

Disgust: function versus mechanism

Armed with the germ theory of disease, several 20th and 21st century scientists noted that many objects that elicit disgust also reliably house pathogens [18–21]. This, in concert with the behaviors associated with disgust (e.g., proximal avoidance and rejection), straightforwardly implied to many scholars that disgust has a *function* — to neutralize infectious disease threats. That said, pathogen avoidance perspectives on disgust might seem incorrect if one assumes that individuals should *invariantly* experience disgust when pathogens are present, or not feel disgust when pathogens are absent. In fact, people often do not experience disgust toward some substances that house pathogens, such as a cooked hamburger that secretly houses *Escherichia coli* bacteria, and they also sometimes experience disgust toward objects that are free of pathogens, such as fudge that is shaped to look like feces [22]. This has led some theorists to propose that disgust has other functions, such as soothing existential anxieties [23]. However, considerations of information processing mechanisms can clarify some of the initially puzzling aspects of disgust. We describe multiple mechanisms within an information processing system, starting with a basic question: how do we detect pathogens in the first place?

How do we detect pathogens?

Any pathogen avoidance system must be capable of first detecting pathogens. This is no small feat, given the microscopic nature of microbes. If pathogens are reliably housed in certain locations, though, our sensory systems can evolve to detect cues associated with those locations. Consider where human-infecting microbes reside. They are more likely to be in or on other humans or mammals than in or on plants. They are more likely to be in some parts of a person (e.g., their mouth) than in others (e.g., their hair). They are more likely to be in a person's blood than in their tears. If these facts were invariant across the environments that humans have lived in for many generations, then selection could have shaped our sensory systems to be sensitive to locations that have reliably correlated with pathogen presence. That is, we could evolve pathogen detection systems that treat certain stimuli as *information* regarding the statistical likelihood that pathogens are present. We believe that humans have indeed evolved such systems. Each of the preceding examples types of stimuli are often treated as if they are pathogenic, even if they are, in fact, not [8,20,21,23,24,25••,26•]. Additionally, other stimuli can be perceived as connoting pathogen presence, either via classical conditioning [27,28] or by observing others' disgust reactions toward a stimulus [8,29]. That said, information regarding pathogens is imperfect, and people do not always respond to pathogen cues with avoidance.

Imperfections in pathogen detection

In the late 17th century, Van Leeuwenhoek developed a microscope — a marvel of human engineering — and became the first person to peer into the world of microbes. The fact that humans had been indirectly and non-consciously detecting pathogens for hundreds of thousands of years before this is an equally impressive marvel, but one of *natural* engineering. However, just as blood tests for HIV are imperfect (and, indeed, have calculable false positive and false negative rates, sensitivities, and specificities), so too are our pathogen detection systems. Some of this fallibility results from our inability to detect pathogens in some situations, like when a passenger in the front of an airplane cabin is exposed to a virus expelled from the lungs of a passenger in the rear. Much of the imperfection reflects design, though [3••,25••,30]. One could respond to one of the aforementioned cues with or without avoidance. Both of these possibilities could be an error, depending on whether pathogens are actually present. The first error, a false alarm, would needlessly deploy a pathogen avoidance response — a response that is not without costs. A useful food might not be consumed, a valuable social partner might be avoided or excluded, and energy might be expended by avoiding an area. The second error, a miss, would fail to deploy a pathogen avoidance response — a response that might have prevented the potentially high costs of infection. Assuming the second type of cost is greater, we would expect greater sensitivity to cues to pathogens at the expense of specificity. This can help explain the so-called law of contagion, where objects that come into contact with cues to pathogens are themselves treated as if they are infectious [22,23]. That said, signal detection principles alone do not explain why so many pathogen sources are *not* avoided, even if they possess cues suggesting that pathogens might be present.

Accepting the costs of pathogens

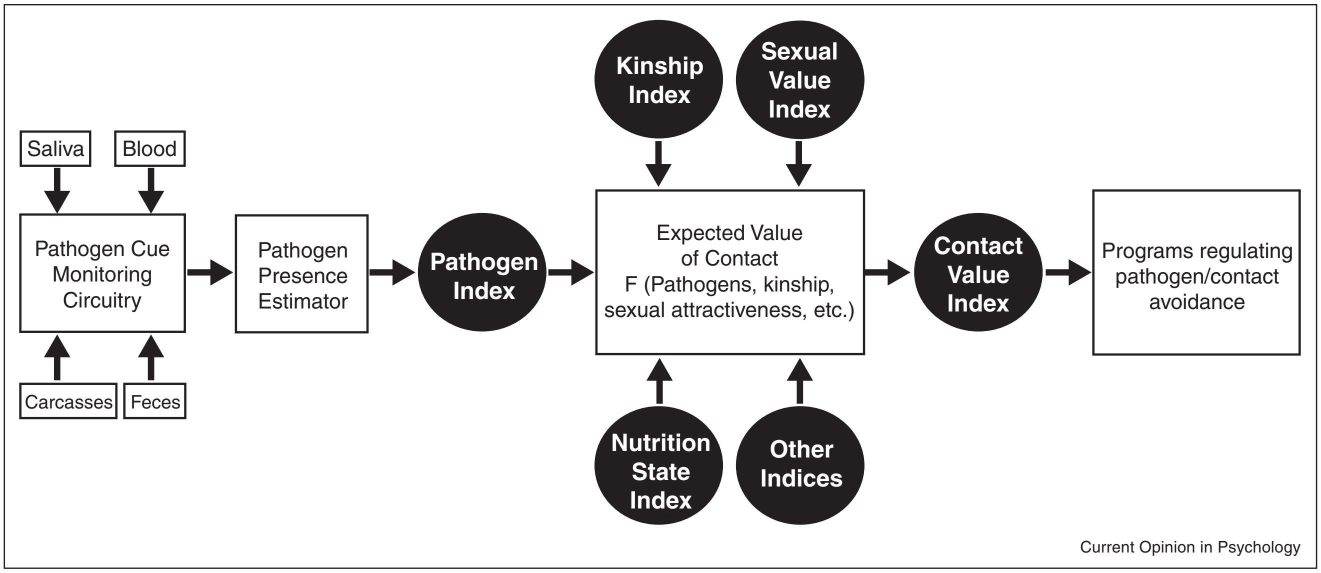
The best strategies for avoiding pathogens would involve never opening our mouths, never opening our eyes, and never touching another person. Needless to say, the type of psychology that would execute this strategy would be unlikely to evolve in humans, since basic fitness enhancing tasks imply non-zero infection risks. Instead, given the benefits of contact with various conspecifics and substances — which vary in their likelihood to house pathogens and their ability to convey benefits — we should have adaptations that tradeoff the costs of pathogen exposure against benefits that require physical contact. These tradeoffs should be designed to weigh several factors, including the probability that pathogens are present, the costs of infection (e.g., in terms of ability to resist pathogens, or in terms of broader investment in future reproduction; [31]), and the benefits of contact. Take the human mouth as an example. Some pathogens can be transmitted via saliva; indeed, some manipulate host behavior (e.g., by inducing sneezing or coughing) as a way to infect others [32]. Hence, given the asymmetry in costs of false alarms versus misses, we might expect people to avoid close contact with others' mouths at all times. This type of strategy, while not as fitness impairing as never eating, would not be cost free.

Consider kissing, which might allow individuals to assess a partner's mate quality or compatibility [33,34]. Even in the absence of direct mouth-to-mouth contact, proximity with the mouth could convey information about a potential sexual partner's health or genes (e.g., via olfaction). If an individual possesses certain characteristics (e.g., is of the opposite sex; has cues to high sexual value), then the pathogen risks of oral contact can be outweighed by reproductive benefits. Hence, even if two mouths are assessed as equally likely to transmit pathogens, one might be avoided if it belongs to someone with low sexual value (e.g., due to age, sex, quality, or compatibility), whereas another might be embraced if it belongs to someone with high sexual value [25••,35•].

The computational architecture of pathogen avoidance

The above considerations imply that the information processing systems underlying pathogen avoidance likely integrate multiple components. We present a model of how such an information processing system might be structured (see Figure 1; see also [25••]). In this model, perceptual systems (e.g., vision, olfaction) monitor the environment for cues to pathogens. Then, a mechanism that functions to integrate cues from different perceptual systems — a pathogen presence estimator — generates a pathogen index, an internal representation of the probability that pathogens are present based on the detection and reliability of cues. But pathogen presence isn't the sole factor governing avoidance. If this were the case, myriad fitness-promoting behaviors (e.g., eating, copulating, caring for offspring) would be avoided when pathogens are detected. Context-dependent avoidance can only occur if additional information is taken as input — if other mechanisms function to trade off pathogen presence against other dimensions impacting fitness across different contexts. Thus, under this model, the pathogen index, along with other indexes relevant to the

Figure 1



One proposed information processing system underlying pathogen avoidance adaptations.

costs and benefits of contact (e.g., kinship, sexual value, current nutrient state, among others) could be integrated into a downstream index, which then regulates approach versus avoidance in an adaptive manner (see [36,37] for examples of other proposed modular systems). We have termed this composite variable *the expected value of contact* [25••]. In Figure 1, the expected value of contact estimator computes a contact value index, which is a function (F) of all inputs to the system. We note that this is just one of many possible information processing architectures underlying pathogen avoidance adaptations. Nevertheless, this model is consistent with several empirical findings of how variables such as sexual value, nutrient state, and immune function influence responses to pathogen cues (see Table 1). Notably, an information processing architecture like this might underlie what has popularly been referred to as the behavioral immune system [3••,38]. In addition to being useful for understanding context-specific pathogen avoidance (that is, the tradeoffs the system was designed to make), information-processing models such as this one can also be used to understand trait-level variation in pathogen avoidance, a topic we turn to next.

Variation in pathogen avoidance

Individuals vary in the degree to which they are generally disgusted by cues to pathogens (disgust sensitivity; [39,40]) and avoidant of situations in which pathogens can be transmitted (germ aversion, or contamination sensitivity; [41]). Although instruments designed to capture this variation are often administered, theory and data informing the sources or meaning of this variability are limited [42]. The information-processing model presented here, which suggests where and why variation could arise, can be used as a framework for understanding individual differences. Assessments of each parameter in the model (e.g., pathogen presence, kinship, hunger, and sexual value) require their own detection systems, each of which are reliant on domain-specific cues. Trait-level pathogen avoidance could result from more sensitive cue detection, or it could result from strategically favoring Type I errors (false alarms) relative to Type II errors (misses), or it could result from greater pursuit of benefits of contact with pathogens (e.g., eating, mating). Disgust sensitivity and germ aversion are sometimes interpreted as reflecting 'investment' in avoiding pathogens — that is, greater avoidance at the expense of eating, mating, or social contact opportunities. Some evidence supports this perspective, with more pathogen avoidant individuals being less open to sexual contact with multiple partners [12•,41,43] and less open to sampling novel cuisines [7].

Outstanding questions

The framework described here poses multiple questions for recent pathogen avoidance proposals. Consider the idea that prejudicial attitudes toward the elderly might result from pathogen avoidance adaptations [16]. This could result either because (1) some physical features of the elderly are treated as cues to pathogens, or (2) physical contact with the elderly is less beneficial than physical contact with younger individuals. The first account could result if (1) pathogen detection mechanisms take departures from prototypes as input, and elderly physical features (e.g., wrinkles, pallor) depart from prototypes,

Table 1

Key findings demonstrating conditions under which a pathogen index is integrated with other information in a manner that affects the avoidance response to pathogen cues.

Information integrated with pathogen index	Benefit of integration	Example of evidence for integration
Sexual value	Sexual arousal can act as a cue to the fitness benefits (gleaned via conception) from contact with an individual with sexual value.	[44] Women who are sexually aroused report less disgust toward pathogen cues and behaviorally avoid cues to pathogens less (see also [45–48])
Kinship	Estimates of kinship can inform the inclusive fitness benefits of helping behaviors that requires physical contact	[49] Mothers perceive their own baby's feces soiled diaper to smell less bad than other babies' diapers, both when the source of the diaper is known and when the mother is blind to the identity of the diaper
Nutritional status	Individuals should be more willing to accept the potential costs of infection via food if nutrients are more needed	[50] Participants who fasted before an experiment expressed less disgust toward images of spoiled foods than participants who had not fasted (see also [51])
Ability to combat pathogens	The immune system might be more heavily taxed after illness, and contact with pathogens may be more costly	[52] Individuals who have been ill in the past week allocate more attention to cues to pathogens and behaviorally avoid cues to pathogens more than participants who have not been recently ill (see also [5•,53]).
Hormonal status	Progesterone might reduce ability to fight infection, or it might act as a cue to increased susceptibility to infection	[54] Women with higher progesterone levels experience more disgust toward and avoid cues to pathogens more than women with lower progesterone (see also [55,56])

(2) pathogen detection mechanisms take the specific features of the elderly as input (e.g., body scent), but not because these features departure from prototypes per se, or (3) the physical features of the elderly are not processed as cues to pathogens per se, but elderly individuals are associated with hospitals or poor hygiene, and hence the concept 'elderly' is processed as connoting infection. The second account could result if information about the elderly is not processed as posing any greater infection risk than information about younger individuals, but sexual or cooperative contact with the elderly is processed as yielding fewer benefits, and hence the contact with the elderly is avoided. Each of these possibilities can be used to generate distinct testable predictions within a pathogen avoidance account of ageism. Similar approaches might be useful for better understanding pathogen avoidance accounts of other prejudices, food preferences, and mate selection, among other topics.

Summary

Pathogen avoidance adaptations likely have strong and widespread effects on human psychology. Important first steps have been made in testing hypotheses of function in this area. Further consideration of and research into the information processing mechanisms underlying such adaptations can generate new knowledge in this area and clarify existing findings. These endeavors can uncover how and why information in the environment is processed as connoting pathogen presence and how, when, and why pathogen avoidance responses are executed in response to this information.

Conflict of interest statement

None declared.

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