Psychological Review
2013, Vol. 120, No. 1, 65–84

© 2012 American Psychological Association
0033-295X/13/$12.00 DOI: 10.1037/a0030778

Disgust: Evolved Function and Structure

Joshua M. Tybur
VU University Amsterdam

Debra Lieberman
University of Miami

Robert Kurzban
University of Pennsylvania

Peter DeScioli
Brandeis University

Interest in and research on disgust has surged over the past few decades. The field, however, still lacks a coherent theoretical framework for understanding the evolved function or functions of disgust. Here we present such a framework, emphasizing 2 levels of analysis: that of evolved function and that of information processing. Although there is widespread agreement that disgust evolved to motivate the avoidance of contact with disease-causing organisms, there is no consensus about the functions disgust serves when evoked by acts unrelated to pathogen avoidance. Here we suggest that in addition to motivating pathogen avoidance, disgust evolved to regulate decisions in the domains of mate choice and morality. For each proposed evolved function, we posit distinct information processing systems that integrate function-relevant information and account for the trade-offs required of each disgust system. By refocusing the discussion of disgust on computational mechanisms, we recast prior theorizing on disgust into a framework that can generate new lines of empirical and theoretical inquiry.

Keywords: disgust, adaptation, evolutionary psychology, emotion, cognition

Research concerning disgust has expanded in recent years (Olatunji & Sawchuk, 2005; Rozin, Haidt, & McCauley, 2009), and contemporary disgust researchers generally agree that an evolutionary perspective is necessary for a comprehensive understanding of the development and function of this emotion (e.g., Chapman, Kim, Susskind, & Anderson, 2009; Curtis, de Barra, & Aunger, 2011; Kelly, 2011; Oaten, Stevenson, & Case, 2009; Rozin, Haidt, & McCauley, 2008; Tybur, Lieberman, & Griskevicius, 2009). Contributing to this consensus are the cross-cultural consistency in expressions of disgust (Ekman, 1972), the straightforward connection between common disgust elicitors and infectious disease threats (e.g., rotting meat; Curtis & Biran, 2001), and the recognition that pathogens have imposed strong selection pressures on the evolution of most organisms (Fumagalli et al., 2011; Tooby, 1982).

Despite recent advances, important issues remain. Disgust researchers have been explicit in identifying pathogens as the key selection pressure driving the evolution of the disgust system, but there has been less precision in identifying the selection pressures driving the evolution of disgust systems unrelated to pathogen avoidance (e.g., behavior in the sexual and moral domains). Although multiple researchers have suggested that pathogen disgust was "co-opted" or "modified" to execute new functions (e.g., Rozin et al., 2008), exactly how these new domains functionally differ from pathogen-related disgust has not always been specified. Hence, one of our goals here is to articulate the selection pressures that led to the evolution of separate disgust adaptations that perform distinct functions in the domains of pathogen avoidance, mate choice, and moral judgment.

Further, in contrast to the widespread appeal to function, there has been far less work specifying the underlying psychological mechanisms that generate the specified disgust responses. In addition to specifying function, then, we examine the computational structure of disgust. Whereas an examination of evolved function addresses the ultimate level of explanation of behavior, that is, why disgust exists and operates the way it does, a description of information processing structure provides a proximate level of explanation, that is, how each disgust system carries out its function (Tinbergen, 1963; Tooby & Cosmides, 1992). For each function disgust performs, psychological mechanisms must take specific inputs, integrate them with fitness-relevant moderating factors, and then set in motion the constellation of behavioral, cognitive, and physiological processes naturally selected to perform the function at hand. For instance, pathogen disgust requires (a) detection systems that take as input cues associated with pathogen presence and (b) integration systems that weigh cue-based pathogen threat level with other fitness relevant factors (e.g., hunger) and then adaptively regulate withdrawal and avoidance behaviors accordingly.

Joshua M. Tybur, Department of Social and Organizational Psychology, VU University Amsterdam, Amsterdam, the Netherlands; Debra Lieberman, Department of Psychology, University of Miami; Robert Kurzban, Department of Psychology, University of Pennsylvania; Peter DeScioli, Department of Psychology, Brandeis University.

We thank Vladas Griskevicius for helpful comments on an earlier form of this article. We also thank Jon Haidt and Randy Thornhill for helpful comments.

Correspondence concerning this article should be addressed to Joshua M. Tybur, VU University Amsterdam, Department of Social and Organizational Psychology, Van der Boechorstraat 1, 1081 BT Amsterdam, the Netherlands. E-mail: j.m.tybur@vu.nl

Here we outline the possible information processing structures required by pathogen, sexual, and moral disgust systems, with a focus on the trade-offs each system was designed to make (e.g., the trade-off between the costs of infection vs. eating made by pathogen disgust; the trade-off between inbreeding vs. having sex made by sexual disgust; the trade-off between endorsing or rejecting moralized rules). We argue that the development of such computational models is a useful tool to help make explicit the information required to perform a particular function, and in so doing it can help generate hypotheses regarding functional design, loci of individual differences, potential sources of impairment, development, and cross-cultural variability.

To begin, we briefly review the current dominant perspective on disgust and suggest that limitations associated with this perspective necessitate an alternate approach. We summarize the details of an evolutionary-computational approach for understanding emotions and apply this to disgust. In so doing, we specify the selection pressures that led to the evolution of pathogen, sexual, and moral disgust. For each adaptation, we describe a computational structure that considers the trade-offs the system was selected to make. Finally, we explain how a computational model can generate novel testable hypotheses and inform programs of research across multiple disciplines, including developmental, clinical, personality, cognitive, and social psychology.

Contemporary Disgust Theory

There is a growing consensus within the social sciences that disgust plays a key role in motivating behavior that probabilistically reduces exposure to pathogens—organisms that exploit their hosts for resources critical to the pathogen's own survival and replication (Calder, Keane, Manes, Antoun, & Young, 2000; Curtis, Aunger, & Rabie, 2004; Curtis & Biran, 2001; Curtis et al., 2011; Fessler, Eng, & Navarrete, 2005; Fessler & Navarrete, 2003a; Fleischman & Fessler, 2011; Kelly, 2011; Marzillier & Davey, 2004; Oaten et al., 2009; Olatunji & Sawchuk, 2005; Rozin et al., 2008; Stevenson & Repacholi, 2005; Susskind et al., 2008; Tybur, Bryan, Magnan, & Caldwell Hooper, 2011; Tybur, Merriman, Caldwell, McDonald, & Navarrete, 2010). Many of the substances that people across cultures find intuitively disgusting, such as feces, dead bodies, and sexual fluids, reliably contain harmful bacteria (see Curtis & Biran, 2001, Table 6, for a summary). However, as multiple disgust researchers have noted, many objects, acts, and concepts that do not pose objective infectious-disease threats also elicit disgust. For example, feces-shaped fudge, apple juice in bedpans, and sterilized plastic cockroaches elicit reports of disgust, as do many sexual concepts and noninfectious social transgressions (Borg, de Jong, & Schultz, 2010; Cannon, Schnall, & White, 2011; Chapman et al., 2009; Hutcherson & Gross, 2011; Koukounas & McCabe, 1997; Rozin, Millman, & Nemeroff, 1986). A critical issue for disgust researchers has been to generate a theoretical model to account for the heterogeneity of disgust elicitors outside of the domain of pathogen avoidance.

The theoretical model of disgust put forth by Rozin, Haidt, McCauley, and colleagues, which we refer to as the Rozin–Haidt–McCauley (RHM) model, has become the gold standard within the disgust literature over the past two decades (Haidt, McCauley, & Rozin, 1994; Haidt, Rozin, McCauley, & Imada, 1997; Rozin & Fallon, 1987; Rozin, Haidt, & McCauley, 2008, 2009). The RHM model is explicitly based on considerations of evolved function, and it proposes several "stages" through which disgust has expanded to multiple domains. RHM propose that "core disgust"—disgust toward food, animals, and body products—evolved from a toxin-based food-rejection system (distaste) and functions to motivate pathogen avoidance. RHM further suggest that core disgust was co-opted to address a putative separate function: neutralizing reminders that humans are animals. In particular, the RHM model posits that animal-reminder disgust functions to protects us from seeing "ourselves as lowered, debased, and mortal" (Rozin et al., 2008, p. 762) by rejecting any reminders of our animal nature and mortality, and it is elicited primarily by sex, death (e.g., corpses), bad hygiene, and body envelope violations (e.g., gore, wounds, disfigurement). Hence, animal reminder disgust is thought to function to "protect the body and the soul" (Rozin et al., 2008, p. 764). RHM suggest the presence of two additional domains of disgust: interpersonal disgust, which functions to protect the body, soul, and social order and is elicited by contact with strangers or undesirables, and moral disgust, which functions to protect the social order and is elicited by moral violations (see Figure 1 for a comparison of the model proposed by RHM, 2008, and the model proposed herein).

Despite its ubiquitous use across disparate fields, the RHM model has key shortcomings. For example, animal reminder disgust is consistently posited to "protect the soul," a function purported to be unique to humans (Rozin, Haidt, & McCauley, 2008, 2009; Rozin, Lowery, Imada, & Haidt, 1999). However, avoidance of corpses—the prototypical elicitor of animal reminder disgust under the RHM model—is ubiquitous across other species (Wagner, Stroud, & Meckley, 2011; Yao et al., 2009). The literature on this topic suggests that corpse avoidance in nonhuman animals functions to protect against threats posed by infectious microbes that may have killed the other organism or that are rapidly colonizing the corpse. Other aspects of animal reminder disgust—disgust toward sex, poor hygiene, and deformity—likely have more specific functions that are well grounded within an evolutionary framework but are not articulated under the RHM model (e.g., Fessler & Navarrete, 2003a; Oaten, Stevenson, & Case, 2011; Ryan, Oaten, Stevenson, & Case, in press; Tybur et al., 2009). Moreover, the animal reminder perspective is tied to a questionable assumption about human nature: that "anything that reminds us that we are animals elicits disgust" (Rozin et al., 2008, p. 761). Nonhuman animals can be readily observed running and jumping like humans, breathing like humans, sleeping like humans, and caring for their offspring like humans, yet none of these behaviors elicit disgust. In fact, humans often view comparisons to animals positively rather than with disgust (see Royzman & Sabini, 2001; Tybur et al., 2009). In general, the rapidly developing evolutionary literature—notably the literature on behavioral adaptations for pathogen avoidance (see Curtis, 2007; Curtis & Biran, 2001; Curtis et al., 2004, 2011; Hart, 2011; Schaller & Park, 2011)—suggests that an examination of functions not articulated in the RHM model can offer great utility for understanding disgust.

Another shortcoming of the RHM model is that, much like Darwin's (1872/1965) initial account of disgust, it relied on circular functional definitions. Darwin initially defined disgust as a reaction to "something revolting, primarily in relation to the sense of taste, as actually perceived or vividly imagined" (p. 250).

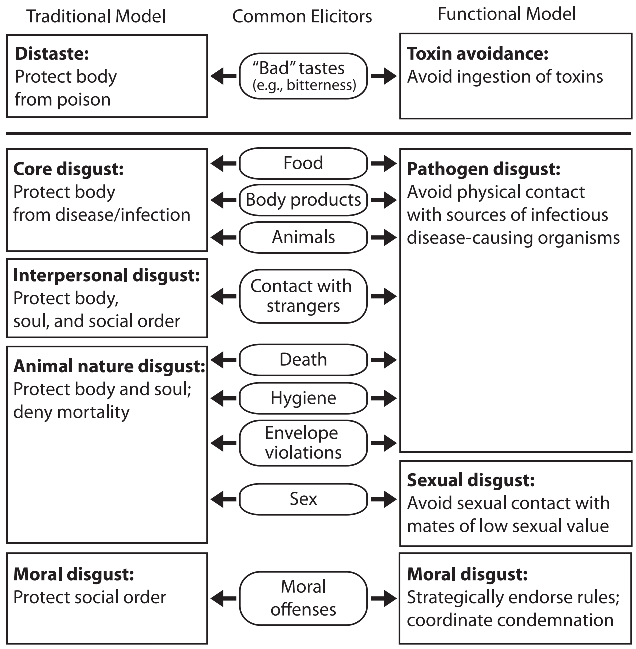

Figure 1. Comparison of disgust models. The traditional model proposed by Rozin, Haidt, and McCauley (2008; RHM) and the functional model proposed herein group the elicitors of disgust differently. According to the RHM model, multiple domains of disgust emerged from distaste, which functions to protect the body from poisons. RHM's model proposes four types of disgust with distinct elicitors: core disgust, interpersonal disgust, animal nature disgust, and moral disgust. By contrast, a functional perspective indicates that all of these elicitors, with the exception of sex and moral offenses, are better interpreted as different sources of infectious agents. Sex under the traditional model is thought to elicit disgust because it reminds humans of their animal nature. From a functional perspective, decisions about sexual behavior constitute a separate adaptive problem related to avoiding sexual contact with fitness-jeopardizing reproductive partners. Both models propose a separate domain of moral disgust. Whereas RHM interprets its function as benefiting the group by protecting the larger social order, the framework proposed here suggests that moral disgust serves individual fitness interests by communicating condemnation of rule violators with other people. In addition, the functional model suggests that behaviors eliciting sexual and pathogen disgust feed into systems strategically sifting for behaviors to condemn, addressing the functionally distinct question of why some disgusting acts are perceived as morally wrong.

According to this perspective (notably provided before the germ theory of disease was widely disseminated), disgust is both the reason for the response (the object is revolting) and the output of the response. Similarly, the animal reminder perspective suggests that people feel disgust toward behaviors that threaten to remind people that they are animals, but the disgust response appears to also serve as the criteria by which a behavior is identified as reminding people that they are animals (so, some animal behaviors, such as urinating and copulating, are argued to remind people that they are animals because they elicit disgust, whereas other behaviors that are no less animal, such as breathing and sleeping, are not argued to remind people that they are animals because they do not elicit disgust). Further, RHM (2008) argued that (in the United States, at least) moral disgust is elicited by sleazy acts. Accounts such as this beg the further question of what renders an act sleazy. We argue that considerations of evolved function and structure can help overcome some of these challenges.

An Evolutionary View of Emotion

Our examination of disgust draws heavily on an evolutionary perspective of emotion (Keltner & Gross, 1999; Keltner, Haidt, & Shiota, 2006; Nesse & Ellsworth, 2009; Tooby & Cosmides, 1990, 2008; Pinker, 1997; Tooby & Cosmides, 2008). This perspective has been fruitfully applied to other psychological states, including anger (Sell, Tooby, & Cosmides, 2009), fear (Öhman & Mineka, 2001; Tooby & Cosmides, 1990), jealousy (Buss & Haselton, 2005), and depression (Andrews & Thompson, 2009; Hagen, 2002; Keller & Nesse, 2006). Here, we apply this logic to three proposed functionally distinct domains of disgust: pathogen, sexual, and moral disgust.

Accordingly, we provide descriptions of each functional domain at two separate levels of analysis. The first, that of deciphering evolved function, requires a description of the historically recurring conditions that led to the emotion's evolution and subsequent maintenance. This level of analysis specifies the small subset of responses, out of the unbounded set of all possible responses, that would have overcome the conditions posed by the posited selection pressures and led, on average, to an increased rate of survival and reproduction. Taken together, a description of selection pressures and subsequent solutions to the conditions they posed constitute an analysis of evolved function.

Whereas an explanation of evolved function (an *ultimate* explanation) requires consideration of the selective conditions that persisted over many thousands of generations, our second level of analysis—that of information processing structure (a *proximate* explanation akin to the algorithmic level of analysis proposed by Marr, 1982)—specifies how the selected design feature operates within an individual organism (Tinbergen, 1963). Given the different adaptive problems disgust solves (e.g., decisions regarding mate choice vs. pathogen avoidance), many of the procedures that give rise to disgust are predicted to differ. We suggest that these computational processes occur nonconsciously but that they lead to consciously accessible states (the experienced sensation of disgust).

The evolutionary analysis of disgust we offer thus builds on components of the RHM model—most notably the idea that disgust has multiple functions, one of which is to deter contact with pathogenic substances—but differs markedly in that we specify the selection pressures that led to the expansion of disgust into domains beyond pathogen avoidance and an engineering account of how each function is executed.

Pathogen Disgust: The Avoidance of Disease-Causing Organisms

Selection Pressures

Parasitic microorganisms, though small in scale, pose large selection pressures on all long-lived, multicellular organisms. Pathogens' rapid reproduction at the expense of their hosts creates a coevolutionary arms race between host avoidance and pathogen transmission (Ewald, 1994; Nesse & Williams, 1994). The dynamic of pathogen–host interactions has been implicated as a major selective force in the evolution of phenomena ranging from sexual reproduction, cellular differentiation, and an immune system (Fumagalli et al., 2011; Ridley, 1993; Tooby, 1982) to the decorative plumage on birds (Hamilton & Zuk, 1982), to personality and cultural variation (Mortensen, Becker, Ackerman, Neuberg, & Kenrick, 2010; Schaller & Murray, 2008; Thornhill, Fincher, Murray, & Schaller, 2010). Like a wide range of other taxa, including roundworms, lizards, and chimpanzees, humans have elaborate defensive physiological, cognitive, and behavioral adaptations that evolved because of the selection pressures posed by pathogens (Curtis, 2007; Curtis et al., 2011; Kluger, Ringler, & Anver, 1975; Schaller & Duncan, 2007; Schaller & Park, 2011; Zhang, Lu, & Bargmann, 2005). We argue that *pathogen disgust* is one such adaptation and serves as an initial line of defense against pathogen infection. Pathogen disgust largely captures what others have called core disgust (Rozin et al., 2008), primary disgust (Marzillier & Davey, 2004), theoretical disgust (Nabi, 2002), pure disgust (Zhong & Liljenquist, 2006), and basic disgust (Chapman et al., 2009; Inbar, Pizarro, & Bloom, 2009). We suggest that the label *pathogen disgust* best describes this domain because it refers to the system's evolved function and describes the types of cues taken as input.

Infectious microorganisms cannot rapidly travel large distances the same way that other, larger predators (e.g., tigers) can. To move to a new host, pathogens need to exploit points of contact between habitable regions of their current and future hosts. The following areas of animal bodies are particularly useful as exit and entry points.

1. The mouth. The mouth is a primary source of transit utilized by many micropredators. For example, *Mycobacterium tuberculosis* exits a host via saliva droplets that are expelled by speaking, coughing, and sneezing and enters a new host through the mouth when airborne droplets are inhaled. The mouth's digestive function also provides useful avenues of food-borne infection. Microbes such as *Escherichia coli* can gain entry into the body through the mouth when infected animal products (e.g., meat, wastes) are ingested as food. In addition to exploiting behaviors such as breathing and eating, pathogens can induce host behaviors that facilitate transmission, such as sneezing and vomiting. For instance, *Vibrio cholerae* uses the mouth as a digestive exit through vomit.

2. The skin. As the surface of the body, the skin is an obvious launchpad for infectious attacks. Transmission can occur through skin-to-skin contact as well as through skin lesions that exude pus or blood. For example, the varicella zoster virus (chicken pox) travels via contact with infected skin lesions and moreover causes itching that promote skin-based transmission to another host. Further, pathogens that do not directly infect via the skin can be housed on the skin and make their way into the body via the other entry points discussed. For example, fecal contamination of unbroken skin may not directly cause infection. However, touching the mouth or eyes with this skin can lead to infection.

3. The anus. The excretory function of the anus makes it well suited for pathogen exit. After exiting the body in feces, infectious agents can gain entry into a new host through the mouth, such as from contaminated water. For instance, *Salmonella enterica*, which causes typhoid fever, exits the body in feces and enters new hosts through ingested food and water. Infectious disease transmission can also occur during anal penetration (Varghese, Maher, Peterman, Branson, & Steketee, 2001).

4. The genitals. The sex organs are designed to transport gametes between organisms, which creates cross-body pathways that can be exploited by micropredators. For instance, *Chlamydia trachomatis* gains access to new hosts via sexual fluids, as do many other sexually transmitted diseases (Holmes et al., 2007).

To avoid the costs of infection, humans need counteradaptations to prevent pathogen transmission. These mechanisms must defend the key entry points, such as the mouth and skin, and they need to avoid other individuals' exit points and the substances leaving these points, such as sneezes and feces. Pathogen disgust offers a first line of defense by physically steering people away from conspecifics, nonhuman animals, objects, and locations that could make them vulnerable to contact with pathogens. Naturally, maximum pathogen avoidance, such as never eating, touching others, or having sex, would have carried substantial fitness costs. To make adaptive trade-offs, psychological mechanisms need to estimate magnitudes of pathogen-transmission risk and weigh them against magnitudes of expected benefits associated with engaging in these other behaviors. We detail these computational mechanisms below.

Information Processing Architecture of Pathogen Avoidance

At least three sets of information processing systems are needed to avoid pathogens: (a) perceptual systems that monitor the environment for cues that reliably correlate with pathogen presence, (b) intermediate computational processes that integrate the probability of pathogen presence with other factors that should influence the intensity of the pathogen disgust response and then output this integrated information, and (c) a system that sets in motion the specific psychological and physiological processes involved in the pathogen avoidance response (see Table 1).

Inputs: Cues to pathogen presence. Although most infectious microorganisms are too small for humans to observe directly, we are able to detect various properties reliably associated with their presence. For instance, pathogens flourish in some environments more than others—generally those that provide a source of nutrients and minimal antipathogen defenses (e.g., corpses).

Over evolutionary history, natural selection likely favored perceptual systems that reliably detect those properties associated with pathogen presence. Color, for example, reliably indicates whether fruit is unripe, ripe, or rotten due to the effects that infectious microorganisms have on fruit pigmentation (Giovannoni, 2001). Other visual cues, including texture and viscosity, can identify potentially pathogenic substances (e.g., blood, pus, semen, feces; see Curtis et al., 2004). Similarly, the visual cues associated with "creepy crawlers" (e.g., maggots and worms) can act as a time stamp of the length of time an organism has been deceased and hence left undefended against infectious microorganisms. Unlike a freshly killed animal, a body that has been dead longer will have a greater probability of having been successfully colonized by micro- and macro-organisms. Thus, the presence of maggots, flies, and worms indicates a greater likelihood of bacterial contamination. Olfactory, gustatory, and tactile cues also indicate the presence of pathogens. For instance, research on olfaction and disgust

Table 1
Information Processing Structure of the Functional Domains of Disgust

Adaptive problem	Cues that indicate probable presence of adaptive problem	Additional factors modulating response	Expected value estimator	Computed internal regulatory variable	Output
Avoiding contact with infectious disease-causing organisms	Bodily fluids and products, animals, poor hygiene, decomposing or rotting organic matter	Nutritional state, relationship to cue source (e.g., friendship, kinship), sexual arousal	Integrates contact avoidance benefits (reduced infection risk) with costs (e.g., not eating, not having sex)	Expected value of contact	Pathogen disgust: Sensation of disgust, disgust facial expression, motivation to avoid contact, and deployment of other functionally coordinated systems according to the magnitude of the expected value of contact
Avoiding sexual contact with individuals jeopardizing fitness	Sexual interest from individuals with poor genetic compatibility (kin) and with low mate value	Availability of alternative mates, one's own mate value (opportunity costs)	Integrates sexual avoidance benefits (reproductive opportunities saved for better partner) with costs (e.g., missed reproductive opportunities, impaired social relationship with target)	Expected sexual value	Sexual disgust: Sensation of disgust, disgust facial expression, motivation to avoid sexual contact, and deployment of functionally coordinated systems according to the magnitude of the expected sexual value
Communicating and coordinating condemnation with other people	Behaviors likely to be condemned by others (lying, cheating, stealing, rule violations)	Relationship to target (e.g., friendship, kinship)	Integrates condemnation benefits (mitigating conflict escalation) with costs (e.g., impaired social relationship with target)	Expected condemnation value	Moral disgust: Motivation to signal condemnation of the behavior/person and facial and vocal expressions of disgust

has identified the specific chemical compounds in feces that elicit disgust (e.g., Wicker et al., 2003). Sour taste buds can detect lactic acid, an indication of elevated bacterial concentrations (DeSimone, Lyall, Heck, & Feldman, 2001). Touch also provides information regarding moisture content and animacy, two factors predictive of both pathogenic growth (Lovanh, Cook, Rothrock, Miles, & Sistani, 2007) and disgust reactions (Oum, Lieberman, & Aylward, 2011).

Intermediate computational processes: The probability of pathogen presence and the expected value of contact. Once pathogen detection systems have responded to incoming cues, additional systems assess the likelihood of the presence of an actual threat. Much like a blip on a submariner's sonar, perceptual activation can be caused by environmental noise or a true signal. For this reason, we posit a set of systems that integrate the detected pathogen cues, perform a signal detection analysis, and generate an internal estimate of the probability of pathogen presence. The signal detection process that occurs should be tuned to reflect the costs of committing two possible errors: Type I (assuming a threat when none is actually present—a false alarm) and Type II (failing to detect a threat when one is present—a miss; Haselton & Nettle, 2006; Nesse, 2005; Tooby & Cosmides, 1990). In the context of pathogen detection, a miss involves high costs, including the costs of the immune response to fight the infection (e.g., metabolic costs; damage caused by inflammatory responses), any tissue damage done by the pathogen, and, in some cases, death. In contrast, the costs of a false alarm, although non-zero, might include what are often relatively small costs, such as proximal avoidance or declining to ingest a food. Generally, then, humans are predicted to be biased toward having a relatively low threshold for acting on ambiguous cues to infection risks (Ackerman et al., 2009; Kurzban & Leary, 2001; Neuberg, Kenrick, & Schaller, 2011; Oaten et al., 2011; Park, Faulkner, & Schaller, 2003; Park, Schaller, & Crandall, 2007; Schaller, Miller, Gervais, Yager, & Chen, 2010; Schaller & Park, 2011).

The possibility of pathogen presence should not lead to automatic behavioral avoidance across all contexts. Instead, the expected, probabilistic costs of pathogen infection should be set against other exigencies, such as acquiring nutrients and calories by ingesting the soon-to-be rotting flesh of a dead animal. For this reason, additional procedures are needed to integrate the computed pathogen threat with other indices that influence the costs versus benefits of avoiding pathogens in a given context. Consider sexual behavior as an example. For sexual behaviors to take place—behaviors that bring individuals into contact with foreign pathogens via physical proximity with a conspecific and exposure to various bodily fluids—the pathogen avoidance response must be down-regulated. This could be engineered by a system that integrates estimates of pathogen presence with other information regarding sexual arousal and then outputs an expected value of contact that reflects the cost–benefit ratio of contact versus avoidance in a given context.

Under the model we are proposing, the magnitude of pathogen disgust depends on the computed expected value of contact. Indeed, we claim that the sensation of disgust might just be the felt output of this computation. Critically, this value should reflect the trade-offs inherent in avoiding pathogens versus obtaining other benefits. For instance, pathogen avoidance might be traded off against the benefits of helping kin or obtaining nutrients when scarce. Stevenson and Repacholi (2005), for example, found that the level of disgust associated with a pathogen-related odorant depends on the source of the odorant, with kin eliciting significantly less disgust than strangers. Importantly, such flexibility requires that cues to kinship modulate the pathogen disgust response, an outcome that is possible if the probability of relatedness (see, e.g., Lieberman, Tooby, & Cosmides, 2007) serves as an additional input to systems computing the expected value of contact. Similarly, foods with cues to pathogen presence might be avoided when alternative foods are available but consumed when they are not, as in times of prolonged famine (e.g., Hoefling et al., 2009). Hence, internal states correlated with hunger (e.g., low blood-glucose levels) might serve as yet other inputs to a system that computes the expected value of contact. Internal states indicating greater vulnerability to pathogens, including progesterone, can act as an additional input to modulate the disgust response (Fessler et al., 2005; Fleischman & Fessler, 2011). In general, the modular architecture we are proposing allows for flexibility in the disgust response by virtue of the variety of inputs required to compute an expected value of contact (see Barrett and Kurzban, 2006, for a discussion on modularity).

Outputs: The evolved response to pathogen presence. The expected value of contact is predicted to initiate the cascade of events required to neutralize the threat of pathogen infection. A system well designed to perform this function should activate the behavioral, cognitive, and physiological processes that help defend against the various modes of pathogen transmission. A key (perhaps the key) response of pathogen disgust is the motivation to avoid contact with mouths, skin surfaces, anuses, genitals, and other surfaces, portals, or substances capable of transmitting disease-causing organisms. Avoiding the spray of sneezes and coughs and contact with skin lesions or body fluids would have reduced the probability of pathogen infection. Indeed, comparisons of action tendencies associated with several affective states indicate that disgust is uniquely related to physical avoidance and pushing away (Hertenstein, Keltner, App, Bulleit, & Jaskolka, 2006; Roseman, Wiest, & Swartz, 1994). Myriad studies have shown that, when individuals possess cues for pathogen presence, they are proximally avoided and/or stigmatized (Kleck, 1969; Kurzban & Leary, 2001; Oaten et al., 2011; Schaller & Duncan, 2007; Worthington, 1974) and that contextual or chronic motivations to avoid disease exacerbate such distancing (Mortensen et al., 2010; Park et al., 2003, 2007).

The pathogen disgust system should also adaptively regulate other psychological processes that could aid in avoiding contact with pathogens. For instance, (carefully) gathering more information about possible sources of contaminants would have been beneficial, especially under conditions of uncertainty. Additional scrutiny with the senses or social communication might help corroborate suspicions of pathogen presence; this might account for the otherwise odd phenomenon in which people, on eating something that does not taste right, seem inclined to get a second opinion (e.g., “Does this milk taste spoiled to you? Here . . .”).

In the case that a pathogenic substance has been ingested and has caused a physiological response such as nausea or expulsion, memory systems should be engaged to store the likely source of the contaminant (see, e.g., Seligman & Hager, 1972, on the “sauce béarnaise” effect). These memory traces should be very specific and tailored toward retrieving information about items ingested because of the causal relationship between ingesting food substances and pathogenic infection (Garcia, Kimeldorf, & Koelling, 1955). Thus, upon feeling nausea, for instance, one’s memory systems should be organized to recall substances ingested rather than pathogen-irrelevant conditions, such as the weather or the color of one’s clothing. In addition, pathogen disgust should regulate attention (directed toward avenues of pathogen transmission), conceptual frameworks (to activate concepts such as cleanliness, health, and infection), reasoning (to infer that if one has been touched, one could be contaminated), learning mechanisms (to encode cues that predict the transmission of pathogens such as the “ah-ah-ah” that precedes the “chooo”), and so on in a manner that would have aided in the neutralization of pathogen threats (Ackerman et al., 2009; Faulkner, Schaller, Park, & Duncan, 2004; Mortensen et al., 2010; Navarrete & Fessler, 2006; Park et al., 2003; Tybur, Bryan, Magnan, & Caldwell Hooper, 2011).

Pathogen disgust is also associated with various physiological responses posited to reduce the probability that pathogenic substances will enter the body and cause infection. The prototypical disgust facial expression appears to restrict airflow through the nose, to reduce the exposed surface area of the eyes, and to prevent potentially infectious substances from entering the mouth (Fessler & Haley, 2006; Rozin, Lowery, & Ebert, 1994; Rozin et al., 1995; Susskind et al., 2008). Disgust is often accompanied by nausea, a desire to vomit, and a loss of appetite (Rozin & Fallon, 1987; Rozin et al., 2008), all of which may contribute to ridding the body of pathogens that have already been ingested or to decreasing the probability of ingesting materials housing pathogens.

Perception of pathogen cues also appears to prime our immunological defense systems. For example, Stevenson, Hodgson, Oaten, Barouei, and Case (2011) recently observed increases in salivary tumor necrotizing factor alpha, a cytokine that plays a role in the inflammatory process that clears infection, in participants exposed to cues to pathogen presence. Similarly, Schaller et al. (2010) demonstrated that, relative to participants in a control condition, participants who viewed images of faces sneezing or marked with pox produced higher levels of interleukin-6 (IL-6), a cytokine that plays a key role in the inflammatory process that clears infections. Hence, visual cues to pathogen presence prepare the body to fight pathogenic invaders. Notably, differences in IL-6 observed by Schaller et al. were not mediated by differences in self-reports of disgust toward the stimuli. Instead, self-reports of disgust were inversely related to IL-6 activation among participants who viewed pathogenic faces, suggesting that individuals may follow distinct strategies for countering pathogen threats, with some preparing a strengthened immune response and others investing in avoidance.

In sum, there are numerous psychological abilities and physiological systems that could be activated to solve the problem of pathogen transmission. Identifying those that might have assisted in the avoidance of pathogen threats can help generate hypotheses about the structure of pathogen disgust. Importantly, activation or deactivation of each system should contribute to the specific function of defending against pathogens. That is, rather than suggesting that disgust functions to generally “protect the self” (e.g., Miller, 2004), we posit that the disgust response is tailored to the particular problem of avoiding pathogens and that evidence of this functionality should be apparent in the activation of the various psychological and physiological programs. Beyond the systems mentioned above, we point out, additional features of a pathogen disgust system include the calibration processes that guide the learning of which cues are indicative of pathogens during development and the feedback processes that disengage the pathogen disgust response.

As others have suggested, disgust seems to have expanded to operate in domains beyond pathogen avoidance. Here we argue that the pathogen disgust system was co-opted and modified for the additional function of avoiding biologically costly sexual partners, leading to a distinct and distinguishable sexual disgust adaptation.

Sexual Disgust: The Avoidance of Fitness-Jeopardizing Sexual Partners

Despite the long-standing recognition that disgust plays an important role in human sexuality (Angyal, 1941; Mosher & O'Grady, 1979; Tomkins, 1963) and more recent work demonstrating empirical links between certain sexual behaviors and disgust (Ackerman, Kenrick, & Schaller, 2007; Borg et al., 2010; Fessler & Navarrete, 2003a, 2004; Haidt et al., 1994; Koukounas & McCabe, 1997; Lieberman et al., 2007; Park, 2008; Schaich Borg, Lieberman, & Kiehl, 2008; Stevenson, Case, & Oaten, 2011; Tybur et al., 2009; Vonderheide & Mosher, 1988), no consensus has been reached on the precise function or functions of sexual disgust. For example, Goldenberg et al. (2000) implied that sexual avoidance functions to neutralize existential threats: "Because the human species has intercourse and reproduces just as other animals do, the physical aspects of sex make apparent our animalistic creaturely nature" (p. 206). Similarly, Rozin et al. (2008) considered sex a prototypical example of animal reminder disgust, and they argued that sexual disgust functions to motivate rejection of reminders that human bodies are similar to animal bodies. As discussed above, this perspective runs into difficulties when one considers that humans breathe and sleep just as other animals do; yet these other "animal" activities are not posited to make apparent our animal nature, nor do they elicit disgust (Royzman & Sabini, 2001; Tybur et al., 2009).

But the question remains: Why do some sexual acts elicit disgust whereas others elicit sexual arousal? For example, a 20-year-old man might find the thought of sexual intercourse with an 80-year-old woman disgusting, but the exact same sexual act with an 18-year-old female lingerie model would elicit a markedly different response. The animal reminder construct promoted by Rozin et al. (2008) cannot account for these differences, as both acts are "animalistic" (Tybur et al., 2009). We propose an alternative perspective: that sexual disgust functions to motivate the avoidance of sexual behaviors with partners imposing potentially high fitness costs.

Selection Pressures Imposed by Sexual Decision Making

Although sexual intercourse is necessary for reproduction, it carries several direct costs, including tissue damage during intercourse, the risk of pathogen transmission, and social risks in the form of reputational damage and direct aggression from intrasexual competitors (see Hoffman et al., 2008; Penn & Smith, 2007; Perilloux et al., 2010; Tybur & Gangestad, 2011). Sexual interactions with the vast majority of organisms in the ecology impose such probabilistic costs without yielding any potential reproductive benefits. For example, sex with members of other species, individuals of the same species who are post-reproductive (i.e., the elderly) or pre-reproductive (i.e., children), and members of the same sex cannot yield reproductive benefits yet still extract nonzero (and potentially substantial) costs.

Perhaps more important, sex entails significant *opportunity costs*. Time and energy spent courting, copulating, and raising offspring with one individual generally cannot be invested in acquiring other mates or other fitness-enhancing behaviors (see Kenrick, Griskevicius, Neuberg, & Schaller, 2010). Hence, selection should have fine-tuned psychological adaptations for estimating the projected fitness value of a particular individual as a sexual partner given the alternatives present. Critically, males and females have different opportunity costs on average—that is, they are typically precluding different amounts of prospective alternative reproduction by engaging in sex that leads to fertilization (Trivers, 1972). Whereas females, in producing one offspring, are precluded from the production of another offspring due to their minimum investment of 9–10 months gestation and subsequent nursing, a male need only minimally invest the trivial time and metabolic resources needed to inseminate the female. These disparate selective forces should have generated psychological structures with different sensitivities to the costs of committing versus forgoing various sexual opportunities (Buss & Schmitt, 1993).

Here we discuss two main dimensions that contribute to the opportunity costs involved in selecting one sexual partner over another: genetic compatibility and mate quality (Jennions & Petrie, 2000; Neff & Pitcher, 2005; Zeh & Zeh, 1996). Genetic compatibility has been defined as the nonadditive genetic variance in fitness (Puurtinen, Ketola, & Kotiaho, 2009). Put differently, it is a relative measure of how compatible (fitness-promoting) another individual's genotype is with one's own. The most notable instances of incompatibility involve close kin, who are much more likely than nonrelatives to share identical deleterious recessive alleles that could jeopardize the health of resulting offspring (Bittles & Neel, 1994; Charlesworth & Charlesworth, 1999; Haig, 1999). By virtue of producing offspring who are more similar biochemically to their parents, inbreeding also increases the probability that pathogens will disrupt offspring development (Tooby, 1982). Other factors can influence genetic compatibility, including immunological compatibility, which can be assessed via chemical signatures associated with genes that govern the immune response (e.g., major histocompatibility complex; see Ober et al., 1997; Thornhill et al., 2003; Wedekind & Furi, 1997).

Mate quality, on the other hand, is a composite of the nonrelative dimensions along which potential sexual partners may vary. One such dimension, intrinsic genetic quality—that is, alleles that increase fitness in an additive fashion—generates what has come to be known as "good genes" (Neff & Pitcher, 2005). Evolutionary biologists and psychologists have proposed that various visible aspects of the phenotype—generally, what is perceived as "attractive" (Grammer, Fink, Møller, & Thornhill, 2003)—can carry information regarding intrinsic quality (Møller & Swaddle, 1997; Singh, 1993; Thornhill & Gangestad, 1993, 2006). Other dimensions also contribute to the magnitude of opportunity costs posed by potential sexual partners. For instance, the ability and willingness to invest in offspring, current health, intrasexual competitive ability, and residual reproductive value (e.g., age) would all factor into mate quality (though these dimensions may not be entirely independent of good genes).

In summary, there are multiple selection pressures that would have shaped sexual decision making. The presence of individuals who varied in terms of their genetic compatibility, genetic quality, and other attributes known to govern sexual attraction (Buss, 1992; Ellis, 1992; Thornhill & Gangestad, 1999) created the adaptive problem of avoiding those who posed the greatest reproductive threats. We propose that disgust, which initially evolved as a motivator of pathogen avoidance, was co-opted to motivate the avoidance and rejection of sexual contact with those whose sexual value was relatively low among the potential pool of mates. Critically, given the nature of these adaptive problems, the inputs that lead to sexual disgust should differ from those involved in the pathogen disgust system. Before we turn to an information processing model of sexual disgust, though, we briefly address the question, Why disgust?

Sexual attraction and arousal fulfill important functions in mating decisions: They motivate courtship, copulation, and pair bonding with individuals of high sexual value. The absence of attraction and arousal could thus potentially perform the function of steering individuals away from mates of low sexual value. However, the absence of sexual arousal would not prevent that individual from being sexually pursued by other people who possess their own reproductive agendas. To reject and avoid unwanted sexual advances and behaviors another response is required. Emotions such as fear and anger are not well suited to avoiding potentially costly mates. Fear can lead to immobilization or rapid flight (Öhman & Mineka, 2001) the former of which likely does not impede sexual pursuit, and the latter of which is metabolically costly and often unnecessary (e.g., if social allies and kin can prevent another's sexual interest from progressing to sexual aggression). Similarly, anger often acts as an "approach" emotion (Carver & Harmon-Jones, 2009), and associated aggression can lead to costly counteraggression (Sell et al., 2009).

We suggest that the phylogenetically ancient (Curtis, 2007; Zhang et al., 2005) pathogen disgust was a felicitous system to co-opt to perform the function of avoiding biologically costly mates. First, pathogen disgust motivates withdrawal and physical avoidance, cost-effective behaviors that solve the problem of staying out of arm's reach (we note that flight motivated by fear could also contribute to sexual avoidance when a sexual threat involves active pursuit). Second, pathogen avoidance is already linked to sexual behavior. If other individuals and their bodily fluids represent planets of potentially infectious microorganisms, then pathogen disgust must be down-regulated for sex to occur (Angyal, 1941). Indeed, sexual arousal appears to dramatically down-regulate pathogen disgust, as evidenced by particular sexual fetishes (e.g., eproctophilia and coprophilia; Symons, 2007; see also Borg & de Jong, 2012). If instead of being down-regulated, disgust was up-regulated in response to particular traits (e.g., kinship estimates; see below), evolution would have been well on its way to fashioning a sexual avoidance mechanism from a pathogen avoidance mechanism.

Information Processing Architecture of Sexual Avoidance

Sexual avoidance requires a different suite of mechanisms compared to pathogen avoidance. Here we posit: (a) perceptual systems that take cues associated with genetic compatibility and mate value as input; (b) intermediate computational processes that integrate information regarding genetic compatibility, mate value, and other context-dependent indices to compute for each individual an expected value as a sexual partner, which reflects the expected fitness outcome of avoiding versus selecting that individual as a sexual partner; and (c) a system that uses this expected value to set in motion the specific psychological and physiological processes involved in sexual avoidance (see Table 1).

Inputs: Cues to compatibility and quality. Just as pathogen avoidance systems monitor for cues associated with pathogen presence, mate selection systems monitor for cues associated with genetic compatibility and mate value. Kinship is one important dimension contributing to genetic compatibility. Recent research has demonstrated that multiple cues are used to assess the relatedness of others. These cues include childhood coresidence duration (Bevc & Silverman, 1993, 2000; Fessler & Navarrete, 2004; Lieberman, Tooby, & Cosmides, 2003; Lieberman et al., 2007), exposure to one's mother caring for a newborn (Lieberman et al., 2007), and perhaps facial and attitudinal similarity (DeBruine, 2005; Park & Schaller, 2005). As suggested by a recent model of kin detection (Lieberman et al., 2007), kinship cues feed into a kinship estimator that computes an index of genetic relatedness. This index, we suggest, is one input to systems assessing sexual value.

Other aspects of genetic compatibility require dedicated detection systems. The extent to which one differs immunologically might be computed by a separate system. For instance, humans, primarily women, prefer the scent of individuals with dissimilar ajor histocompatibility complex (MHC) types (Thornhill et al., 2003; Wedekind & Furi, 1997). This preference, at least in mice, appears to be calibrated during development (Penn & Potts, 1999; Yamazaki et al., 1988) and might represent in humans a separate dimension along which potential sexual partners are evaluated.

Other systems should be functionally specialized for detecting and assessing traits contributing to mate quality. With respect to intrinsic quality, there might be systems that assess symmetry, skin tone, skin texture, and so forth (Fink, Grammer, & Thornhill, 2001; Grammer et al., 2003; Scott, Pound, Stephen, Clark, & Penton-Voak, 2010; Symons, 1979). Many such dimensions will be used to assess the quality of potential mates for both males and females (B. C. Jones et al., 2001; Thornhill & Gangestad, 2006; Zebrowitz & Rhodes, 2004). Because the properties that influence mate value vary across the sexes, some of the features that determine mate quality differ between men and women (Buss, 2003). Whereas some dimensions might be given greater weight by males in assessing the qualities of females (e.g., cues that relate to youth and fertility, Buss, 1989; Kenrick & Keefe, 1992; Singh, 1993), others might be given more weight by females in assessing the qualities of males (e.g., cues of direct intrasexual competitiveness; Gangestad, Simpson, Cousins, Garver-Apgar, & Christensen, 2004; Little, Jones,

& DeBruine, 2008; Puts, 2010; Snyder, Kirkpatrick, & Barrett, 2008).

Intermediate systems for integrating intrinsic quality and genetic compatibility. Once cues to genetic compatibility and mate quality have been detected and assessed, they must be combined in a manner that allows for the adaptive regulation of mating decisions. One possibility is that they combine to produce an expected value as a sexual partner (see also Tooby and Cosmides, 2008). The expected sexual value system outputs different magnitudes depending on inputs. When below the minimum threshold for acceptability as a mate, it outputs a magnitude that is felt as sexual disgust, which serves as input to systems motivating sexual avoidance. For an individual with a high degree of relatedness and a high mate quality (e.g., a physically attractive sister), information about relatedness should generally trump information regarding mate value due to the costs associated with inbreeding, leading to a low expected sexual value. This decision should also take as input other factors such as the availability of alternative mates and the pathogen load of the environment (Schaller & Murray, 2008). The expected value of an individual as a sexual partner should reflect the integration of all these factors and thus represents an index of the context-dependent fitness consequences of pursuing versus avoiding an individual as a sexual partner. But this only addresses systems regulating one's own sexual interests. Other individuals compute their own distinct estimates of expected sexual value and can act accordingly. For instance, a 50-year-old man may find an 18-year-old woman sexually attractive despite her aversion toward him. Perceived sexual intent from a conspecific should therefore interact with expected sexual value to output sexual avoidance.

Outputs: The evolved response to partners of low sexual value. In line with our definition of pathogen disgust, we argue that sexual disgust is just the felt output of computational procedures estimating expected sexual value. When sexual value estimates reach a lower threshold and sexual interest has been detected, behavioral strategies, cognitive mechanisms, and physiological systems that facilitate sexual avoidance should be activated. We propose that the ancient psychological processes involved in avoiding pathogens were co-opted for the function of sexual avoidance because of the delicate nature of avoidance that is optimal for sexual interactions. Again, the behavioral avoidance of macropredators motivated by fear (e.g., rapid flight) is inefficient for neutralizing many (perhaps most) poor sexual partners, just as it would be inefficient for neutralizing pathogens. Although rapid flight may neutralize such threats, it is metabolically expensive and may preclude benefits associated with interacting with individuals (e.g., kin) in a nonsexual manner. Certainly, other cues (e.g., ambient darkness; pursuit from a sexually aggressive conspecific) may interact with cues related to quality and compatibility to output rapid flight, but threats posed by many poor-quality mates can be neutralized with less costly avoidance.

Although presumably co-opted from initial pathogen avoidance mechanisms, the collection of systems entrained to avoid an individual sexually should differ in important ways. Whereas proximal avoidance (i.e., not touching) mitigates the dangers of pathogens, specifically sexual avoidance mitigates the reproductive threats posed by individuals with low expected sexual value. Similarly, physical contact with an object possessing pathogen cues should elicit avoidance and disgust, whereas physical contact with an individual with low sexual value should not. Take, for example, a woman's father. Despite having cues for poor genetic compatibility, a father should not automatically elicit sexual disgust. Rather, sexual disgust should be aroused only if sexual behavior is considered by the offspring or offered by the father (Westermarck, 1891/1921). The lack of a constant state of sexual disgust toward poor mates reflects the costs associated with avoiding individuals who are otherwise valuable social partners. Although constant motivations to avoid poor mates would certainly decrease the probability of reproducing with them, it would also cripple some beneficial social relationships. Recent research indicates that avoidance behaviors are indeed not constant but instead might fluctuate in adaptive ways (e.g., Lieberman, Pillsworth, & Haselton, 2011).

In addition to distinct behaviors for sexual avoidance, there are likely domain-specific processes that are activated in response to possible or considered sexual engagement with individuals of low sexual value. These include specialized systems for reasoning (if he smiles at me then he is sexually interested in me), attention (directed toward the proximity of interested low sexual value targets), memory (of escape routes, individuals who could come to one's aid), and learning (what locations to avoid when alone). Some of these processes may be shared with pathogen disgust. For example, individuals report feeling nauseated when thinking about sibling incest (Royzman, Leeman, & Sabini, 2008), and rape victims often report feelings of disgust and being soiled (Isac & Schneider, 1992; Petrak, Doyle, Williams, Buchan, & Forster, 1997). Given that sexual disgust likely evolved from an existing pathogen disgust system and that many cues that elicit sexual disgust pertain to pathogens (e.g., intrinsic mate value depends cues signaling the presence of infection), the physiological systems entrained by pathogen avoidance systems may overlap with those designed to avoid certain individuals as sexual partners as a by-product.

In summary, we suggest that sexual disgust, rather than stemming from a need to avoid reminders of our animal nature (Rozin et al., 2008), functions to motivate the avoidance of mates who could potentially jeopardize one's reproductive success. Critical features of our model of sexual disgust include systems that trade off genetic compatibility against other features such as attractiveness and resource status in an adaptive manner. The outputs of these and other systems combine to generate an expected value of an individual as a sexual partner; depending on magnitude, this variable can initiate attraction or avoidance behaviors. The cascade of psychological and physiological systems engaged in sexual avoidance likely forms a unique set but might share components with the pathogen avoidance system (e.g., facial expression and withdrawal behaviors).

Moral Disgust: Navigating the Landscape of Condemnation

Cross-culturally, actions that otherwise elicit pathogen or sexual disgust are often *moralized*. That is, they are viewed as morally wrong and subject to punishment. Examples include taboos about food (especially meat; Fessler & Navarrete, 2003b); sexual acts such as incest, masturbation, bestiality, pedophilia, prostitution, and homosexuality; and behaviors having to do with liquid and solid bodily wastes (Douglas, 1966; Miller, 1997). Further, people report and display disgust toward moralized acts unrelated to pathogen threats or sexuality. Danovitch and Bloom (2009), for instance, found that children as young as 6 years old label moral violations related to harm and fairness as "disgusting" both verbally and via identification of facial expressions. In adults, recent EMG studies have demonstrated the activation of facial muscles associated with pathogen disgust (e.g., the levator labii) after unfair treatment in an ultimatum game (Chapman et al., 2009) and while imagining dishonest behavior (Cannon et al., 2011). Finally, fMRI studies have shown common neural activation for responses to pathogen disgust and unfair offers in an ultimatum game (Sanfey, Rilling, Aronson, Nystrom, & Cohen, 2003), theft and violence (Schaich Borg et al., 2008), and child abuse (Moll et al., 2005). These empirical patterns illustrate a close link between disgust and morality, giving rise to a pair of related but separable questions. The first is why are acts that evoke pathogen or sexual disgust moralized, as in "Having sex with a goat is morally wrong." The second is why do violations of moral rules evoke the language and facial expression of disgust, as in, "The theft of $23 from the Food For Orphans Fund was disgusting." Here we address both questions.

We emphasize that this section is not intended as an extended treatment of morality (for relevant recent work on this topic, see DeScioli and Kurzban, 2009, 2012; Haidt, 2007, 2012; Haidt & Kesebir, 2010; Hauser, 2006; Krebs, 2011) but instead as an examination of how disgust impacts moral cognition and vice versa. We also note that, in contrast to pathogen and sexual disgust, there is little consensus about the measurement, function, and even existence of moral disgust (see Bloom, 2004; Nabi, 2002; Royzman & Kurzban, 2011; Royzman & Sabini, 2001; Rozin et al., 2008; Rozin, Haidt, & McCauley, 2009; Simpson, Carter, Anthony, & Overton, 2006; Tybur et al., 2009). Hence, the ideas discussed in this section are necessarily more exploratory than those in previous sections on pathogen and sexual disgust. Nevertheless, the material presented here includes three novel insights into the connection between morality and disgust. First, unlike other treatments on this topic (e.g., Chapman et al., 2009; Hutcherson & Gross, 2011; Rozin et al., 2008; Rozin, Haidt, & Fincher, 2009; Tybur et al., 2009), ours separates the relationship between disgust and morality into the two questions described above. Second, we offer an explicit computational perspective, proposing aspects of the information processing systems required for each proposed link between disgust and morality (cf. Mikhail, 2007, 2008). Third, in contrast to recent accounts of moral disgust that have been couched in group selection processes (e.g., Haidt, 2007, 2012), we offer alternative approaches based on individual-level selection pressures (see discussion in Pinker, 2012). Our approach follows the same trajectory as the previous sections on pathogen and sexual disgust, with a consideration of selection pressures and computational processes.

Disgust as Input to Moral Decisions: Why Are Disgusting Things "Wrong"?

Haidt (2001, 2006, 2007, 2012) has persuasively argued that moral judgments are often rooted in intuition rather than logical consideration of the consequences of moral violations (see also Greene, 2007; Nichols, 2002). *Disgust* has been implicated as an important source of these intuitions. Indeed, according to moral foundations theory (Graham, Haidt, & Nosek, 2009; Haidt, 2012; Haidt & Joseph, 2004), one basic moral foundation, purity/sanctity, "is based on the emotion of disgust in response to biological contaminants (e.g., feces or rotten food), and to various social contaminants like spiritual corruption, or the inability to control one's base impulses" (Koleva, Graham, Iyer, Ditto, & Haidt, 2012, p. 185). Examples of purity violations include a man having sexual intercourse with a chicken carcass, a brother and sister having sex, and an avant-garde performance art piece in which performers act like nonhuman animals and urinate on stage (see Haidt, 2001, 2006).

Haidt (2007, 2012) provided an evolutionary explanation for the connection between purity/sanctity and morality, arguing that disgust-based morality functions to improve group cohesion—to "bind" people into effective groups. Here we propose alternative functions based on a framework recently used to investigate some of the "mysteries of morality" (DeScioli & Kurzban, 2009, 2012; see also DeScioli, Bruening, & Kurzban, 2011; DeScioli, Christner, & Kurzban, 2011; Kurzban, DeScioli, & Fein, 2012; Weeden, 2003).

Selection pressures. Humans live in groups in which violations of moral rules are condemned and punished. In addition to shaping the evolution of *cultures* (Boyd & Richerson, 1992; Haidt, 2012; Richerson & Boyd, 2005), the existence of moralistic punishment poses adaptive problems for *individuals*—avoiding sanctions from group members. One solution to this problem is for individuals to strategically influence the content of moral rules by supporting or resisting candidate rules based on how the rule, if it were in place, would affect the individual. DeScioli and Kurzban (2009, 2012) suggest that decisions to endorse or oppose a particular rule are influenced by the expected impact of the rule on the endorser's fitness (see also Weeden, 2003). Attitudes toward rules relating to short-term mating can serve as an example. Rules leading to condemnation and punishment of adultery (or, more generally, casual sex) are especially advantageous for individuals invested in a monogamous, pair-bonded mating strategy because they recruit the moralized punishment of a group as a barrier to a current or future mate's infidelity. However, these rules are disadvantageous for individuals whose sexual strategies involve acquiring multiple mates (Gangestad & Simpson, 2000). Hence, individuals should endorse rules that favor their fitness interests and resist rules that run counter to their fitness interests. Consistent with this perspective, individual differences in mating strategy predict endorsement of rules constraining others' sexuality, and experimental primes designed to increase the perceived likelihood of infidelity similarly increase rule endorsement (Kurzban, Dukes, & Weeden, 2010; Li, Cohen, Weeden, & Kenrick, 2010; Weeden, 2003; Weeden, Cohen, & Kenrick, 2008).

Rules can vary tremendously across cultures and times (Shweder, Mahapatra, & Miller, 1987), and new rules appear frequently within groups. For example, in the past century, moral rules have developed around new technologies such as hormonal contraceptives, stem cell therapy, cloning, genetically engineered crops, digital property rights, carbon emissions, cigarette smoking around children, pornography, and taxation on income made from investments. The introduction of new moral rules heightens the problems associated with endorsing or resisting rules in a manner that favors one's fitness. Given the rapid introduction of potential moral rules and the general difficulties of forecasting the consequences of endorsing specific rules, how has selection shaped moral cognition to endorse rules in a fitness-promoting manner?

As discussed above, pathogen and sexual disgust motivate the avoidance of acts or objects due to fitness costs associated with infectious disease or mating, respectively. When one contemplates a given act, then, the extent to which one experiences disgust can function as an index of the fitness costs of engaging in the act in question. The greater the disgust, the more motivated an individual should be to avoid that act. Taken together with a consideration of costs and benefits involved in endorsing rules, this implies that the more the contents of a (potential) moral rule evoke disgust, the greater the probability that the rule would prohibit acts that the individual would prefer not to do even if the rule were not in place. As a strategic matter, there is little disadvantage to the individual to adopt and spread a rule that prevents such acts.

Information processing procedures. Our proposal, then, is that disgust intuitions can serve as input to systems that judge the strategic value of endorsing a rule. Computationally, this could occur if felt disgust, an output of systems assessing the expected value of contact and expected sexual value described in the pathogen and sexual disgust sections above, serves as an input to mechanisms designed to make strategic decisions about which moral rules to endorse and which to resist (see also Pizarro, Inbar, & Helion, 2011.) This computational account is consistent with a number of empirical studies investigating the link between disgust and moral judgment. In general, these investigations have found that activating the pathogen or sexual disgust system increases judgments of moral wrongness, presumably because increased disgust marks the decreased fitness costs of condemnation. For example, Schnall, Haidt, Clore, and Jordan (2008) showed that participants who smell a disgusting odor judge acts to be more morally wrong than control participants. Along similar lines, Eskine, Kacinik, and Prinz (2011) showed that subjects who experienced a disgusting taste judge acts to be more wrong than subjects who experience a sweet one. Wheatley and Haidt (2005) showed that disgust induced under hypnosis similarly increased the extent to which acts are viewed as wrong, and Moretti and di Pellegrino (2010) showed that participants rejected low offers in an ultimatum game more frequently after a viewing images that evoked pathogen disgust. Activation of sexual disgust similarly shapes moral judgments. For instance, Lieberman et al. (2003, 2007) found that the same kinship cues that predict the development of personal sexual aversions toward opposite sex siblings also predict the strength of one's moral opposition to third-party sibling incest. This perspective is consistent with moral foundations theory, which suggests that individuals morally judge certain acts because those acts elicit disgust (Graham et al., 2009; Haidt, 2012).

Importantly, we do not suggest that disgust serves as an input to every moral judgment, nor do we suggest that every act that elicits disgust will inevitably become moralized. There are a multitude of other computational processes that underlie the moral judgment system (Mikhail, 2007, 2008). Some of these processes likely dictate when and how disgust intuitions shape moral rules. For instance, acts must first be assessed as candidates for moralization. When computational processes do not identify an act as a candidate for moralization, disgust intuitions ought not to lead to a moralized disgust. When acts are identified as candidates for moralization, disgust-driven assessments about the fitness outcome of endorsing versus opposing a particular rule are likely integrated with information regarding the number and identity/status of group members who agree with one's assessment, the ability to enforce the rule, the consistency of the rule with other existing rules, and so on (DeScioli & Kurzban, 2012). Likewise, other emotions could provide distinct "intuitions" about the fitness costs associated with rule endorsement and explain additional features of moral rule content (e.g., Haidt & Joseph, 2004; Rozin et al., 1999).

Disgust as Output of Moral Cognition: Why Are Wrongs "Disgusting"?

The previous section proposed an explanation for why people morally condemn acts that elicit (pathogen or sexual) disgust. This section addresses a separate connection between disgust and moral judgment: the fact that people report being disgusted by acts that they view as morally wrong, even when these acts have no pathogen or sexual content. For instance, people asked to consider behaviors such as stealing a purse from a blind person evaluate such acts as morally disgusting (Hutcherson & Gross, 2011; Nabi, 2002), and individuals asked to recall a time that they were "disgusted" often refer to violations of a moral rule related to harm or fairness (Curtis & Biran, 2001; Haidt et al., 1994, 1997; Tybur et al., 2009). Further, recent evidence suggests that a signature feature of pathogen disgust—the canonical facial expression—is observed in domains that have moral but no pathogen or sexual content (Cannon et al., 2011; Chapman et al., 2009). Here, we propose an explanation for this connection between disgust and morality.

Selection pressures: Condemnation coordination. When individuals observe other people violate rules that are subject to punishment, third parties (observers) are faced with a dilemma. If third parties condemn opposing sides in a dispute, they risk creating new enemies and increasing the intensity of the conflict. That is, as compared to a highly skewed distribution of condemners (e.g., when almost everyone condemns the same individual or act), an equal number of supporters on both sides of a dispute can escalate and prolong the costs associated with the conflict. Coordination of condemnation attenuates costs, but to achieve coordination, individuals must signal (communicate) whom they condemn to other people, and they must detect other people's signals of condemnation (see DeScioli and Kurzban, 2012, for an extensive description of this adaptive problem).

We suggest that expressions of disgust, which are easily, rapidly, and cross-culturally recognized (Ekman, 1972; Sauter & Eimer, 2010; Sauter, Eisner, Ekman, & Scott, 2010), might be particularly effective for coordinating condemnation. As proposed above, disgust intuitions act as inputs to wrongness judgments. Hence, people can use an expression of disgust as a reliable cue that other people oppose and moralize a given action. In turn, individuals can signal their opposition to an action by broadcasting a disgust display, even when no pathogen or sexual risks are present. By using the vocal and facial expressions of disgust, third parties signal to others that they oppose the individual who has committed an action they find punishable. We contrast this signaling view with the idea that moral disgust has a function in causing people to avoid some set of objects, behaviors, or people, as is the case with pathogen and sexual disgust.

Information processing procedures and expressions of disgust. There are distinct information processing systems required to perform the function of condemnation coordination.

Naturally, systems must first detect when a rule has been violated (see Cosmides, 1989, and Delton, Cosmides, Robertson, Guemo, & Tooby, 2012, for discussions of detecting cheaters and free riders). Once a violation has been detected, separate systems requiring additional information must assess the value of broadcasting condemnation. One critical input to these systems ought to be whether other people are present to receive the signal (e.g., Fridlund, 1991). Other inputs might relate to the value of signaling one's side in a conflict. For example, when the side one is likely to take is uncertain to third parties (perhaps when one's friends or kin have violated the moral rule), disgust can serve to signal and clarify one's side. Further, in cases in which one risks condemning alone, the language of disgust might be deployed as a tool to recruit punishment from others. That is, because disgust can act as an input to moral judgment (as detailed above), expressing disgust toward another individual may help persuade others that the target of disgust expressions should be punished. In general, we suggest that inputs are integrated to assess an expected value of signaling, as is the case with sexual and pathogen disgust. Once this expected value surpasses a minimum threshold, individuals should activate facial and vocal expressions of disgust.

Given the arguments detailed above, similarities between the pathogen and sexual disgust outputs described previously and disgust toward rule violations ought to primarily involve the expressive components. That is, the disgust facial expression that appears designed to shield the body from pathogens or expel potentially pathogenic material from the mouth (Rozin et al., 2008; Susskind et al., 2008) is common across disgust domains, but the "do not touch" motivation that accompanies pathogen disgust does not appear to accompany moral disgust. For example, reports of moral disgust strongly covary with reports of anger, which motivates approach (Carver & Harmon-Jones, 2009), or with desires to violently "lash out" at rather than avoid the offending party (Marzillier & Davey, 2004; Olatunji et al., 2012; Royzman et al., 2008; Simpson et al., 2006). Further, although people use some components of disgust language to describe rule violations, they do not typically use other terms that correspond with other aspects of disgust that presumably reflect internal states that function to expel pathogens (e.g., grossed out; see Nabi, 2002). Connections that do seem to support a link between moral disgust and avoidance may be better described in terms of punishment and communication. Chapman et al. (2009), for example, reported some evidence that self-reports and facial signatures of disgust expressed toward unfair treatment relate to rejection of offers in an ultimatum game. Rather than rejecting something in terms of minimizing its contact and thus mitigating the possibility of infection, "rejection" in this context is a form of punishment. The expressive component of disgust might function to communicate intention to condemn and potentially recruit others in collective punishment.

Alternative views. We emphasize that there are other proposals to explain why people use the language of disgust to refer to moral violations. For instance, Hutcherson and Gross (2011) argued that "the primary function of both moral disgust and contempt [is] to mark individuals whose behavior suggests that they represent a threat and avoid them, thereby reducing the risk of exposure to harm" (p. 720; see also A. Jones & Fitness, 2008; Rozin et al., 2008; Tybur et al., 2009). Some observations seem to sit uneasily with this explanation. Moral violations that evoke the language of disgust do not uniformly relate to harm, as in a case such as "a company executive refuses to sit next to a laborer on a train" (Hutcherson & Gross, 2011). Further, moral violations generally evoke the motivation to punish wrongdoers as opposed to avoid them (Kurzban, DeScioli, &O'Brien, 2007), although of course both motivations might simultaneously occur. Finally, a system designed to identify potentially harmful people might be expected to attend to the extent to which others intentionally do harm, rather than the extent to which they have violated a moral rule. However, a signature feature of moral judgment is that it frequently does not track intended harm (DeScioli & Kurzban, 2009; Mikhail, 2007).

A possibility related to this idea and which connects to our proposal is that moral disgust functions to motivate social distancing, rather than physical distancing, from an individual who has committed a serious wrong (Curtis & Biran, 2001; Tybur et al., 2009). If, for instance, those who are perceived as having committed moral sins—and their allies—are at risk of being punished by observers (DeScioli & Kurzban, 2012; Neuberg, Smith, Hoffman, & Russell, 1994; Tooby & Cosmides, 2010), there could be value in signaling to observers that one condemns the wrongdoer's actions. Such distancing could defend against being lumped in with the condemned individual during subsequent aggression by moral mobs. However, again, the expressive aspect of disgust may mitigate this problem as effectively as (if not more effectively than) actual physical distance.

Summary

Here we addressed two separate yet related issues regarding the link between disgust and morality. With regard to why disgusting acts are often moralized, we argued that the pathogen and sexual disgust systems provide an index of the fitness value of engaging in particular behaviors oneself and that these indices serve as input for systems assessing the costs of condemning third-party behavior. In general, rules prohibiting behaviors that people find disgusting do not substantially encroach on one's freedom or ability to pursue one's fitness interests. Individuals are thus more likely to endorse rules that involve punishing behaviors that elicit disgust, and such rules are likely to be agreed upon and prevalent across groups (see, e.g., Heath, Bell, & Sternberg, 2001). With regard to why violations of a broad array of moral rules elicit expressions of disgust, we argued that expressions of disgust function to advertise and coordinate intentions to condemn. Further, if an important part of moral discourse is bringing other third parties around to one's agenda of imposing costs on others (DeScioli & Kurzban, 2012; Tooby & Cosmides, 2010), one would expect moralizers to use language well suited to recruiting third parties. Because disgust is an input to the moral judgment system, agents trying to persuade others about the immorality of an action might use disgust to gain support against rule violators. On this view, the answer to the question as to why wrong things are "disgusting" is located in the possibility that expressions of disgust serve a persuasive function on the part of receivers, explaining their use by signalers.

In closing this section, we note that there is great potential for future investigations into the link between disgust and morality. Up to this point, research has primarily focused on establishing whether there is a link between disgust and morality and how that link is best measured (e.g., facial expressions, verbal self-reports, priming effects). Here we differentiate two different disgust and morality connections, describe these connections using a computational perspective, and propose potential functions for moral disgust using in a newly developed theory of moral punishment and coordination. Future investigations can continue to leverage recent advances in evolutionary perspectives on disgust (e.g., Curtis et al., 2011; Tybur et al., 2009) and morality (DeScioli & Kurzban, 2009, 2012; Haidt, 2007, 2012) to accelerate our understanding of moral disgust.

Discussion and Future Research Directions

We began our treatment on disgust with the observation that, although evolutionary theory has implicitly guided much of the rapidly increasing interest in and research on disgust over the past 20 years, the field has lacked an explicit conceptual framework that is grounded in evolutionary theory for understanding disgust. Our goal here has been to address this gap by using a computational approach to understanding emotion (Tooby & Cosmides, 1990, 2008) and by considering research and theory relating to pathogen avoidance (Curtis et al., 2011; Schaller & Park, 2011), sexual decision making (Buss, 1992; Gangestad & Simpson, 2000; Thornhill & Gangestad, 2008), and moral condemnation (DeScioli & Kurzban, 2009, 2012; Haidt, 2007, 2012; Mikhail, 2008). In doing so, we have proposed selection pressures and computational processes underlying functionally specific disgust domains. Our hope is that this attention to the evolved function and associated computational processes can help synthesize the voluminous existing literature on disgust and stimulate avenues for novel research. In closing, we briefly sketch some of the implications this framework can have for varied research areas, specifically investigations into disgust sensitivity, the development of disgust, and cross-cultural variability in disgust.

Individual Differences

A substantial portion of disgust research over past decades has involved empirical observations of covariation between measures of disgust sensitivity (i.e., self-reports of how disgusting people find common disgust elicitors) and other constructs such as political ideology (Hodson & Costello, 2007; Inbar et al., 2009; Tybur et al., 2010), obsessive and compulsive traits (Olatunji et al., 2007), and five-factor model personality dimensions (Druschel & Sherman, 1999). Most of these investigations have focused on domain specificity articulated under the RHM model, an approach that has encountered psychometric and conceptual difficulties (Olatunji et al., 2007; Tybur, Bryan, Lieberman, Caldwell Hooper, & Merriman, 2011; Tybur et al., 2009, 2010). An alternative strategy following the framework we have described involves examining variation in three domains independently, separating pathogen, sexual, and moral disgust. This approach has shown early promise, with recent investigations illuminating pathogen avoidance, mate preferences, moral inclinations, and aggression (see, e.g., DeBruine, Jones, Tybur, Lieberman, & Griskevicius, 2010; Kurzban et al., 2010; Olatujni et al., 2012; Pond et al., 2012; Tybur et al., 2009, 2010).

Each of the computational processes described here points to a difference potential source (cause) of individual differences. For example, we have suggested that the pathogen disgust system detects pathogens, integrates the probability of pathogen presence with other inputs (e.g., cues to kinship, nutritional status, sexual arousal), computes expected values of contact, and then outputs disgust. The model therefore predicts that some of the variation in propensity and intensity of pathogen disgust will stem from individual differences in (a) the ability to detect cues associated with pathogen threats (e.g., olfactory sensitivity); (b) signal detection analyses for estimating pathogen threat level; (c) how pathogen threat estimates are traded off against levels of nutrient depletion (hunger) and other states; (d) how feedback processes return to baseline after removal of the pathogen threat; and (e) immunocompetence (e.g., Schaller et al., 2010; Stevenson, Hodgson, et al., 2011). Uncovering potential underlying sources of variation across the multiple facets of disgust sensitivity might especially benefit clinicians dealing with populations suspected of impairments to the disgust system, including individuals with obsessive compulsive disorder or individuals with sexual disorders (Borg et al., 2010; Olatunji & McKay, 2009; Olatunji & Sawchuk, 2005).

Disgust and Development

This framework might also help clarify how and when disgust develops. Pathogen disgust, for example, is notoriously absent (or, at least, not fully developed) in young children (see Rozin et al., 2008). This absence might stem from the fact that, in environments similar to those in which humans evolved, infants obtain nutrition directly from their mother in the form of breast milk, often exclusively until age 2 or 3 (and sometimes until age 4 or 5; Konner & Shostak, 1987). In ancestral environments, children were also likely carried throughout the first few years of life, and mothers might have steered infants away from likely pathogen sources, reducing or eliminating the need for the disgust system early in development. Further, the pathogen disgust system may not function until an individual reaches other developmental points. For instance, individuals must acquire culturally evolved information regarding those items with high expected benefits of contact (e.g., edible foods) and the locally adapted hygiene rituals (Schaller & Murray, 2008). That is, they may need to acquire information from their social group to deploy disgust in a fitness promoting fashion. Considerations such as these can be used to uncover functional design in the developmental timing of pathogen disgust, which can in turn contribute to understanding of behavioral antipathogen systems (cf. Schaller & Park, 2011).

Because the other disgust systems described here have different functions, they should have different developmental trajectories depending on when in the life span individuals encounter the relevant adaptive problems. For example, sexual disgust might develop later than pathogen disgust because individuals are typically not targeted as sexual partners until they are sexually mature. Moral disgust may have yet another distinct trajectory, with development coinciding with periods in which rule endorsement and condemnation reliably become part of an individual's social world. Although previous disgust theories have explicitly referenced domain specificity in function (e.g., Rozin et al., 2008; Tybur et al., 2009), investigations have not explicitly tested for domain specificity in the timing of development and factors shaping development. The theoretical framework we present here implies very different developmental trajectories for the different varieties of disgust, and it can be used to guide investigations into such domain specificity. In contrast, finding similar trajectories for all three types of disgust would undermine our proposal.

Cross-Cultural Variability

Cultural variability in disgust might partially reflect adaptive responses to ecologically specific conditions (Gangestad, Haselton, & Buss, 2006; Tooby & Cosmides, 1992). For instance, individuals in India are, on average, exposed to more pathogens (and presumably cues to pathogens) than individuals living in Ireland (Murray & Schaller, 2010). Cultural differences in pathogen disgust propensity and intensity could thus vary as a function of ecological differences in these inputs. Further, if pathogen disgust is one input into the computational systems governing moral judgment, as we argue, we might further observe cultural differences in the strength to which disgust intuitions shape moral rules based on local pathogen ecologies (Graham et al., 2009; Haidt, 2012; Haidt, Koller, & Dias, 1993). Indeed, recent work has found support for hypotheses that ecological pathogen presence relates to group level morals (Fincher & Thornhill, 2012; Schaller & Murray, 2008), and individuals located in areas with greater pathogen stress appear to put more emphasis on disgust intuitions in moral decision making (Van Leeuwen, Park, Koenig, & Graham, 2012).

Other aspects of cross-cultural variability in disgust could arise via cultural evolutionary processes. Elicitors of pathogen disgust, for example, may relate to the food preparation habits that have culturally evolved to neutralize pathogens endemic to a specific ecology (e.g., Billing & Sherman, 1998; Henrich & Henrich, 2010; Schaller & Murray, 2008). Differences in the targets of sexual disgust may vary as a function of the manner in which group norms for kinship categorizations and family structures have evolved (Lieberman & Lobel, 2012). If the experience of pathogen or sexual disgust serves as (one) input into systems for moral condemnation, markedly different disgust-based moral rules can exist in different cultures. Further, if rules evolve culturally (Richerson & Boyd, 2005), expressions of moral disgust could be targeted toward violations of culturally specific rules, such as those governing monogamous marriage (Henrich, Boyd, & Richerson, 2012), spiritual ritual (Haidt, 2006), or property rights (Boyd & Richerson, 1983).

Conclusions

Three important advances in disgust research and theory have occurred over the past 20 years. First, researchers have developed a sophisticated evolutionary framework for understanding how disgust functions as an antipathogen adaptation. Second, researchers have begun to document how disgust is elicited in situations beyond pathogen avoidance. Third, researchers have demonstrated connections between disgust and other topics in psychology such as psychopathology (Davey, 2011; Olatunji & McKay, 2009; Olatunji et al., 2007), stigma and prejudice (Cottrell & Neuberg, 2005; Lieberman, Tybur, & Latner, 2012; Navarrete & Fessler, 2006; Oaten et al., 2011), and cooperation and punishment (Chapman et al., 2009; Moretti & di Pelligrino, 2010). These developments suggest that disgust sits at the nexus of a number of important aspects of human nature. We hope that a focus on the evolved functions and cognitive processes underlying disgust will continue to assist in unraveling the science of aversion.

References

Ackerman, J. M., Becker, D. V., Mortensen, C. R., Sasaki, T., Neuberg, S. L., & Kenrick, D. T. (2009). A pox on the mind: Disjunction of attention and memory in the processing of physical disfigurement. *Journal of Experimental Social Psychology, 45,* 478–485. doi:10.1016/j.jesp.2008.12.008

Ackerman, J. M., Kenrick, D. T., & Schaller, M. (2007). Is friendship akin to kinship? *Evolution and Human Behavior, 28,* 365–374. doi:10.1016/j.evolhumbehav.2007.04.004

Andrews, P. W., & Thompson, J. A. (2009). The bright side of being blue: Depression as an adaptation for analyzing complex problems. *Psychological Review, 116,* 620–654. doi:10.1037/a0016242

Angyal, A. (1941). Disgust and related aversions. *Journal of Abnormal and Social Psychology, 36,* 393–412. doi:10.1037/h0058254

Barrett, H. C., & Kurzban, R. (2006). Modularity in cognition: Framing the debate. *Psychological Review, 113,* 628–647. doi:10.1037/0033-295X.113.3.628

Bevc, I., & Silverman, I. (1993). Early proximity and intimacy between siblings and incestuous behavior: A test of the Westermarck theory. *Ethology and Sociobiology, 14,* 171–181. doi:10.1016/0162-3095(93)90004-2

Bevc, I., & Silverman, I. (2000). Early separation and sibling incest: A test of the revised Westermarck theory. *Evolution and Human Behavior, 21,* 151–161. doi:10.1016/S1090-5138(99)00041-0

Billing, J., & Sherman, P. W. (1998). Antimicrobial functions of spices: Why some like it hot. *Quarterly Review of Biology, 73,* 3–49. doi:10.1086/420058

Bittles, A. H., & Neel, J. V. (1994). The costs of human inbreeding and their implications for variations at the DNA level. *Nature Genetics, 8,* 117–121. doi:10.1038/ng1094-117

Bloom, P. (2004). *Descartes' baby: How the science of child development explains what makes us human*. New York, NY: Basic Books.

Borg, C., & de Jong, P. J. (2012). Feelings of disgust and disgust-induced avoidance weaken following induced sexual arousal in women. *PLoS ONE, 7,* e44111. doi:10.1371/journal.pone.0044111

Borg, C., de Jong, P. J., & Schultz, W. W. (2010). Vaginismus and dyspareunia: Automatic vs. deliberate disgust responsivity. *Journal of Sexual Medicine, 7,* 2149–2157. doi:10.1111/j.1743-6109.2010.01800.x

Boyd, R., & Richerson, P. J. (1983). Why is culture adaptive? *Quarterly Review of Biology, 58,* 209–214. doi:10.1086/413217

Boyd, R., & Richerson, P. J. (1992). Punishment allows the evolution of cooperation (or anything else) in sizable groups. *Ethology and Sociobiology, 13,* 171–195. doi:10.1016/0162-3095(92)90032-Y

Buss, D. M. (1989). Sex differences in human mate preferences: Evolutionary hypotheses tested in 37 cultures. *Behavioral and Brain Sciences, 12,* 1–49. doi:10.1017/S0140525X00023992

Buss, D. M. (2003). *The evolution of desire*. New York, NY: Basic Books.

Buss, D. M. (1992). Mate preference mechanisms: Consequences for partner choice and intrasexual competition. In J. H. Barkow, L. Cosmides, & J. Tooby (Eds.), *The adapted mind* (pp. 249–266). New York, NY: Oxford University Press.

Buss, D. M., & Haselton, M. G. (2005). The evolution of jealousy. *Trends in Cognitive Sciences, 9,* 506–507. doi:10.1016/j.tics.2005.09.006

Buss, D. M., & Schmitt, D. P. (1993). Sexual strategies theory: An evolutionary perspective on human mating. *Psychological Review, 100,* 204–232. doi:10.1037/0033-295X.100.2.204

Calder, A. J., Keane, J., Manes, F., Antoun, N., & Young, A. W. (2000). Impaired recognition and experience of disgust following brain injury. *Nature Neuroscience, 3,* 1077–1078. doi:10.1038/80586

Cannon, R. P., Schnall, S., & White, M. (2011). Transgressions and expressions: Affective facial muscle activity predicts moral judgments. *Social Psychological & Personality Science, 2,* 325–331. doi:10.1177/1948550610390525

Carver, C. S., & Harmon-Jones, E. (2009). Anger is an approach-related affect: Evidence and implications. *Psychological Bulletin, 135,* 183–204. doi:10.1037/a0013965

Chapman, H. A., Kim, D. A., Susskind, J. M., & Anderson, A. K. (2009, February 27). In bad taste: Evidence for the oral origins of moral disgust. *Science, 323,* 1222–1226. doi:10.1126/science.1165565

Charlesworth, B., & Charlesworth, D. (1999). The genetic basis of inbreeding depression. *Genetics Research, 74,* 329–340. doi:10.1017/S0016672399004152

Cosmides, L. (1989). The logic of social exchange: Has natural selection shaped how humans reason? Studies with the Wason Selection Task. *Cognition, 31,* 187–276.

Cottrell, C. A., & Neuberg, S. L. (2005). Different emotional reactions to different groups: A sociofunctional threat-based approach to "prejudice." *Journal of Personality and Social Psychology, 88,* 770–789. doi:10.1037/0022-3514.88.5.770

Curtis, V. A. (2007). A natural history of hygiene. *Canadian Journal of Infectious Diseases & Medical Microbiology, 18,* 11–14.

Curtis, V., Aunger, R., & Rabie, T. (2004). Evidence that disgust evolved to protect from risk of disease. *Proceedings of the Royal Society: Series B: Biological Sciences, 271*(Suppl. 4), S131–S133. doi:10.1098/rsbl.2003.0144

Curtis, V., & Biran, A. (2001). Dirt, disgust, and disease: Is hygiene in our genes? *Perspectives in Biology and Medicine, 44,* 17–31. doi:10.1353/pbm.2001.0001

Curtis, V., de Barra, M., & Aunger, R. (2011). Disgust as an adaptive system for disease avoidance behaviour. *Philosophical Transactions of the Royal Society: Series B: Biological Sciences, 366,* 389–401. doi:10.1098/rstb.2010.0117

Danovitch, J., & Bloom, P. (2009). Children's extension of disgust to physical and moral events. *Emotion, 9,* 107–112. doi:10.1037/a0014113

Darwin, C. (1965). *The expression of emotions in man and animal*. Chicago, IL: University of Chicago Press. (Original work published 1872)

Davey, G. C. L. (2011). Disgust: The disease-avoidance emotion and its dysfunctions. *Philosophical Transactions of the Royal Society: Series B: Biological Sciences, 366,* 3453–3465. doi:10.1098/rstb.2011.0039

DeBruine, L. M. (2005). Trustworthy but not lust-worthy: Context-specific effects of facial resemblance. *Proceedings of the Royal Society of London: Series B: Biological Sciences, 272,* 919–922. doi:10.1098/rspb.2004.3003

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

Delton, A. W., Cosmides, L., Robertson, T. E., Guemo, M., & Tooby, J. (2012). The psychosemantics of free riding: Dissecting the architecture of a moral concept. *Journal of Personality and Social Psychology, 102,* 1252–1270. doi:10.1037/a0027026

DeScioli, P., Bruening, R., & Kurzban, R. (2011). The omission effect in moral cognition: Toward a functional explanation. *Evolution and Human Behavior, 32,* 204–215. doi:10.1016/j.evolhumbehav.2011.01.003

DeScioli, P., Christner, J., & Kurzban, R. (2011). The omission strategy. *Psychological Science, 22,* 442–446. doi:10.1177/0956797611400616

DeScioli, P., & Kurzban, R. (2009). Mysteries of morality. *Cognition, 112,* 281–299. doi:10.1016/j.cognition.2009.05.008

DeScioli, P., & Kurzban, R. (2012). A solution to the mysteries of morality. *Psychological Bulletin*. Advance online publication. doi:10.1037/a0029065

DeSimone, J. A., Lyall, V., Heck, G. L., & Feldman, G. M. (2001). Acid detection by taste receptor cells. *Respiration Physiology, 129,* 231–245. doi:10.1016/S0034-5687(01)00293-6

Douglas, M. (1966). *Purity and danger: An analysis of concepts of pollution and taboo*. London, England: Routledge.

Druschel, B. A., & Sherman, M. F. (1999). Disgust sensitivity as a function of the Big Five and gender. *Personality and Individual Differences, 26,* 739–748. doi:10.1016/S0191-8869(98)00196-2

Ekman, P. (1972). Universals and cultural differences in facial expressions of emotion. In J. Cole (Ed.), *Nebraska Symposium on Motivation* (Vol. 19, pp. 207–282). Lincoln: University of Nebraska.

Ellis, B. J. (1992). The evolution of sexual attraction: Evaluative mechanisms in women. In J. H. Barkow, L. Cosmides, & J. Tooby (Eds.), *The adapted mind* (pp. 267–288). New York, NY: Oxford University Press.

Eskine, K. J., Kacinik, N. A., & Prinz, J. J. (2011). A bad taste in the mouth: Gustatory disgust influences moral judgment. *Psychological Science, 22,* 295–299. doi:10.1177/0956797611398497

Ewald, P. W. (1994). *The evolution of infectious disease*. Oxford, England: Oxford University Press.

Faulkner, J., Schaller, M., Park, J. H., & Duncan, L. A. (2004). Evolved disease-avoidance mechanisms and contemporary xenophobic attitudes. *Group Processes & Intergroup Relations, 7,* 333–353. doi:10.1177/1368430204046142

Fessler, D. M. T., Eng, S. J., & Navarrete, C. D. (2005). Disgust sensitivity is elevated in the first trimester of pregnancy: Evidence supporting the compensatory prophylaxis hypothesis. *Evolution and Human Behavior, 26,* 344–351. doi:10.1016/j.evolhumbehav.2004.12.001

Fessler, D. M. T., & Haley, K. J. (2006). Guarding the perimeter: The outside–inside dichotomy in disgust and bodily experience. *Cognition & Emotion, 20,* 3–19. doi:10.1080/02699930500215181

Fessler, D. M. T., & Navarrete, C. D. (2003a). Domain-specific variation in disgust sensitivity across the menstrual cycle. *Evolution and Human Behavior, 24,* 406–417. doi:10.1016/S1090-5138(03)00054-0

Fessler, D. M. T., & Navarrete, C. D. (2003b). Meat is good to taboo: Dietary proscriptions as a product of the interaction of psychological mechanisms and social processes. *Journal of Cognition and Culture, 3,* 1–40. doi:10.1163/156853703321598563

Fessler, D. M. T., & Navarrete, C. D. (2004). Third-party attitudes toward sibling incest: Evidence for Westermarck's hypotheses. *Evolution and Human Behavior, 25,* 277–294.

Fincher, C. L., & Thornhill, R. (2012). Parasite-stress promotes in-group assortative sociality: The cases of strong family ties and heightened religiosity. *Behavioral and Brain Sciences, 35,* 1–59.

Fink, B., Grammer, K., & Thornhill, R. (2001). Human (Homo sapiens) facial attractiveness in relation to skin texture and color. *Journal of Comparative Psychology, 115,* 92–99. doi:10.1037/0735-7036.115.1.92

Fleischman, D. S., & Fessler, D. M. T. (2011). Progesterone's effects on measures of disease avoidance: Support for the compensatory prophylaxis hypothesis. *Hormones and Behavior, 59,* 271–275. doi:10.1016/j.yhbeh.2010.11.014

Fridlund, A. J. (1991). Sociality of social smiling: Potentiation by an implicit audience. *Journal of Personality and Social Psychology, 60,* 229–240. doi:10.1037/0022-3514.60.2.229

Fumagalli, M., Sironi, M., Pozzoli, U., Ferrer-Admetlla, A., Pattini, L., & Nielsen, R. (2011). Signatures of environmental genetic adaptation pinpoint pathogens as the main selective pressure throughout human evolution. *PLoS Genetics, 7,* e1002355. doi:10.1371/journal.pgen.1002355

Gangestad, S. W., Haselton, M. G., & Buss, D. M. (2006). Evolutionary foundations of cultural variation: Evoked culture and mate preferences. *Psychological Inquiry, 17,* 75–95. doi:10.1207/s15327965pli1702_1

Gangestad, S. W., & Simpson, J. A. (2000). The evolution of human mating: Trade-offs and strategic pluralism. *Behavioral and Brain Sciences, 23,* 573–587. doi:10.1017/S0140525X0000337X

Gangestad, S. W., Simpson, J. A., Cousins, A. J., Garver-Apgar, C. E., & Christensen, P. N. (2004). Women's preferences for male behavioral displays change across the menstrual cycle. *Psychological Science, 15,* 203–207. doi:10.1111/j.0956-7976.2004.01503010.x

Garcia, J., Kimeldorf, D. J., & Koelling, R. A. (1955, July 22). Conditioned aversion to saccharin resulting from exposure to gamma radiation. *Science, 122,* 157–158.

Giovannoni, J. (2001). Molecular biology of fruit maturation and ripening. *Annual Review of Plant Physiology and Plant Molecular Biology, 52,* 725–749. doi:10.1146/annurev.arplant.52.1.725

Goldenberg, J. L., Pyszczynski, T., Greenberg, J., & Solomon, S. (2000). Fleeing the body: A terror management perspective on the problem of human corporeality. *Personality and Social Psychology Review, 4,* 200–218.

Graham, J., Haidt, J., & Nosek, B. (2009). Liberals and conservatives use different sets of moral foundations. *Journal of Personality and Social Psychology, 96,* 1029–1046. doi:10.1037/a0015141

Grammer, K., Fink, B., Møller, A. P., & Thornhill, R. (2003). Darwinian aesthetics: Sexual selection and the biology of beauty. *Biological Reviews, 78,* 385–407. doi:10.1017/S1464793102006085

Greene, J. D. (2007). The secret joke in Kant's soul. In W. Sinnott-Armstrong (Ed.), *Moral psychology: Vol. 3. The neuroscience of morality: Emotion, disease, and development* (pp. 35–80). Cambridge, MA: MIT Press.

Hagen, E. H. (2002). Depression as bargaining: The case postpartum. *Evolution and Human Behavior, 23,* 323–336. doi:10.1016/S1090-5138(01)00102-7

Haidt, J. (2001). The emotional dog and its rational tail: A social intuitionist approach to moral judgment. *Psychological Review, 108,* 814–834. doi:10.1037/0033-295X.108.4.814

Haidt, J. (2006). *The happiness hypothesis: Finding modern truth in ancient wisdom*. New York, NY: Basic Books.

Haidt, J. (2007, May 18). The new synthesis in moral psychology. *Science, 316,* 998–1002. doi:10.1126/science.1137651

Haidt, J. (2012). *The righteous mind: Why good people are divided by politics and religion*. New York, NY: Paragon.

Haidt, J., & Joseph, C. (2004). Intuitive ethics: How innately prepared intuitions generate culturally variable virtues. *Daedalus, 133,* 55–66. doi:10.1162/0011526042365555

Haidt, J., & Kesebir, S. (2010). Morality. In S. Fiske, D. Gilbert, & G. Lindzey (Eds.), *Handbook of social psychology* (5th ed., pp. 797–832). Hoboken, NJ: Wiley.

Haidt, J., Koller, S., & Dias, M. (1993). Affect, culture, and morality, or is it wrong to eat your dog? *Journal of Personality and Social Psychology, 65,* 613–628. doi:10.1037/0022-3514.65.4.613

Haidt, J., McCauley, C., & Rozin, P. (1994). Individual differences in sensitivity to disgust: A scale sampling seven domains of disgust elicitors. *Personality and Individual Differences, 16,* 701–713. doi:10.1016/0191-8869(94)90212-7

Haidt, J., Rozin, P., McCauley, C., & Imada, S. (1997). Body, psyche, and culture: The relationship of disgust to morality. *Psychology and Developing Societies, 9,* 107–131. doi:10.1177/097133369700900105

Haig, D. (1999). Asymmetric relations: Internal conflicts and the horror of incest. *Evolution and Human Behavior, 20,* 83–98. doi:10.1016/S1090-5138(98)00042-7

Hamilton, W. D., & Zuk, M. (1982, October 22). Heritable true fitness and bright birds: A role for parasites? *Science, 218,* 384–387. doi:10.1126/science.7123238

Hart, B. L. (2011). Behavioural defences in animals against pathogens and parasites: Parallels with the pillars of medicine in humans. *Philosophical Transactions of the Royal Society: Series B: Biological Sciences, 366,* 3406–3417. doi:10.1098/rstb.2011.0092

Haselton, M. G., & Nettle, D. (2006). The paranoid optimist: An integrative evolutionary model of cognitive biases. *Personality and Social Psychology Review, 10,* 47–66. doi:10.1207/s15327957pspr1001_3

Hauser, M. D. (2006). *Moral minds: How nature designed a universal sense of right and wrong*. New York, NY: Harper Collins.

Heath, C., Bell, C., & Sternberg, E. (2001). Emotional selection in memes: The case of urban legends. *Journal of Personality and Social Psychology, 81,* 1028–1041. doi:10.1037/0022-3514.81.6.1028

Henrich, J., Boyd, R., & Richerson, P. J. (2012). The puzzle of monogamous marriage. *Philosophical Transactions of the Royal Society: Series B: Biological Sciences, 367,* 657–669. doi:10.1098/rstb.2011.0290

Henrich, J., & Henrich, N. (2010). The evolution of cultural adaptations: Fijian food taboos protect against dangerous marine toxins. *Proceedings of the Royal Society: Series B: Biological Sciences, 277,* 3715–3724. doi:10.1098/rspb.2010.1191

Hertenstein, M. J., Keltner, D., App, B., Bulleit, B. A., & Jaskolka, A. R. (2006). Touch communicates distinct emotions. *Emotion, 6,* 528–533. doi:10.1037/1528-3542.6.3.528

Hodson, G., & Costello, K. (2007). Interpersonal disgust, ideological orientations, and dehumanization as predictors of intergroup attitudes. *Psychological Science, 18,* 691–698. doi:10.1111/j.1467-9280.2007.01962.x

Hoefling, A., Likowski, K. U., Deutsch, R., Häfner, M., Seibt, B., Mühlberger, A., . . . Strack, F. (2009). When hunger finds no fault with moldy corn: Food deprivation reduces food-related disgust. *Emotion, 9,* 50–58. doi:10.1037/a0014449

Hoffman, C. L., Ruiz-Lambides, A. V., Davila, E., Maldonado, E., Gerald, M. S., & Maestripieri, D. (2008). Sex differences in survival costs of reproduction in a promiscuous primate. *Behavioral Ecology and Sociobiology, 62,* 1711–1718. doi:10.1007/s00265-008-0599-z

Holmes, K., Sparling, P., Stamm, W., Piot, P., Wasserheit, J., Corey, L., & Cohen, M. (2007). *Sexually transmitted diseases* (4th ed.). New York, NY: McGraw-Hill.

Hutcherson, C. A., & Gross, J. J. (2011). The moral emotions: A social-functionalist account of anger, disgust, and contempt. *Journal of Personality and Social Psychology, 100,* 719–737. doi:10.1037/a0022408

Inbar, Y., Pizarro, D. A., & Bloom, P. (2009). Conservatives are more easily disgusted than liberals. *Cognition & Emotion, 23,* 714–725. doi:10.1080/02699930802110007

Isac, M., & Schneider, S. (1992). Some psychological reactions of rape victims. *Medicine & Law, 11,* 303–308.

Jennions, M. D., & Petrie, M. (2000). Why do females mate multiply? A review of the genetic benefits. *Biological Review, 75,* 21–64. doi:10.1017/S0006323199005423

Jones, A., & Fitness, J. (2008). Moral hypervigilance: The influence of disgust sensitivity in the moral domain. *Emotion, 8,* 613–627. doi:10.1037/a0013435

Jones, B. C., Little, A. C., Penton-Voak, I. S., Tiddeman, B. P., Burt, D. M., & Perrett, D. I. (2001). Facial symmetry and judgments of apparent health: Support for a "good genes" explanation of the attractiveness–symmetry relationship. *Evolution and Human Behavior, 22,* 417–429. doi:10.1016/S1090-5138(01)00083-6

Keller, M. C., & Nesse, R. M. (2006). The evolutionary significance of depressive symptoms: Different adverse situations lead to different depressive symptom patterns. *Journal of Personality and Social Psychology, 91,* 316–330. doi:10.1037/0022-3514.91.2.316

Kelly, D. (2011). *Yuck! The nature and moral significance of disgust*. Cambridge, MA: MIT Press.

Keltner, D., & Gross, J. J. (1999). Functional accounts of emotions. *Cognition & Emotion, 13,* 467–480. doi:10.1080/026999399379140

Keltner, D., Haidt, J., & Shiota, L. (2006). Social functionalism and the evolution of emotions. In M. Schaller, D. Kenrick, & J. Simpson (Eds.), *Evolution and social psychology* (pp. 115–142). New York, NY: Psychology Press.

Kenrick, D. T., Griskevicius, V., Neuberg, S. L., & Schaller, M. (2010). Renovating the pyramid of needs: Contemporary extensions built upon ancient foundations. *Perspectives on Psychological Science, 5,* 292–314. doi:10.1177/1745691610369469

Kenrick, D. T., & Keefe, R. C. (1992). Age preferences in mates reflect sex differences in human reproductive strategies. *Behavioral and Brain Sciences, 15,* 75–91. doi:10.1017/S0140525X00067595

Kleck, R. (1969). Physical stigma and task oriented interactions. *Human Relations, 22,* 53–60. doi:10.1177/001872676902200103

Kluger, M. J., Ringler, D. H., & Anver, M. R. (1975, April 11). Fever and survival. *Science, 188,* 166–168. doi:10.1126/science.1114347

Koleva, S. P., Graham, J., Iyer, R., Ditto, P. H., & Haidt, J. (2012). Tracing the threads: How five moral concerns (especially purity) help explain culture war attitudes. *Journal of Research in Personality, 46,* 184–194. doi:10.1016/j.jrp.2012.01.006

Konner, M., & Shostak, M. (1987). Timing and management of birth among the !Kung: Biocultural interaction in reproductive adaptation. *Cultural Anthropology, 2,* 11–28. doi:10.1525/can.1987.2.1.02a00030

Koukounas, E., & McCabe, M. (1997). Sexual and emotional variables influencing sexual response to erotica. *Behaviour Research and Therapy, 35,* 221–230. doi:10.1016/S0005-7967(96)00097-6

Krebs, D. (2011). *The origins of morality: An evolutionary account*. New York, NY: Oxford University Press.

Kurzban, R., DeScioli, P., & Fein, D. (2012). Hamilton vs. Kant: Pitting adaptations for altruism against adaptations for moral judgment. *Evolution and Human Behavior, 33,* 323–333. doi:10.1016/j.evolhumbehav.2011.11.002

Kurzban, R., DeScioli, P., & O'Brien, E. (2007). Audience effects on moralistic punishment. *Evolution and Human Behavior, 28,* 75–84. doi:10.1016/j.evolhumbehav.2006.06.001

Kurzban, R., Dukes, A., & Weeden, J. (2010). Sex, drugs, and moral goals: Reproductive strategies and views about recreational drugs. *Proceedings of the Royal Society of London: Series B: Biological Sciences, 277,* 3501–3508. doi:10.1098/rspb.2010.0608

Kurzban, R., & Leary, M. R. (2001). Evolutionary origins of stigmatization: The functions of social exclusion. *Psychological Bulletin, 127,* 187–208. doi:10.1037/0033-2909.127.2.187

Li, Y. J., Cohen, A. B., Weeden, J., & Kenrick, D. T. (2010). Mating competitors increase religious beliefs. *Journal of Experimental Social Psychology, 46,* 428–431. doi:10.1016/j.jesp.2009.10.017

Lieberman, D., & Lobel, T. (2012). Kinship on the kibbutz: Coresidence duration predicts altruism, personal sexual aversions and moral attitudes among communally raised peers. *Evolution and Human Behavior, 33,* 26–34. doi:10.1016/j.evolhumbehav.2011.05.002

Lieberman, D., Pillsworth, E. G., & Haselton, M. G. (2011). Kin affiliation across the ovulatory cycle: Females avoid fathers when fertile. *Psychological Science, 22,* 13–18. doi:10.1177/0956797610390385

Lieberman, D., Tooby, J., & Cosmides, L. (2003). Does morality have a biological basis? An empirical test of the factors governing moral sentiments regarding incest. *Proceedings of the Royal Society of London: Series B: Biological Sciences, 270,* 819–826. doi:10.1098/rspb.2002.2290

Lieberman, D., Tooby, J., & Cosmides, L. (2007, February 15). The architecture of human kin detection. *Nature, 445,* 727–731. doi:10.1038/nature05510

Lieberman, D., Tybur, J. M., & Latner, J. (2012). Disgust sensitivity, obesity stigma, and gender: Contamination psychology predicts weight bias for women, not men. *Obesity, 20,* 1808–1814. doi:10.1038/oby.2011.247

Little, A. C., Jones, B. C., & DeBruine, L. M. (2008). Preferences for variation in masculinity in real male faces change across the menstrual cycle. *Personality and Individual Differences, 45,* 478–482. doi:10.1016/j.paid.2008.05.024

Lovanh, N., Cook, K. L., Rothrock, M. J., Miles, D. M., & Sistani, J. (2007). Spatial shifts in microbial population structure within poultry litter associated with physicochemical properties. *Poultry Science, 86,* 1840–1849.

Marr, D. (1982). *Vision: A computational investigation into the human representations and processing of visual information*. New York, NY: Freeman.

Marzillier, S. L., & Davey, G. C. L. (2004). The emotional profiling of disgust eliciting stimuli: Evidence for primary and complex disgusts. *Cognition & Emotion, 18,* 313–336. doi:10.1080/02699930341000130

Mikhail, J. (2007). Universal moral grammar: Theory, evidence, and the future. *Trends in Cognitive Sciences, 11,* 143–152. doi:10.1016/j.tics.2006.12.007

Mikhail, J. (2008). Moral cognition in computational theory. In W. Sinnott-Armstrong (Ed.), Moral psychology: Vol. 3. *The neuroscience of morality: Emotion, disease, and development* (pp. 81–92). Cambridge, MA: MIT Press.

Miller, S. B. (2004). *Disgust: The gatekeeper emotion*. Mahwah, NJ: Analytic Press.

Miller, W. I. (1997). *The anatomy of disgust*. Cambridge, MA: Harvard University Press.

Moll, J., de Oliveira-Souza, R., Moll, F. T., Ignacio, F. A., Bramati, I. E., Caparelli-Dáquer, E. M., & Enslinger, P. J. (2005). The moral affiliations of disgust: A functional MRI study. *Cognitive and Behavioral Neurology, 18,* 68–78. doi:10.1097/01.wnn.0000152236.46475.a7

Møller, A. P., & Swaddle, J. P. (1997). *Asymmetry, developmental stability and evolution*. New York, NY: Oxford University Press.

Moretti, L., & di Pellegrino, G. (2010). Disgust selectively modulates reciprocal fairness in economic interaction. *Emotion, 10,* 169–180. doi:10.1037/a0017826

Mortensen, C. R., Becker, D. V., Ackerman, J. M., Neuberg, S. L., & Kenrick, D. T. (2010). Infection breeds reticence: The effects of disease salience on self-perceptions of personality and behavioral tendencies. *Psychological Science, 21,* 440–447. doi:10.1177/0956797610361706

Mosher, D. L., & O'Grady, K. E. (1979). Homosexual threat, negative attitudes toward masturbation, sex guilt, and males' sexual and affective reactions to explicit sexual films. *Journal of Consulting and Clinical Psychology, 47,* 860–873. doi:10.1037/0022-006X.47.5.860

Murray, D. R., & Schaller, M. (2010). Historical prevalence of infectious disease within 230 geopolitical regions: A tool for investigating origins of culture. *Journal of Cross-Cultural Psychology, 41,* 99–108. doi:10.1177/0022022109349510

Nabi, R. (2002). The theoretical versus the lay meaning of disgust: Implications for emotion research. *Cognition & Emotion, 16,* 695–703. doi:10.1080/02699930143000437

Navarrete, C. D., & Fessler, D. M. T. (2006). Disease avoidance and ethnocentrism: The effects of disease vulnerability and disgust sensitivity on intergroup attitudes. *Evolution and Human Behavior, 27,* 270–282. doi:10.1016/j.evolhumbehav.2005.12.001

Neff, B. D., & Pitcher, T. E. (2005). Genetic quality and sexual selection: An integrated framework for good genes and compatible genes. *Molecular Ecology, 14,* 19–38. doi:10.1111/j.1365-294X.2004.02395.x

Nesse, R. M. (2005). Natural selection and the regulation of defenses: A signal detection analysis of the smoke detector problem. *Evolution and Human Behavior, 26,* 88–105. doi:10.1016/j.evolhumbehav.2004.08.002

Nesse, R., & Ellsworth, P. (2009). Evolution, emotions, and emotional disorders. *American Psychologist, 64,* 129–139.

Nesse, R., & Williams, G. C. (1994). *Why we get sick: The new science of Darwinian medicine*. New York, NY: Times Books.

Neuberg, S. L., Kenrick, D. T., & Schaller, M. (2011). Human threat management systems: Self-protection and disease-avoidance. *Neuroscience & Biobehavioral Reviews, 35,* 1042–1051. doi:10.1016/j.neubiorev.2010.08.011

Neuberg, S. L., Smith, D. M., Hoffman, J. C., & Russell, F. J. (1994). When we observe stigmatized and "normal" individuals interacting: Stigma by association. *Personality and Social Psychology Bulletin, 20,* 196–209. doi:10.1177/0146167294202007

Nichols, S. (2002). Norms with feeling: Towards a psychological account of moral judgment. *Cognition, 84,* 221–236. doi:10.1016/S0010-0277(02)00048-3

Oaten, M., Stevenson, R. J., & Case, T. I. (2009). Disgust as a disease-avoidance mechanism. *Psychological Bulletin, 135,* 303–321. doi: 10.1037/a0014823

Oaten, M., Stevenson, R. J., & Case, T. I. (2011). Disease avoidance as a functional basis for stigmatization. *Proceedings of the Royal Society of London: Series B: Biological Sciences, 366,* 3433–3452. doi:10.1098/rstb.2011.0095

Ober, C., Weitkamp, L. R., Cox, N., Dytch, H., Kostyu, D., & Elias, S. (1997). HLA and mate choice in humans. *American Journal of Human Genetics, 61,* 497–504. doi:10.1086/515511

Öhman, A., & Mineka, S. (2001). Fears, phobias, and preparedness: Toward an evolved module of fear and fear learning. *Psychological Review, 108,* 483–522. doi:10.1037/0033-295X.108.3.483

Olatunji, B. O., Adams, T., Ciesielski, B., Bieke, D., Sarawgi, S., & Broman-Fulks, J. (2012). The Three Domains of Disgust Scale: Factor structure, psychometric properties, and conceptual limitations. *Assessment, 19,* 202–225. doi:10.1177/1073191111432881

Olatunji, B. O., & McKay, D. (2009). *Disgust and its disorders: Theory, assessment, and treatment implications*. Washington, DC: American Psychological Association. doi:10. 1037/11856-000

Olatunji, B. O., & Sawchuk, C. N. (2005). Disgust: Characteristic features, social implications, and clinical manifestations. *Journal of Social and Clinical Psychology, 24,* 932–962. doi:10.1521/jscp.2005.24.7.932

Olatunji, B. O., Williams, N. L., Tolin, D. F., Sawchuk, C. N., Abramowitz, J. S., Lohr, J. M., & Elwood, L. (2007). The Disgust Scale: Item analysis, factor structure, and suggestions for refinement. *Psychological Assessment, 19,* 281–297. doi:10.1037/1040-3590.19.3.281

Oum, R. E., Lieberman, D., & Aylward, A. (2011). A feel for disgust: Tactile cues to pathogen presence. *Cognition & Emotion, 25,* 717–725. doi:10.1080/02699931.2010.496997

Park, J. H. (2008). Is aversion to incest psychologically privileged? When sex and sociosexuality do not predict sexual willingness. *Personality and Individual Differences, 45,* 661–665. doi:10.1016/j.paid.2008.07.011

Park, J. H., Faulkner, J., & Schaller, M. (2003). Evolved disease-avoidance processes and contemporary anti-social behavior: Prejudicial attitudes and avoidance of people with physical disabilities. *Journal of Nonverbal Behavior, 27,* 65–87. doi:10.1023/A:1023910408854

Park, J. H., & Schaller, M. (2005). Does attitude similarity serve as a heuristic cue for kinship? Evidence of an implicit cognitive association. *Evolution and Human Behavior, 26,* 158–170. doi:10.1016/j.evolhumbehav.2004.08.013

Park, J. H., Schaller, M., & Crandall, C. S. (2007). Pathogen-avoidance mechanisms and the stigmatization of obese people. *Evolution and Human Behavior, 28,* 410–414. doi:10.1016/j.evolhumbehav.2007.05.008

Penn, D. J., & Potts, W. K. (1999). The evolution of mating preferences and major histocompatibility complex genes. *American Naturalist, 153,* 145–164.

Penn, D. J., & Smith, K. R. (2007). Differential fitness costs of reproduction between the sexes. *Proceedings of the National Academy of Sciences, USA, 104,* 553–558. doi:10.1073/pnas.0609301103

Perilloux, C., Lewis, D. M. G., Goetz, C. D., Fleischman, D. S., Easton, J. A., Confer, J. C., & Buss, D. M. (2010). Trade-offs, individual differences, and misunderstandings about evolutionary psychology. *American Psychologist, 65,* 930–932. doi:10.1037/a0021635

Petrak, J., Doyle, A.-M., Williams, L., Buchan, L., & Forster, G. (1997). The psychological impact of sexual assault: A study of female attenders of a sexual health psychology service. *Sexual & Marital Therapy, 12,* 339–345. doi:10.1080/02674659708408177

Pinker, S. (1997). *How the mind works*. New York, NY: Norton

Pinker, S. (2012). *The false allure of group selection*. Retrieved from http://www.edge.org

Pizarro, D. A., Inbar, Y., & Helion, C. (2011). On disgust and moral judgment, *Emotion Review, 3,* 267–268. doi:10.1177/1754073911402394

Pond, R. S., DeWall, C. N., Lambert, N. M., Deckman, T., Bonser, I. M., & Fincham, F. D. (2012). Repulsed by violence: Disgust sensitivity buffers trait, behavioral, and daily aggression. *Journal of Personality and Social Psychology, 102,* 175–188. doi:10.1037/a0024296

Puts, D. A. (2010). Beauty and the beast: Mechanisms of sexual selection in humans. *Evolution and Human Behavior, 31,* 157–175. doi:10.1016/j.evolhumbehav.2010.02.005

Puurtinen, M., Ketola, T., & Kotiaho, J. S. (2009). The good-genes and compatible genes benefits of mate choice. *American Naturalist, 174,* 741–752. doi:10.1086/606024

Richerson, P. J., & Boyd, R. (2005). *Not by genes alone: How culture transformed human evolution*. Chicago, IL: University of Chicago Press.

Ridley, M. (1993). *The Red Queen: Sex and the evolution of human nature*. London, England: Viking.

Roseman, I. J., Wiest, C., & Swartz, T. S. (1994). Phenomenology, behaviors, and goals differentiate discrete emotions. *Journal of Personality and Social Psychology, 67,* 206–221. doi:10.1037/0022-3514.67.2.206

Royzman, E., & Kurzban, R. (2011). Minding the metaphor: The elusive character of moral disgust. *Emotion Review, 3,* 269–271. doi:10.1177/1754073911402371

Royzman, E. B., Leeman, R. F., & Sabini, J. (2008). "You make me sick": Moral dyspepsia as a reaction to third-party sibling incest. *Motivation and Emotion, 32,* 100–108. doi:10.1007/s11031-008-9089-x

Royzman, E. B., & Sabini, J. (2001). Something it takes to be an emotion: The interesting case of disgust. *Journal for the Theory of Social Behaviour, 31,* 29–59. doi:10.1111/1468-5914.00145

Rozin, P., & Fallon, A. (1987). A perspective on disgust. *Psychological Review, 94,* 23–41. doi:10.1037/0033-295X.94.1.23

Rozin, P., Haidt, J., & Fincher, K. (2009, February 27). From oral to moral. *Science, 323,* 1179–1180. doi:10.1126/science.1170492

Rozin, P., Haidt, J., & McCauley, C. R. (2008). Disgust. In M. Lewis, J. M. Haviland-Jones, & L. F. Barrett (Eds.), *Handbook of emotions* (3rd ed., pp. 757–776). New York, NY: Guilford Press.

Rozin, P., Haidt, J., & McCauley, C. R. (2009). Disgust: The body and soul emotion in the 21st century. In D. McKay & O. Olatunji (Eds.), *Disgust and its disorders* (pp. 9–29). Washington, DC: American Psychological Association.

Rozin, P., Lowery, L., & Ebert, R. (1994). Varieties of disgust faces and the structure of disgust. *Journal of Personality and Social Psychology, 66,* 870–881. doi:10.1037/0022-3514.66.5.870

Rozin, P., Lowery, L., Imada, S., & Haidt, J. (1999). The CAD triad hypothesis: A mapping between three moral emotions (contempt, anger, disgust) and three moral codes (community, autonomy, divinity). *Journal of Personality and Social Psychology, 76,* 574–586.

Rozin, P., Millman, L., & Nemeroff, C. (1986). Operation of the laws of sympathetic magic in disgust and other domains. *Journal of Personality and Social Psychology, 50,* 703–712. doi:10.1037/0022-3514.50.4.703

Rozin, P., Nemeroff, C., Horowitz, M., Gordon, B., & Voet, W. (1995). The borders of the self: Contamination sensitivity and potency of the mouth, other apertures and body parts. *Journal of Research in Personality, 29,* 318–340. doi:10.1006/jrpe.1995.1019

Ryan, S., Oaten, M., Stevenson, R. J., & Case, T. I. (in press). Facial disfigurement is treated like an infectious disease. *Evolution and Human Behavior*.

Sanfey, A. G., Rilling, J. K., Aronson, J. A., Nystrom, L. E., & Cohen, J. D. (2003, June 13). The neural basis of economic decision-making in the ultimatum game. *Science, 300,* 1755–1758. doi:10.1126/science.1082976

Sauter, D. A., & Eimer, M. (2010). Rapid detection of emotion from human vocalizations. *Journal of Cognitive Neuroscience, 22,* 474–481.

Sauter, D. A., Eisner, F., Ekman, P., & Scott, S. K. (2010). Cross-cultural recognition of basic emotions through nonverbal emotional vocalizations. *Proceedings of the National Academy of Sciences of the United States of America, 107,* 2408–2412.

Schaich Borg, J., Lieberman, D., & Kiehl, K. A. (2008). Infection, incest, and iniquity: Investigating the neural correlates of disgust and morality. *Journal of Cognitive Neuroscience, 20,* 1529–1546. doi:10.1162/jocn.2008.20109

Schaller, M., & Duncan, L. A. (2007). The behavioral immune system: Its evolution and social psychological implications. In J. P. Forgas, M. G. Haselton, & W. von Hippel (Eds.), *Evolution and the social mind: Evolutionary psychology and social cognition* (pp. 293–307). New York, NY: Psychology Press.

Schaller, M., Miller, G. E., Gervais, W. M., Yager, S., & Chen, E. (2010). Mere visual perception of other people's disease symptoms facilitates a more aggressive immune response. *Psychological Science, 21,* 649–652. doi:10.1177/0956797610368064

Schaller, M., & Murray, D. R. (2008). Pathogens, personality and culture: Disease prevalence predicts worldwide variability in sociosexuality, extraversion, and openness to experience. *Journal of Personality and Social Psychology, 95,* 212–221. doi:10.1037/0022-3514.95.1.212

Schaller, M., & Park, J. H. (2011). The behavioral immune system (and why it matters). *Current Directions in Psychological Science, 20,* 99–103. doi:10.1177/0963721411402596

Schnall, S., Haidt, J., Clore, G., & Jordan, A. (2008). Disgust as embodied moral judgment. *Personality and Social Psychology Bulletin, 34,* 1096–1109. doi:10.1177/0146167208317771

Scott, I. M. L., Pound, N., Stephen, I. D., Clark, A. P., & Penton-Voak, I. S. (2010). Does masculinity matter? The contributions of masculine face shape to male attractiveness in humans. *PLoS ONE, 5, e13585*. doi:10.1371/journal.pone.0013585

Seligman, M. E. P., & Hager, J. L. (1972). *Biological boundaries of learning*. New York, NY: Meredith.

Sell, A., Tooby, J., & Cosmides, L. (2009). Formidability and the logic of human anger. *Proceedings of the National Academy of Sciences, USA, 106,* 15073–15078. doi:10.1073/pnas.0904312106

Shweder, R. A., Mahapatra, M., & Miller, J. (1987). Culture and moral development. In J. Kagan & S. Lamb (Eds.), *The emergence of morality in young children* (pp. 1–83). Chicago, IL: University of Chicago Press.

Simpson, J., Carter, S., Anthony, S. H., & Overton, P. G. (2006). Is disgust a homogeneous emotion? *Motivation and Emotion, 30,* 31–41. doi:10.1007/s11031-006-9005-1

Singh, D. (1993). Adaptive significance of female physical attractiveness: Role of waist-to-hip ratio. *Journal of Personality and Social Psychology, 65,* 293–307. doi:10.1037/0022-3514.65.2.293

Snyder, J., Kirkpatrick, L., & Barrett, H. C. (2008). The dominance dilemma: Do women really prefer dominant mates? *Personal Relationships, 15,* 425–444. doi:10.1111/j.1475-6811.2008.00208.x

Stevenson, R. J., Case, T. I., & Oaten, M. J. (2011). Effect of self-reported sexual arousal on responses to sex-related and non-sex-related disgust cues. *Archives of Sexual Behavior, 40,* 79–85. doi:10.1007/s10508-009-9529-z

Stevenson, R. J., Hodgson, D., Oaten, M. J., Barouei, J., & Case, T. I. (2011). The effect of disgust on oral immune function. *Psychophysiology, 48,* 900–907. doi:10.1111/j.1469-8986.2010.01165.x

Stevenson, R. J., & Repacholi, B. M. (2005). Does the source of interpersonal odour affect disgust? A disease risk model and its alternatives. *European Journal of Social Psychology, 35,* 375–401. doi:10.1002/ejsp.263

Susskind, J. M., Lee, D. H., Cusi, A., Feinman, R., Grabski, W., & Anderson, A. K. (2008). Expressing fear enhances sensory acquisition. *Nature Neuroscience, 11,* 843–850. doi:10.1038/nn.2138

Symons, D. (1979). *The evolution of human sexuality*. New York, NY: Oxford University Press.

Symons, M. (2007). *Where do nudists keep their hankies?* New York, NY: HarperCollins.

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

Thornhill, R., & Gangestad, S. W. (1993). Human facial beauty: Averageness, symmetry, and parasite resistance. *Human Nature, 4,* 237–269. doi:10.1007/BF02692201

Thornhill, R., & Gangestad, S. W. (1999). Facial attractiveness. *Trends in Cognitive Sciences, 3,* 452–460. doi:10.1016/S1364-6613(99)01403-5

Thornhill, R., & Gangestad, S. W. (2006). Facial sexual dimorphism, developmental stability, and susceptibility to disease in men and women. *Evolution and Human Behavior, 27,* 131–144. doi:10.1016/j.evolhumbehav.2005.06.001

Thornhill, R., & Gangestad, S. W. (2008). *The evolutionary biology of human female sexuality*. New York, NY: Oxford University Press.

Thornhill, R., Gangestad, S. W., Miller, R., Scheyd, G., Knight, J., & Franklin, M. (2003). Major histocompatibility complex genes, symmetry, and body scent attractiveness in men and women. *Behavioral Ecology, 14,* 668–678. doi:10.1093/beheco/arg043

Tinbergen, N. (1963). On aims and methods in ethology. *Zeitschrift fur Tierpsychologie, 20,* 410–433. doi:10.1111/j.1439-0310.1963.tb01161.x

Tomkins, S. S. (1963). *Affect, imagery, consciousness: Vol. II. The negative affects*. New York, NY: Springer.

Tooby, J. (1982). Pathogens, polymorphism, and the evolution of sex. *Journal of Theoretical Biology, 97,* 557–576. doi:10.1016/0022-5193(82)90358-7

Tooby, J., & Cosmides, L. (1990). The past explains the present: Emotional adaptations and the structure of ancestral environments. *Ethology and Sociobiology, 11,* 375–424. doi:10.1016/0162-3095(90)90017-Z

Tooby, J., & Cosmides, L. (1992). The psychological foundations of culture. In J. Barkow, L. Cosmides, & J. Tooby (Eds.), *The adapted mind: Evolutionary psychology and the generation of culture* (pp. 19–136). New York, NY: Oxford University Press.

Tooby, J., & Cosmides, L. (2008). The evolutionary psychology of the emotions and their relationship to internal regulatory variables. In M. Lewis, J. M. Haviland-Jones, & L. F. Barrett (Eds.), *Handbook of emotions* (3rd ed., pp. 114–137). New York, NY: Guilford Press.

Tooby, J., & Cosmides, L. (2010). Groups in mind: The coalitional roots of war and morality. In Henrik H/ogh-Olesen (Ed.), *Human morality and sociality: Evolutionary and comparative perspectives* (pp. 91–234). New York, NY: Palgrave Macmillan.

Trivers, R. (1972). Parental investment and sexual selection. In B. Campbell (Ed.), *Sexual selection and the descent of man, 1871–1971* (pp. 136–179). Chicago, IL: Aldine-Atherton.

Tybur, J. M., Bryan, A. D., Lieberman, D., Caldwell Hooper, A. E., & Merriman, L. A. (2011). Sex differences and sex similarities in disgust sensitivity. *Personality and Individual Differences, 51,* 343–348. doi:10.1016/j.paid.2011.04.003

Tybur, J. M., Bryan, A. D., Magnan, R. E., & Caldwell Hooper, A. E. (2011). Smells like safe sex: Olfactory pathogen primes increase intentions to use condoms. *Psychological Science, 22,* 478–480. doi:10.1177/0956797611400096

Tybur, J. M., & Gangestad, S. W. (2011). Mate preferences and infectious disease: Theoretical considerations and evidence in humans. *Philosophical Transactions of the Royal Society: Series B: Biological Sciences, 366,* 3375–3388. doi:10.1098/rstb.2011.0136

Tybur, J. M., Lieberman, D., & Griskevicius, V. (2009). Microbes, mating, and morality: Individual differences in three functional domains of disgust. *Journal of Personality and Social Psychology, 97,* 103–122. doi:10.1037/a0015474

Tybur, J. M., Merriman, L. A., Caldwell, A. E., McDonald, M. M., & Navarrete, C. D. (2010). Extending the behavioral immune system to political psychology: Are political conservativism and disgust sensitivity really related? *Evolutionary Psychology, 8,* 599–616.

Van Leeuwen, F., Park, J. H., Koenig, B. L., & Graham, J. (2012). Regional variation in pathogen prevalence predicts endorsement of group-focused moral concerns. *Evolution and Human Behavior, 33,* 429–437. doi:10.1016.j.evol.humbehav.2011.12.005

Varghese, B., Maher, J. E., Peterman, T. A., Branson, B. A., & Steketee, R. W. (2002). Reducing the risk of sexual HIV transmission: Quantifying the per-act risk for HIV on the basis of choice of partner, sex act, and condom use. *Sexually Transmitted Diseases, 29,* 38–43. doi:10.1097/00007435-200201000-00007

Vonderheide, S. G., & Mosher, D. L. (1988). Should I put in my diaphragm? Sex-guilt and turn-offs. *Journal of Psychology & Human Sexuality, 1,* 97–111. doi:10.1300/J056v01n01_08

Wagner, C. M., Stroud, E. M., & Meckley, T. D. (2011). A deathly odor suggests a new sustainable tool for controlling a costly invasive species. *Canadian Journal of Fisheries and Aquatic Sciences, 68,* 1157–1160. doi:10.1139/f2011-072

Wedekind, C., & Furi, S. (1997). Body odour preferences in men and women: Do they aim for specific MHC combinations or simply heterozygosity? *Proceedings of the Royal Society of London: Series B: Biological Sciences, 264,* 1471–1479. doi:10.1098/rspb.1997.0204

Weeden, J. (2003). *Genetic interests, life histories, and attitudes towards abortions* (Unpublished doctoral dissertation). University of Pennsylvania.

Weeden, J., Cohen, A. B., & Kenrick, D. T. (2008). Religious participation and reproductive strategies. *Evolution and Human Behavior, 29,* 327–334. doi:10.1016/j.evolhumbehav.2008.03.004

Westermarck, E. A. (1921). *The history of human marriage*. London, England: Macmillan. (Original work published 1891)

Wheatley, T., & Haidt, J. (2005). Hypnotic disgust makes moral judgments more severe. *Psychological Science, 16,* 780–784. doi:10.1111/j.1467-9280.2005.01614.x

Wicker, B., Keysers, C., Plailly, J., Royet, J.-P., Gallese, V., & Rizzolatti, G. (2003). Both of us disgusted in my insula: The common neural basis of seeing and feeling disgust. *Neuron, 40,* 655–664. doi:10.1016/S0896-6273(03)00679-2

Worthington, M. E. (1974). Personal space as a function of the stigma effect. *Environment and Behavior, 6,* 289–294. doi:10.1177/001391657400600302

Yamazaki, K., Beauchamp, G. K., Kupniewski, D., Bard, J., Thomas, L., & Boyse, E. A. (1988, June 3). Familial imprinting determines H-2 selective mating preferences. *Science, 240,* 1331–1332. doi:10.1126/science.3375818

Yao, M., Rosenfeld, J., Attridge, S., Sidhu, S., Aksenov, V., & Rollo, C. D. (2009). The ancient chemistry of avoiding risks of predation and disease. *Evolutionary Biology, 36,* 267–281. doi:10.1007/s11692-009-9069-4

Zebrowitz, L. A., & Rhodes, G. (2004). Sensitivity to "bad genes" and the anomalous face overgeneralization effect: Cue validity, cue utilization, and accuracy in judging intelligence and health. *Journal of Nonverbal Behavior, 28,* 167–185. doi:10.1023/B:JONB.0000039648.30935.1b

Zeh, J. A., & Zeh, D. W. (1996). The evolution of polyandry I: Intragenomic conflict and genetic incompatibility. *Proceedings of the Royal Society of London: Series B: Biological Sciences, 263,* 1711–1717. doi:10.1098/rspb.1996.0250

Zhang, Y., Lu, H., & Bargmann, C. I. (2005, November 10). Pathogenic bacteria induce aversive olfactory learning in *Caenorhabditis elegans*. *Nature, 438,* 179–184. doi:10.1038/nature04216

Zhong, C. B., & Liljenquist, K. (2006, September 8). Washing away your sins: Threatened morality and physical cleansing. *Science, 313,* 1451–1452. doi:10.1126/science.1130726

Received February 11, 2012
Revision received August 16, 2012
Accepted September 11, 2012 ■