Women's Disgust Adaptations

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Diana Santos Fleischman

Consider for a moment a few things that you find disgusting. You may find that these disgust elicitors have a few things in common such as the ability to make you sick or poison you, or, perhaps, you will have a more diverse set of ideas on mind. In many ways disgust is one of the more straightforward emotional motivational states given that it distances individuals from cues of contamination or disease, and yet it is evoked in diverse contexts. You may be disgusted by thinking of eating meat with maggots in it, feeling a stranger sneeze all over your arm, considering someone who steals from the disabled, or imagining having sex with a relative or unattractive person. Like many aspects of evolved psychology considered in this volume, disgust is one emotional domain in which men and women have faced somewhat different selection pressures, in this case the costs and benefits related to disease avoidance.

Why Disgust?

Pathogens are a central adaptive problem almost all organisms face; even the pathogens themselves sometimes have pathogens! Pathogens, like parasitic bacteria, helminths, viruses, and protozoa, derive nutrients and shelter and breed grounds from hosts who are then often disadvantaged in terms of both survival and reproductive success. Pathogens like bacteria and viruses have advantages over complex multicellular organisms like humans. Their arsenal, mutations and short generational times along with gene swapping and recombination, can enable them to adapt quickly to exploit host environments and overcome defenses. In response to this constant threat, immune systems of incredible complexity and adaptability have been developed. Humans come preequipped to build billions of antibodies and antigen receptors, molecules that bind to parasitic elements and by-products. However, mounting a defense against pathogens is costly. It is estimated in humans that metabolic demands go up by 16 % after a vaccine and 30 % during sepsis (Lochmiller & Deerenberg, 2000). Moreover, immune activation doesn't come without collateral damage. Immune products and inflammation that fight infection can have harmful effects that last long after the infection is cleared; macrophages that consume bacteria leak digestive enzymes, damaging surrounding tissues (Clark, 2007, p. 16). In the case of diseases such as tuberculosis and hepatitis B, it is the immune system that destroys the lungs and liver, respectively, not the pathogen itself (Clark, 2007).

Given these high costs, prevention is indeed the best medicine; if and when recurrent and reliable cues to disease exist, one should expect that organisms will adapt to identify and avoid

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them. There are many examples of disease avoidance analogous to disgust in nonhuman animals. Sheep, horses, and cows avoid grazing in areas heavily contaminated with fecal matter (Hart, 1990). Eating conspecifics offers a nearly optimal nutrient balance; however, many omnivores and carnivores display a "cannibalism taboo" because, even in this case, the cost of contracting illness exceeds the nutritional benefits (Hart, 1990). Acquired taste aversions, that is, avoiding foods that taste like ones that previously caused illness, are well documented, especially in animals like rats that cannot vomit (Hart, 1990). Many nonhuman animals also avoid mating with kin or sick conspecifics (Hart, 1990). However, while disgust may be a disease avoidance system, not all disease avoidance systems are disgust.

What Is Disgust?

Although nonhuman animals engage in some very complex disease avoidance strategies, disgust, when defined as an emotion, is distinctively human. But what is disgust? It seems difficult to define disgust without referencing the very things we find disgusting. Darwin defined disgust as referring to "something revolting, primarily in relation to the sense of taste, as actually perceived or vividly imagined; and secondarily to anything which causes a similar feeling, through the sense of smell, touch and even of eyesight" (Darwin, 1872, p. 253). Many definitions tend to be similarly circuitous and appealing to intuitive understanding; disgusting stuff is, well, disgusting. More enlightening is to consider disgust within the framework of computational theory of mind as a motivational system with inputs and outputs including the adaptive salience of the cue and the condition of the organism.

Disgust can be called an "affect program," an emotional response that is automatically triggered, coordinated, and often elicited by adaptively relevant stimuli (Kelly, 2011, p. 15). Disgust is associated with a number of defined physiological correlates including activation of the parasympathetic nervous system, reduced heart rate, heightened galvanic skin response (Rohrmann & Hopp, 2008), and increased salivation (saliva prevents damage to tooth enamel during vomiting) (Angyal, 1941). The facial expression associated with disgust is similarly specific and considered one of the five basic universal emotional expressions (Ekman & Friesen, 1971). Moreover, disgust shows consistent neural localization in the anterior insular cortex which responds preferentially to images of contamination and facial expressions of disgust (Stark et al., 2003, 2007; Wright, He, Shapira, Goodman, & Liu, 2004) including heightened activation in those with elevated disgust sensitivity or obsessive–compulsive disorder (OCD) (Calder et al., 2007; Shapira et al., 2003).

Although the function of disgust may seem straightforward, coming up with an explanation that encompasses not just obvious cues of pathogen presence but also myriad other disgust elicitors has been the focus of some debate. One of the dominant paradigms has been the model of Rozin, Haidt, McCauley, and colleagues (Rozin & Fallon, 1987; Rozin, Haidt, & McCauley, 2008). Rozin et al. (2008) state that disgust begins its evolutionary trajectory as a distaste response focused on the mouth. Certainly there is evidence for this in the emotion-specific expression of disgust (Ekman & Friesen, 1971) (e.g., dropping the corners of the mouth) which plausibly imitate the facial movements of retching. This explains the so-called "core disgust," but for many other common disgust elicitors, Rozin and colleagues developed "animal reminder disgust," a domain that spans everything from corpses and wounds to sexual behavior (Rozin et al., 2008). Because (a) nonhuman animals do not have disgust or awareness of their own mortality and (b) humans have mortality in common with animals, Rozin and colleagues hypothesized that animal reminder disgust serves to manage the existential fear of one's own mortality ("Terror Management"). Terror management as an explanation for disgust sensitivity has been heavily critiqued from an adaptationist perspective (e.g., Fessler & Navarrete, 2005). Moreover, most things animals do are not disgusting: "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" (Tybur, Lieberman, Kurzban, & DeScioli, 2012, p. 2).

There is a now good deal of consensus that a central adaptive function of disgust is to reduce the risk of infection by distancing one from cues of the presence of pathogens (Curtis, Aunger, & Rabie, 2004; Fessler, Eng, & Navarrete, 2005; Laland & Brown, 2011; Oaten, Stevenson, & Case, 2009; Schaller & Duncan, 2007; Tybur et al., 2012), but disgust is obviously elicited by many other kinds of stimuli. Even if sensitivities to all domains of disgust are related, an adaptationist perspective suggests sex differences in specific domains.

Measures of Disgust Sensitivity

In order to understand how disgust has been studied and how different domains are defined, what follows is a short introduction on the common measures of disgust sensitivity.

Disgust Sensitivity Scale and Disgust Sensitivity Scale Revised

The Disgust Sensitivity (DS) scale was one of the first measures of disgust sensitivity widely used. It contains 32 items and specifies seven domains of disgust: food, animals, body products, sex, envelope violations, death, and hygiene. The DS was criticized and subsequently revised (Olatunji, Haidt, McKay, & David, 2008) creating the disgust scale revised (DS-R) which has fewer items and three factors, core disgust, animal reminder disgust, and contamination-based disgust, showing good validity and reliability (Van Overveld, De Jong, Peters, & Schouten, 2011). The DS scale is an outgrowth of the idea that disgust began as a response against oral incorporation and serves in part to distance oneself from reminders of mortality and animal nature.

Three Domains of Disgust Scale

A more recent scale developed divides disgust into three domains (Tybur, Lieberman, & Griskevicius, 2009) using a 21-item questionnaire. The three domains are pathogen disgust (regarding cues or contexts of disease that aren't sexual (e.g., stepping on dog poop)), sexual disgust (which motivates away from cues or context that could jeopardize reproductive success (e.g., hearing two strangers have sex)), and moral disgust (which facilitates coordinating judgment against norm violations (e.g., deceiving a friend)) (Tybur et al., 2012).

Image-Based Rating Systems

The disgust scales above require the respondent to read and imagine various disgusting scenarios. A potentially more ecologically valid way to measure disgust is through images or behavioral measures. One of the better-known image sets used to measure disgust was used by Curtis et al. (2004) and contains 19 images of varying disease salience (e.g., a bowl of blue viscous liquid compared to a bowl of yellow viscous liquid with red flecks). Images from the International Affective Picture System (Lang, Bradley, & Cuthbert, 1999) are also used to both elicit disgust and measure disgust sensitivity. Behavioral measures used to measure disgust sensitivity (e.g., (Borg & De Jong, 2012; Rozin, Haidt, McCauley, Dunlop, & Ashmore, 1999)) will be discussed more in detail below.

Measures of Disgust Facial Expression

Disgust has very specific muscular activity associated with it including gaping, retracting the upper lip, wrinkling the nose, and dropping the corners of the mouth (Ekman & Friesen, 1971). Disgust studies have used coders to rate the degree of disgust expressed facially (De Jong, Peters, & Vanderhallen, 2002); the most rigorous is the Facial Action Coding System (Ekman, Friesen, & Hager, 2002). Other studies use facial electromyography (fEMG) where electrodes sense movements in the face in response to stimuli (e.g., Borg, De Jong, & Schultz, 2010; De Jong et al., 2002).

Sex Differences in Disgust

One of the most consistent findings in the disgust literature is that women are more disgust-sensitive than men. Women score significantly higher in total on the DS-R (Olatunji et al., 2008, 2009) with the largest effects in core disgust (Olatunji, personal communication). Studies using the original DS found that women were more disgust-sensitive overall (Quigley, Sherman, & Sherman, 1997) and across all domains (Haidt, McCauley, & Rozin, 1994; Schienle, Stark, Walter, & Vaitl, 2003). Using the DS with seven domains, Haidt et al. (1994) found the largest sex differences in animal disgust (e.g., it would bother me to see a rat run across my path) and magic (e.g., a friend offers you a piece of chocolate shaped like dog-doo) and the smallest sex difference in the sex domain (e.g., I think homosexual activities are immoral). In contrast, the Three Domains of Disgust scale (TDD) has found that the largest and most consistent sex difference between men and women is in the sexual domain d (475), 1.44, as compared to pathogen d (475), 0.32, and moral domains d (475), 0.23 (Tybur, Bryan, Lieberman, Caldwell Hooper, & Merriman, 2011). Women are also more disgusted by pornography than men (Koukounas & McCabe, 1997). Relatedly, women are more disgusted by a thought experiment involving transplanting organs including genital transplant (Fessler & Haley, 2006).

The sex difference in pathogen disgust holds when using images and behavioral measures as well. Using 19 images and nearly 40,000 participants, Curtis et al. (2004) found women showed higher disgust scores on the seven specifically disease-salient images (e.g., oozing wound). Rozin et al. (1999) found that women were significantly less likely than men to engage fully with 26 tasks designed to elicit disgust (e.g., eating a piece of fudge in the shape of feces).

The contamination obsessions and washing compulsions that are commonly seen in OCD may be an overexpression of motivations and behaviors that have adaptively reduced the probability of infection. In nonclinical samples, women score higher than men on measures of OCD-related contamination fear (Mancini, Gragnani, & D'Olimpio, 2001; Mancini, Gragnani, Orazi, & Grazia Pietrangeli, 1999; Van Oppen, 1992). Estimates suggest that women tend to be more at risk for developing OCD (Weissman, Bland, Canino, & Greenwald, 1994). Specifically, OCD-related cleaning compulsions are more likely to develop in females (Zohar, 1999; Zohar & Bruno, 2006).

These sex differences in disgust sensitivity do not seem to manifest until puberty or young adulthood. One of the only studies investigating disgust sensitivity in children did not find significant gender differences. Using both parental reports of children's (mean age 7 years old) disgust reactions and behavioral tasks intended to elicit disgust in children, gender did not come out as a significant predictor (Stevenson, Oaten, Case, Repacholi, & Wagland, 2010). This implies that sex difference in disgust sensitivity takes some time to socialize or that these differences are related functionally and physiologically to reproduction and mating.

Why Are Women More Disgust-Sensitive Than Men?

For a variety of functional reasons, both for the protection of self and offspring, women may have had unique selection pressure for increased disgust sensitivity, especially with regard to sexually transmitted diseases, pathogen cues, and suboptimal mate choice.

Functional Reasons for Heightened Disgust in Women

With regard to danger to self and future reproductive success, women have a great deal more at stake when engaging in sexual behavior than men. The problem of avoiding sexually transmitted infections (STIs) is complicated in that these pathogens rely on their hosts to be chosen as mates. Therefore, sexually transmitted pathogens are under unique selection pressure to cryptically infect hosts, that is, to show few signs of infection that would cause them to be detectable (Tybur & Gangestad, 2011). Women have a greater area of mucous membranes and experience more tissue damage during intercourse than heterosexual men, making them more prone to STIs such as human immunodeficiency virus, human papilloma virus, and human herpesvirus (Madkan, Giancola, Sra, & Tyring, 2006). Women are more than three times as likely to contract chlamydia (Madkan et al., 2006). It is perhaps one explanation for why women high in sexual disgust as measured by the TDD are more avoidant of sex generally (Kurzban, Dukes, & Weeden, 2010).

When women contract STIs they suffer a much greater disease burden than men because of pelvic inflammatory disease (PID), an infection of the upper genital tract affecting the ovaries, uterus, and fallopian tubes. PID is uniquely possible because human female anatomy is such that pathogens can travel through the vagina and into the peritoneal cavity (Madkan et al., 2006). Of women with untreated chlamydia, 40 % will develop (PID) (Madkan et al., 2006). Of women with a single episode of PID, 8 % are rendered infertile; more rarely acute PID develops into a systemic infection (Madkan et al., 2006). STIs can also cause other long-term and systemic diseases; for instance previous gonorrhea infection can cause dermatitis and arthritis (Bleich, Sheffield, Wendel, Sigman, & Cunningham, 2012).

Women, compared to men, are unique in that they can pass disease on to their gestating or nursing offspring, having serious consequences including loss of considerable maternal investment. Babies born to mothers with chlamydia are at risk for pneumonia and eye infections which can result to blindness, and mothers can pass HIV on to offspring during childbirth or while nursing (Madkan et al., 2006). Due to women exclusively breastfeeding and a gender-based division of labor, in traditional hunter-gatherer societies, mothers and other female kin are those most involved in caring for infants and small children. Heightened female disgust sensitivity could also function to protect human infants and children who are highly altricial and vulnerable to disease (Curtis et al., 2004). Many of the diseases used as examples here may be quite recent in our evolutionary history (Diamond, 1999); however, the factors that contribute to greater vulnerability and more serious adaptive consequences in women compared to men have been selection pressures for millions of years.

Women have greater obligate parental investment than men (Trivers, 1996) making it possible for them to have, at most, two offspring in a year. Females are choosier with regard to mates than males (e.g., Clark & Hatfield, 1989). In addition to the more immediate costs of sex including infection, disease burden, and contagion to offspring, female strategy should guide women away from using one of their comparatively few reproductive opportunities on a genetically inferior male. It's unclear whether direct benefits (e.g., not contracting infections either sexually or being in close proximity to someone with an infection) or indirect benefits (i.e., choosing a mate who would produce offspring with less disease susceptibility) are responsible for women's preference for male traits. A treatment of female mate choice for markers of health and immunocompetence in males is beyond the scope of this chapter; however, an adaptationist perspective predicts disgust will augment female choosiness in mate selection. Baseline disgust sensitivity and pathogen priming have been shown to influence aspects of mate choice.

Pathogen disgust but not sexual disgust or moral disgust predicts women's preferences for masculinity in male faces, a putative marker of immunocompetence (DeBruine, Jones, Tybur, Lieberman, & Griskevicius, 2010). Debruine, Jones, Crawford, Welling, and Little (2010) found that a nation's health indicators predict women's preference for facial masculinity. Jones et al. (2008) conclude that preference for health in male faces is more pronounced during the luteal phase when immunocompetence is compromised, while preference for facial masculinity is highest during the ovulatory phase with the highest fertility (more on that later in the chapter). However, Little, DeBruine, and Jones (2011) found that after priming participants with pathogen cues, women showed greater preference for symmetry (another putative indicator of health) and facial masculinity.

Another reason women might show higher disgust sensitivity is because men may have experienced selection pressures to display a *lack* of disgust to cues of contamination. Secondary sexual characteristics such as facial masculinity, low voice pitch, and facial hair advertise high androgen levels, which may have immunosuppressive effects (Moore et al., 2011; Thornhill & Gangestad, 2006). It is hypothesized that these characteristics thus act as a costly signal; a male displaying both health and high androgen features signals to possible mates that he has a robust immune system. Because disgust acts to distance humans from cues of disease, males may also display their robust immunity by showing indifference toward common disgust elicitors or even make a show of their disgust insensitivity (e.g., fraternity induction involving eating vomit (Lohse, 2012)). Males may also display less disgust sensitivity as a by-product; men's greater propensity for risk taking in other domains may also manifest in the domain of disease avoidance (Fessler, Pillsworth, & Flamson, 2004).

The Original Omnivore's Dilemma

Other than sexual disgust there is also reason to believe that women should be more sensitive at the potential evolutionary origin of disgust, food selection. Humans, like other species that are nutrition generalists, face an "omnivore's dilemma"; there are a large number of foods that can be eaten but they differ in their nutritional quality and in the probability that they will contain dangerous pathogens:

> During the evolutionary transition in which our ancestors' brains expanded greatly, so did their production of tools and weapons, and so did their consumption of meat (Leakey, 1994)...But when early humans went for meat, including scavenging the carcasses left by other predators, they exposed themselves to a galaxy of new microbes and parasites, most of which are contagious- they spread by contact. (Haidt, 2006)

Meat, a principal source of foodborne illness, is also a source of potential teratogens, say agents that cause abnormal infant development like *Toxoplasma gondii*; meat is the subject of most food taboos and women may be predisposed to be disgusted by it (for a review see Fessler & Navarrete, 2003a). Four times as many women are vegetarians than men (Neumark-Sztainer, Story, Resnick, & Blum, 1997), and disgust sensitivity is higher in moral vegetarians than meat eaters (Fessler, Arguello, Mekdara, & Macias, 2003).

Women may also have higher disgust sensitivity overall because they go through periods of heightened sensitivity to disease both luteally (during the menstrual cycle) and during pregnancy.

Reproductive Cycle Effects on Disgust Modulation in Women

The Compensatory Behavioral Prophylaxis Hypothesis

Disgust has many possible adaptive effects. However, avoiding cues of contamination isn't always equally advantageous especially when sensing and identifying these cues can be cognitively taxing and ambiguous. Disease avoidant behavior motivated by disgust entails the costs of increased time and energy removed from other adaptive behaviors such as foraging and engaging socially. Hypervigilance in the disgust domain can be debilitating, as OCD aptly shows. Throughout deep time, women have experienced fluctuating vulnerability to infection as a consequence of specific hormonal shifts. The Compensatory Behavioral Prophylaxis Hypothesis or CBPH (Fessler et al., 2005) predicts that reactions to circumstances associated with the risk of pathogen transmission are predicted to vary in an adaptive manner, enhancing prophylactic behavior during times of elevated susceptibility.

Upregulated disgust sensitivity and attention to cues of possible disease in the face of immune vulnerability have been demonstrated in a handful of studies on both men and women. One way such vulnerability has been measured is with the Perceived Vulnerability to Disease scale (PVD) which has two main factors: "perceived infectability" (e.g., if an illness is "going around," I will get it) and germ aversion (Duncan, Schaller, & Park, 2009). Both factors correlate significantly with all three DS-R factors (Olatunji et al., 2008) with germ aversion correlating more highly than perceived infectability (Duncan et al., 2009).

Disease avoidance doesn't just manifest as disgust sensitivity toward pathogen cues but also spills into other domains of social processing. The smoke alarm principle (Nesse, 2005) or error management theory (Haselton & Buss, 2000) posits that given errors with different adaptive consequences, the more costly error will be minimized by skewing response toward the less costly error, in this case reacting with disgust at elements that do not connote contagious disease. Just as the immune system sometimes reacts against elements that are not pathogenic (e.g., dust allergy), so too can psychological mechanisms designed to avoid disease interpret benign cues as disgusting. In many contexts the psychology of disease avoidance seems calibrated in a sensitive way to minimize the number of false negatives and to overinterpret the likelihood of disease presence. For example, birthmarks and other facial irregularities which are not contagious elicit as much avoidance and disgust facial expression as influenza (Ryan, Oaten, Stevenson, & Case, 2012). Those who trigger disease avoidance and disgust may be rejected and stigmatized, and this might be especially likely when (a) there are other cues of disease presence or (b) when one is especially susceptible to infection. Miller and Maner (2011) found that those who had recently been ill and therefore were more susceptible to disease showed heightened attention and avoidance of disfigured individuals. Age and obesity, conditions that alter human morphology, may superficially mimic cues of disease. Stigma against the elderly and obese is associated positively with PVD (Miller & Maner, 2012; Schaller & Park, 2011).

Another aspect of psychology that is associated with disease avoidance and disgust is ethnocentrism and xenophobia. The full reasoning for this connection is beyond the scope of this chapter but some surmise that (a) it is because foreign and unfamiliar people have carried novel and thus potentially fatal diseases and engaged in practices (e.g., cooking, hygiene) that may not be as optimal for disease avoidance as those adopted by the local culture (Diamond, 1999; Schaller, Park, & Faulkner, 2003) and/or (b) foreigners and other out-group members are linguistically and culturally connected to disease (e.g., Jewish vermin) and thus cognitively associated with disease avoidance psychology (Faulkner, Schaller, Park, & Duncan, 2004; Navarette, Fessler, & Eng, 2007). Both disgust and PVD have been shown to positively associate with ethnocentrism (Navarrete & Fessler, 2006), and PVD as well as disease priming has been shown to increase measures of xenophobia (Schaller & Park, 2011).

Pregnancy Is a Dangerous Time Both for the Embryo and for the Mother

Women experience significant immunomodulation during the first trimester as well as fostering a developmentally sensitive embryo. Because the immune system is designed to recognize self from nonself, there is a danger that the maternal immune system will destroy the embryo that is made up of half-paternal genetic material. High progesterone levels stimulate progesterone-induced blocking factor (PIBF). PIBF stimulates the immune system to shift toward more anti-inflammatory immune components to tolerate the conceptus. At the same time a woman's immune functioning is compromised, the embryo is undergoing organogenesis and is most vulnerable to environmental insults: teratogens and infections (for a review see Fessler, 2002). As mentioned previously, food, especially meat, is a major vector for diseases including those with teratogenic effects. During the first trimester in particular, pregnant

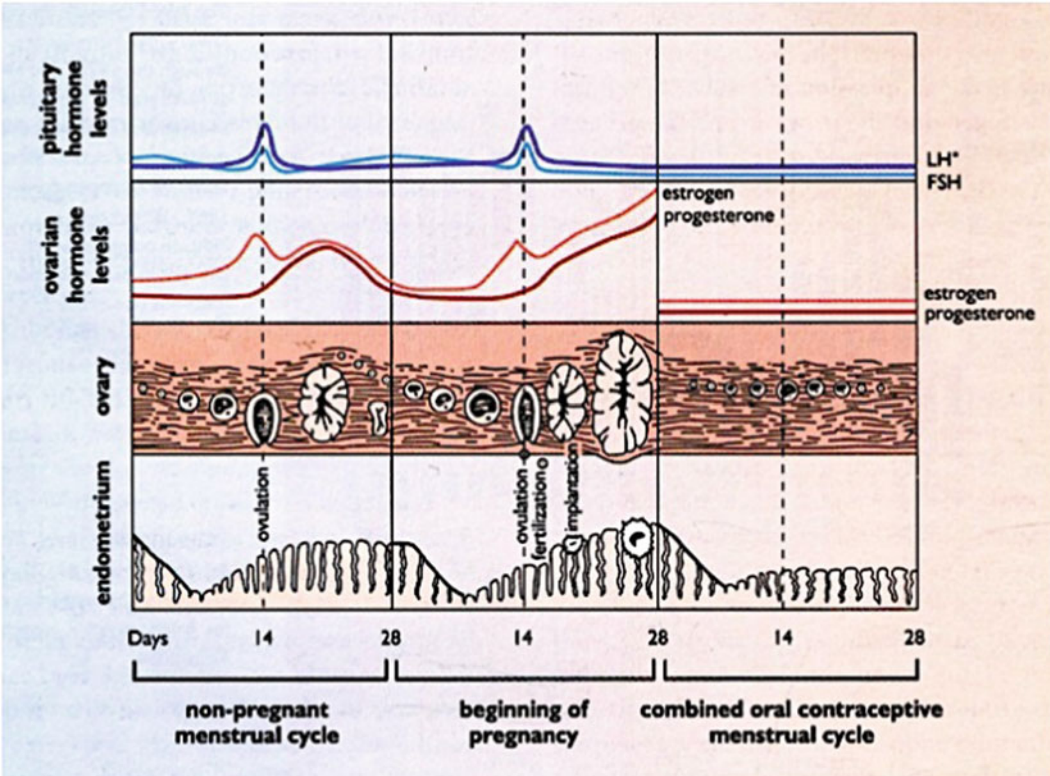


Fig. 15.1 Follicle-stimulating hormone, luteinizing hormone, estrogen, and progesterone in women in normally cycling women, pregnant women, and women on hormonal contraceptives. Taken from Drife (1996) The Benefits and Risks of Oral Contraceptives Today (1st ed.). Informa HealthCare

women often experience nausea and vomiting; these symptoms which may be elicited by smelling or eating specific foods are thought to compensate for vulnerability to infection and the sensitivity of the conceptus (Fessler, 2002; Flaxman & Sherman, 2000). Fessler et al. (2005) found elevated disgust sensitivity, primarily in the food domain of the DS (Haidt et al., 1994) in the first relative to second and third trimesters of pregnancy, a period of heightened vulnerability to infection. Navarette et al. (2007) found the same pattern with regard to hostility toward out-group members.

Progesterone, the Menstrual Cycle and Immunomodulation

The menstrual cycle consists of functionally distinct phases marked by characteristic variations in hormonal levels. Progesterone is also elevated in anticipation of pregnancy during the latter portion of the menstrual cycle. The highest levels of progesterone outside of pregnancy occur during the luteal phase, the period after the rupture of the ovarian follicle in which the corpus luteum secretes progesterone (Hatcher & Namnoum, 2004) (see Fig. 15.1). The body prepares for conception and implantation during the luteal phase by downregulating inflammatory responses. Inflammatory immunity is the first line of defense against foreign agents in the body and thus is less discerning and more likely to destroy an ambiguous entity (Clark, 2007). Luteal phase immunomodulation is hypothesized to be an adaptation much like the immunomodulation in early pregnancy that prevents the maternal immune system from attacking the conceptus, making it possible for implantation and development to occur. Heightened proneness to infection is the cost of this immune tolerance (Fessler, 2001).

The shift in inflammatory immune response during the luteal phase is evident in a variety of ways. Studies have shown that levels of proinflammatory cytokines decline, and natural killer cells are downregulated (Bouman, Moes, Heineman, De Leij, & Faas, 2001; Faas et al., 2000; Trzonkowski et al., 2001). It also appears that TH2 or anti-inflammatory immune response increases relative to the TH1 or inflammatory immune response during the luteal phase (Faas et al., 2000). Autoimmune diseases characterized by proinflammatory activity such as rheumatoid arthritis diminish luteally, while the opposite occurs with disorders such as lupus erythematosus associated with excess anti-inflammatory activity (Kozlowski et al., 2002). Consistent with the important defensive functions of inflammation, chronic infections worsen (Wilder, 2006) and response to vaccination is diminished (Kozlowski et al., 2002). Thus, the menstrual cycle offers a natural experiment for fluctuations in immune susceptibility.

Testing Disgust and the Psychology of Disease Avoidance in the Luteal Phase

Studies have tested how immunomodulation in the luteal phase effects the psychology of disease avoidance with a variety of measures including dietary intake, disgust sensitivity, preference for healthy faces, and hygiene concerns.

As mentioned previously, meat is a principal source of foodborne illness and frequently avoided during pregnancy (Fessler, 2002; Flaxman & Sherman, 2000). However, Fleischman and Fessler (2007) did not find a reduction in meat consumption in a repeated sample using daily food diaries. In a follow-up cross-sectional design study using progesterone salivary assays, Fleischman and Fessler (2009) also did not find that progesterone or luteal phase was associated with disgust at photographs of raw or cooked meat. It may be that evolved mechanisms are calibrated to express disgust at unfamiliar foods or foods that have previously been associated with illness rather than meat. Another possibility is that there has been no selection pressure to avoid meat during the (comparatively short) luteal phase given that incubation period of meat-borne illnesses can be days or weeks long (Bloom, 2002). Finally, cues like smell and taste may be better indicators of disease risk than visual cues in a food context.

Disgust sensitivity has been measured across the menstrual cycle. Using the DS (Haidt et al., 1994), Fessler and Navarrete (2003b) failed to find increases in disgust during the luteal phase. However, as discussed previously, the original DS had some shortcomings in terms of factor structure and may not have been a sensitive or ecologically valid enough instrument to detect effects. In contrast, using the disgust images from Curtis et al. (2004), two studies found an increase in disgust ratings. Fleischman and Fessler (2009) found an effect of cycle phase such that those women in the luteal phase showed significantly higher disgust reactivity than women in the follicular phase. Fleischman and Fessler (2011) found that progesterone is significantly correlated with disgust image ratings (Fig. 15.2).

Disgust facial expressions and facial quality may also be important cues in the psychology of disease avoidance. Looking at facial expressions, the direction of gaze may be important in perceiving these cues such that an averted gaze indicates a looming threat in the environment whereas a direct gaze may imply that *you* are the source of the facial expression. Conway et al. (2007) found that during the luteal phase, women experience others' facial expressions of both fear and disgust as more intense when they display averted as opposed to direct gaze. Although sensitivity to disgust facial expressions is predicted by the CBPH, sensitivity to fear expressions is not. However, it's possible that the same underlying psychological and physiological changes that make increased disgust sensitivity during the luteal phase possible also predispose women to be more sensitive to other negative emotions like fear. Disgust or aversion toward disease cues is one avenue toward disease avoidance, but preferences for cues of health

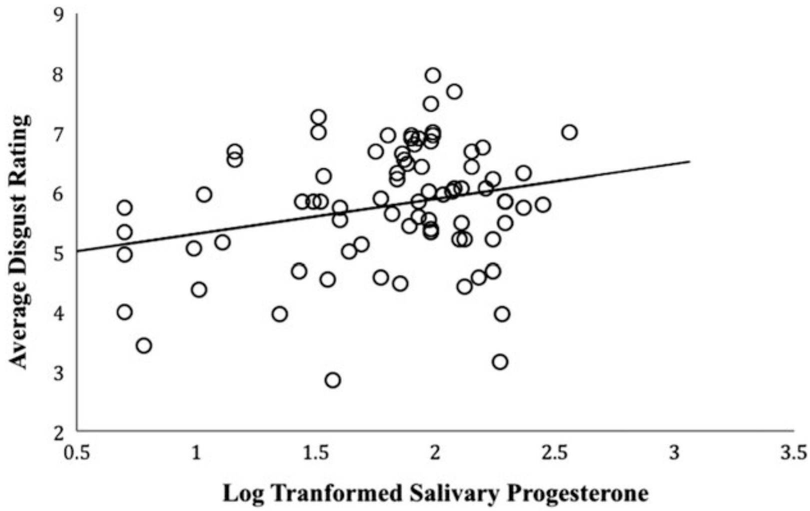


Fig. 15.2 Relationship between log-transformed salivary progesterone and self-reported disgust to photographic stimuli, $n = 97$. Adapted from Fleischman and Fessler (2011)

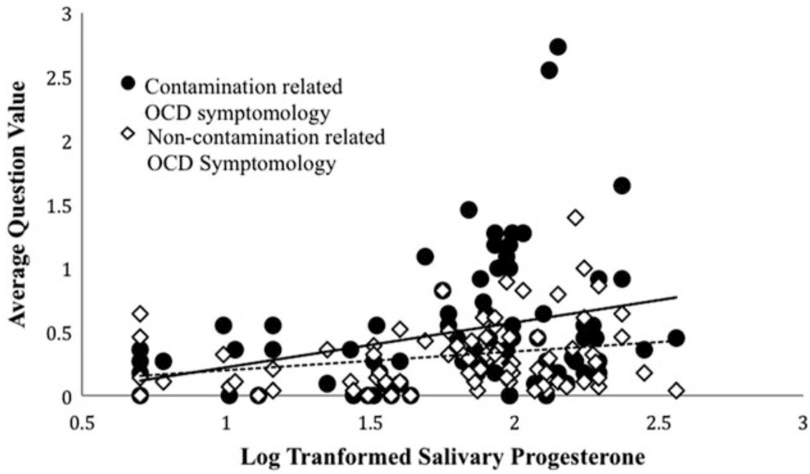
may also change as a function of immunomodulation. In six studies Jones et al. (2005) found increased preference for healthy over unhealthy faces in women who are in the high progesterone period (either estimated or measured directly).

As discussed above, the contamination obsessions and washing compulsions in OCD can be considered an overexpression of disease avoidance behaviors that are adaptive, and this domain of OCD is more frequently expressed in women (Bogetto, Venturello, Albert, Maina, & Ravizza, 1999). In women, OCD onset is also likely to follow significant reproductive milestones like menarche and pregnancy (Labad et al., 2005). Studies of clinical samples have shown that OCD symptoms are heightened during the luteal phase when progesterone is highest (Vulink, Denys, Bus, & Westenberg, 2006; Williams & Koran, 1997), and one study of a nonclinical samples has shown that women engage in more cleaning behavior during the luteal phase (Dillon & Brooks, 1992).

OCD symptomology also encompasses other obsessions and compulsions regarding checking and ritualistic behavior. However, the CBPH only predicts that those behaviors related to disease avoidance will be exacerbated by luteal immunomodulation. Modifying a self-report OCD symptomology scale (Burns, Keortge, Formea, & Sternberger, 1996) and administering to a nonclinical sample, Fleischman and Fessler (2011) tested the CBPH with contamination-related symptomology (e.g., "In the last 24 hours I've felt my hands were dirty when I touched money" and "In the last 24 hours if I touched something I thought was 'contaminated', I immediately had to wash or clean myself") and non-contamination-related symptomology (e.g., "In the last 24 hours before going to sleep, I've had to do certain things in a certain order" and "In the last 24 hours when I heard about a disaster, I've thought it was somehow my fault"). The study found that contamination-related OCD symptomology was significantly correlated with progesterone (Fig. 15.3) but non-contamination-related OCD symptomology was not significantly correlated with progesterone (Fessler & Fleischman, 2011). However, Fleischman and Fessler (2009) found that both aspects of OCD symptomology increased significantly during the luteal phase.

Evidence from Fleischman and Fessler (2011) and Conway et al. (2007) point to the luteal phase's association with not only disgust but also heightened sensitivity to fear and ruminations unrelated to contamination. Perhaps the cognitive readiness needed for sensitivity to disease cues is entangled with other types of fear and anxiety. The area of the brain that responds preferentially to disgust, the anterior insular cortex, is also stimulated by fear-inducing images (Stark et al., 2003). If disgust and fear share a common neurological system that would

Fig. 15.3 Relationship between log-transformed salivary progesterone and self-reported contamination-related and non-contamination-related OCD symptomology. The dashed line represents the trend line for non-contamination-related OCD symptomology



constrain the adaptive expression of one without the other.

Related to disease avoidance, in public restrooms, modern women encounter cues of contamination, and this context poses a problem both in terms of contamination fear and obsessive hand washing for those with OCD (Abramowitz, Braddock, & Moore, 2008). Fleischman and Fessler (2011) found that salivary progesterone in women was correlated with disease avoidance behaviors in public restrooms (e.g., "In the last 24 h, have you used a paper towel or anything else to open a bathroom door rather than touching it with your hands?" and "In the last 24 h, have you washed your hands two or more times in the bathroom?") in a nonclinical sample.

Another facet of disease avoidance that humans have in common with nonhuman animals is grooming and ectoparasite removal. When they feed on blood, organisms like ticks, lice, and flies bypass the skin barrier and transmit disease. Just as OCD may be an overexpression of adaptive disease avoidance, trichotillomania may be an overexpression of the prophylactic behavior of grooming, removing parasites, and preventing them from penetrating the body envelope wherein they can cause infection. Women with trichotillomania exhibit increased symptoms during the early stages of pregnancy and the luteal phase (Keuthen et al., 1997). Fleischman and Fessler (2011) found that self-grooming behavior (e.g., "In the last 24 h, have you picked at a scab?" and "In the last 24 h, have you picked at or around your eyes?") was correlated with salivary progesterone. This area of disease avoidance and behavior generally has hardly been explored in the literature.

Immunomodulation, Progesterone, and Exogenous Progestins

Combined hormonal contraceptives, so-called because they contain both synthetic estradiol and progesterone, inhibit the natural production of these hormones, essentially flatlining any menstrual cycle variability. The rise in progesterone that occurs after ovulation is mainly produced in the empty ovarian follicle (Hatcher & Namnoum, 2004), and because women on hormonal contraceptives don't ovulate, this rise in progesterone does not occur in pill-taking women. Studies have shown that the progesterone and estradiol of nonsmoking women is lower in pill-using women (Arnold, Tóth, & Faredin, 1980; Thorneycroft & Stone, 1972). However, there is some evidence that exogenous progestins, like their natural counterparts, lower inflammatory immune responses. The progestins found in commonly prescribed oral contraceptives have been shown to lessen the severity of the autoimmune disease, lupus (Buyon, 1996), and reduce natural killer cell numbers and cytotoxicity (Scanlan, Werner, Legg, & Laudenslager, 1995). Women on the pill report more gastrointestinal distress

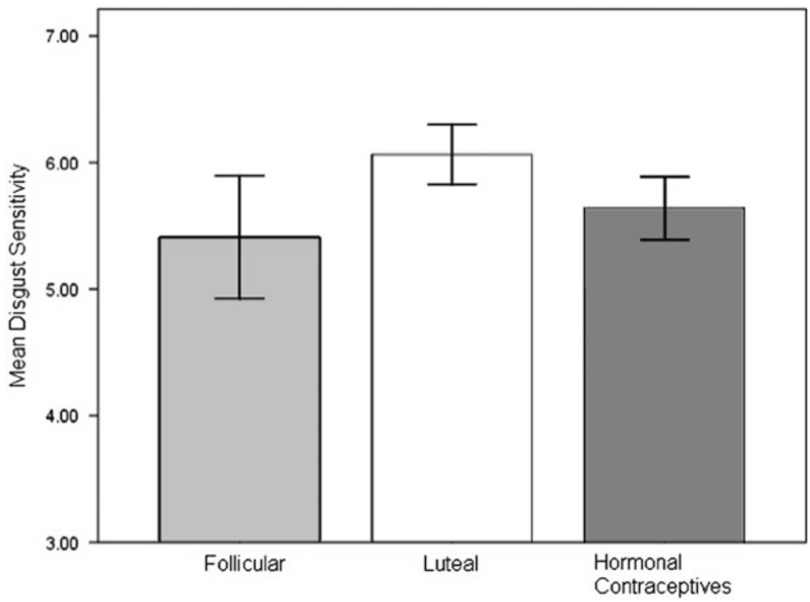


Fig. 15.4 Differences in disgust sensitivity between women in the follicular phase, women in the luteal phase, and women on hormonal contraceptives in response to images. Follicular $n = 25$, luteal $n = 40$, and hormonal contraceptive $n = 41$

and respiratory illness than nonusers (Auerbach, Hafner, Huber, & Panzer, 2002).

Previous research has shown that women using the pill offer a quasi-control group for research on hormonal and menstrual cycle effects on behavior, showing a lower frequency of hormonally mediated behaviors (Chavanne & Gallup, 1998; Miller, Tybur, & Jordan, 2007; Wedekind, Seebeck, Bettens, & Paepke, 1995). Fleischman and Fessler (2009) found that pill-using women showed significantly lower salivary progesterone than women in the luteal phase and that women on hormonal contraceptives showed no heightened disgust sensitivity or other disease avoidance behaviors relative to nonusers in the follicular or the luteal phase. The reason for this is unclear. Perhaps only endogenously produced progesterone acts as a proximate indicator of disease susceptibility, or the level of progesterone relative to estrogen may be the relevant proximate cue. Another possibility is that ovulation and heightened progesterone must occur in proximity with one another to cause the relevant increase in disgust sensitivity (Fig. 15.4).

Sexual Disgust and Ovulation

If one accepts that sexual disgust is a means toward the functional goal of avoiding contexts that jeopardize reproductive success, we should also see that the salience of sexual disgust elicitors varies across the menstrual cycle as a function of conception risk. One mating behavior significantly associated with disgust sensitivity is incest avoidance as inbreeding depression increases the likelihood of recessive alleles in offspring ultimately making it more likely that reproduction will be unsuccessful (e.g., miscarriage) or result in reduced fitness in resultant offspring. There have been no studies of disgust toward incest across the menstrual cycle; however, one study has shown that women are less likely to interact with their fathers around ovulation (Lieberman, Pillsworth, & Haselton, 2011). Fessler and Navarrete (2003a, 2003b) found that women were more likely to exhibit disgust in the sexual domain when fertile. Of the women's disgust adaptations thus far, this area is one in most need of further research especially in combination with biomarkers of high fertility (e.g., estrogen, luteinizing hormone).

Disgust and Sexual Arousal

Although humans generally avoid being in close proximity with disease cues; such avoidance is fundamentally incompatible with engaging in sexual behavior. Reproductive success is the currency of fitness, yet sex involves extensive exposure to stimuli that indicate disease risk. Sexual behavior entails increased contact with disease cues but also increased vulnerability to disease. The direct exchange of body fluids and exposure of mucous membranes—along with abrasion associated with the friction of intercourse—present an entry possibility for pathogenic microorganisms. Moreover, close proximity and fast breathing increase the risk of contracting airborne pathogens from a sexual partner or surrounding environment. In line with the possible disease risk of sexual behavior, one study in men has shown an increase in lymphocytes in sexually aroused men (Haake et al., 2004).

Secretions and odors frequently encountered in sexual contexts are strong disgust elicitors (Rozin & Fallon, 1987). However, intuitively it seems that disgust is not an integral part of normal sexual activity. If stimuli are found disgusting outside of a sexual context but not in one, does sexual arousal have the evolved function of dispelling the emotion of disgust?

How Sexual Arousal Influences Disgust Reactions

Two studies with male samples have looked at how sexual arousal influences disgust. Ariely and Loewenstein (2006) found that men who were exposed to photos of naked women compared to those men who viewed photos of clothed women were significantly more likely to state they would engage in a variety of potentially disgusting sexual acts such as having sexual contact with an animal, having anal sex, or watching a woman urinating. Stevenson, Case, and Oaten (2011) investigated the hypothesis that sexual arousal would specifically influence disgust at sexually relevant disgust cues. Stevenson et al. (2011) used three modalities (aural, visual, and tactile) of disgust stimuli with one sex-related stimulus (e.g., feeling lubricated condoms in a bowl, looking at a picture of a woman's torso with a large scar) and one non-sex-related stimulus presented in each modality (e.g., feeling cold ham and pea soup, looking at a picture of a polluted landscape). Men who had viewed sexually arousing images versus other images (e.g., positive arousal such as images of skydiving) showed reduced disgust reactions in the sexual domain, but arousal had no effect on disgust reactions to nonsexual stimuli (Stevenson et al., 2011).

The ultimate adaptive function of sexual arousal, achieving reproductive success, is the same for men as it is for women and similarly for women can only happen in contexts with intimate contact with pathogen cues. On the other hand, as explained above, women are uniquely vulnerable to infection during coitus, and thus, sexual arousal may not have the same dampening effect on disgust sensitivity in women as in men. Two studies have looked at how women respond to disgust when sexually aroused. Borg and De Jong (2012) split women into one of three mood induction groups: positive arousal, negative arousal, and sexual arousal. Women watched a mood induction video and intermittently "completed" disgust tasks (rather than doing the task participants could choose to imagine how disgusted they would be to engage with the task). They found that there was a significant main effect of group on approach and completion of the tasks such that the sexual arousal group conducted significantly more tasks than either the positive arousal or the neutral control groups. Women in the sexual arousal condition compared to women in the positive arousal and negative arousal conditions reported less disgust at the sexually disgusting tasks (e.g., lubricating a vibrator, handling a pair of stained underwear). Borg and De Jong (2012) also found those in the sexual arousal group compared to the neutral group found nonsexual disgust tasks (e.g., inserting a pin into a cow eyeball) less disgusting.

Fleischman, Hamilton, Fessler, and Meston (2014) investigated the effect of sexual arousal on disgust sensitivity by dividing women into four groups: neutral film → erotic film → rate disgust images; neutral film → rate disgust images → erotic film; neutral film → rate fear images → erotic film; neutral film → erotic film → rate fear images. None of the disgust or fear images were sexual in nature. All women were between day 5 and 10 of the menstrual cycle in order to homogenize any menstrual cycle effects. Genital arousal in response to the erotic films was measured using a vaginal photoplethysmograph (Sintchak & Geer, 1975) which measures vaginal engorgement controlling for heartbeat, producing a measurement, vaginal pulse amplitude (VPA). The relevant dependent variable in Fleischman et al. (n.d.) is percent change, that is, the percentage change in VPA from the neutral film to the erotic film.

At the time when this chapter was written data were still being collected. Fleischman et al. (n.d.) did not find that women in the sexual arousal condition (neutral film → erotic film → rate disgust images) showed lower disgust reactivity than women in the other conditions or that the intensity of sexual arousal had any direct effect on disgust reactivity. However, Fleischman et al. (n.d.) did find that the interaction of sexual arousal and a baseline measure of disgust *sensitivity* taken before the experimental protocol began (a subset of the paper and pencil pathogen sensitivity factor from (Tybur et al., 2009)) was the significant predictor of disgust ratings. In this study, women high in disgust sensitivity show a positive association between sexual arousal and disgust reactivity such that increase in sexual arousal causes an increase in disgust ratings, while women who are low in disgust sensitivity show a more similar pattern to studies of sexual arousal's effect on disgust in male participants (e.g., Ariely & Loewenstein, 2006; Stevenson et al., 2011), that is, reduced disgust ratings in response to heightened sexual arousal. In other words, disgust-sensitive women become more disgusted when aroused and less disgust-sensitive women become less disgusted when aroused. There was no effect of self-reported sexual arousal on any measures.

This result is intriguing in light of compensatory behavioral prophylaxis. If low baseline disgust sensitivity is indicative of robust immunity, perhaps the system is calibrated such that those who can afford exposure to disease cues during sexual arousal show decreased disgust reactivity and those that cannot show the opposite effect. The stimuli used in Fleischman et al. (2014) were also very rich in pathogen cues (images included corpses, people vomiting, and feces) indicating that individual differences can fundamentally change the way disease-salient disgust stimuli is processed in the presence of competing motivational states. Further research must disentangle sex differences in sexual disgust. Stevenson et al. (2011) did not find decreased disgust sensitivity in aroused male participants to one image without pathogen salience (the stimuli was of a river covered in garbage). Further research should determine whether men, who tend to have lower disgust sensitivity, show the same reduction in disgust reactivity to pathogen cues overall as those women with low disgust sensitivity.

How Disgust Influences Sexual Arousal

The presence of disgust elicitors or the emotion of disgust may indicate that an unpropitious mating is more likely thus reducing the motivation, through sexual arousal, to mate. Clinically, disgust has been shown to have important effects on women's sexual functioning. Women diagnosed with vaginismus (a condition in which vaginal spasms make intercourse difficult or impossible) were found to have greater overall disgust sensitivity as measured by the DS (Haidt et al., 1994) than women with dyspareunia (genital pain related to intercourse) and women without sexual complaints (De Jong, Van Overveld, Weijmar Schultz, Peters, & Buwalda, 2009). Unexpectedly, this study showed no differences between groups on ratings from the Sexual Disgust Questionnaire (e.g., "To what extent are you willing to lie beneath bedclothes in a hotel that look unwashed, and below which previous guests may have had sexual intercourse?") (De Jong et al., 2009). However, a follow-up study found both women with vaginismus and dyspareunia showed greater implicit disgust associations to sexual stimuli, and that women with vaginismus showed greater facial muscle activation reflecting disgust when viewing an erotic film (Borg et al., 2010).

Although the clinical implications of heightened disgust sensitivity have been explored, how disgust influences sexual arousal has not been tested extensively. Some previous studies have explored how disgust within a sexual context influences reported arousal. Women who report more disgust at erotica also report less sexual arousal (Koukounas & McCabe, 1997). Malamuth and Check (1980) found that males who read vignettes of sexual encounters found those in which the woman was described as disgusted as less sexually arousing. Vonderheide and Mosher (1988) found the more disgust women reported when imagining inserting a contraceptive diaphragm, the less arousal they report at imagining a subsequent sexual interaction, but have evidence this reflects underlying negative attitudes about sexuality. One study is unique in that it tested participants' sexual decision-making after disgust was elicited. Participants exposed to the smell of feces reported greater propensity to wear a condom than controls (Tybur, Bryan, Magnan, & Hooper, 2011).

In the same study described more in detail above, Fleischman et al. (n.d.) induced disgust by having participants rate 18 disgusting images before viewing an erotic video. The study found that those in the disgust before erotic condition showed lower sexual arousal (as gauged with VPA) than women in the other conditions. Moreover, disgust had a linear effect on sexual arousal. There was a strong direct correlation between the strength of disgust ratings and the decrease in subsequent sexual arousal. Disgust, here elicited by extreme cues of pathogen presence, seems well designed to dampen sexual arousal and prevent the motivation to engage in a dangerous or unpropitious mating.

Disgust has been implicated in asexuality (Carrigan, 2011), sexual aversion (Carnes, 1998), and hypoactive sexual desire (Brauer et al., 2012) as well as vaginismus and dyspareunia (Borg et al., 2010; De Jong et al., 2009). Although Fleischman et al. (n.d.) cannot speak to how long the effects of disgust on dampened sexual arousal will last, it is clinically relevant to consider the greater risks of mating for women over evolutionary time when considering female sexual disorders. From an evolutionary perspective, aversion toward sexual contact, especially in the face of cues and contexts of possible disease presence, would no doubt have been adaptive. Moreover, the adaptive payoff of sexual activity is likely part of the information processing. The previous study only involved women between day 5 and 10 of the menstrual cycle; however, hormonal effects on the reciprocal interaction of disgust and sexual arousal in women would be a fruitful new avenue for research.

Conclusions and Future Directions

The study of disgust is still in its infancy in many ways. One of the most intriguing ideas to come out of the disgust literature recently is the idea that the immune system and the disgust system are proximately integrated in some way. As mentioned previously, recently ill participants show enhanced attention to disease cues (S. Miller & Maner, 2011). Schaller, Miller, Gervais, Yager, and Chen (2010) found that mere exposure to pathogen cues increased cytokine circulation in the blood. Men and women have experienced different selection pressures with regard to pathogens and the costs and benefits of disease avoidance. Further work should be conducted using immune markers to investigate men and women's different response to disease cues. Finally, pathogens may alter sexual disgust. Dawkins (2006) speculated that sexually transmitted diseases might increase the libido of their hosts. Certainly it could also be in sexually transmitted pathogens' best interest to decrease the sexual disgust of their hosts.

References

Abramowitz, J. S., Braddock, A. E., & Moore, E. L. (2008). Psychological treatment of obsessive-compulsive disorder. In M. M. Antony & M. B. Stein (Eds.), *Oxford handbook of anxiety and related disorders: Oxford library of psychology* (pp. 391–404). New York: Oxford University Press. Retrieved from http://books.google.co.uk/books?hl=en&lr=&id=DKDDqOw6Y7wC&oi=fnd&pg=PA391&dq=abramowitz+oxford+handbook+of+anxiety+moore&ots=oRvJSWntb1&sig=5FLIdu7DCdgIeTjz6woHUHty2eE#v=onepage&q=abramowitz%20oxford%20handbook%20of%20anxiety%20moore&f=false

Angyal, A. (1941). Disgust and related aversions. *The Journal of Abnormal and Social Psychology, 36*(3), 393.

Ariely, D., & Loewenstein, G. (2006). The heat of the moment: The effect of sexual arousal on sexual decision making. *Journal of Behavioral Decision Making, 19*(2), 87–98.

Arnold, M., Tóth, I., & Faredin, I. (1980). Radioimmunological study of the effect of hormonal contraceptives upon the progesterone level of saliva (author's transl). *Zahn-, Mund-, und Kieferheilkunde mit Zentralblatt, 68*(7), 713.

Auerbach, L., Hafner, T., Huber, J. C., & Panzer, S. (2002). Influence of low-dose oral contraception on peripheral blood lymphocyte subsets at particular phases of the hormonal cycle. *Fertility and Sterility, 78*(1), 83–89.

Bleich, A. T., Sheffield, J. S., Wendel, G. D., Sigman, A., & Cunningham, F. G. (2012). Disseminated gonococcal infection in women. *Obstetrics & Gynecology, 119*(3), 597–602. doi:10.1097/AOG.0b013e318244eda9.

Bloom, S. (2002). *Practical gastroenterology: A comprehensive guide*. London: Martin Dunitz.

Bogetto, F., Venturello, S., Albert, U., Maina, G., & Ravizza, L. (1999). Gender-related clinical differences in obsessive-compulsive disorder. *European Psychiatry, 14*(8), 434–441.

Borg, C., & De Jong, P. J. (2012). Feelings of disgust and disgust-induced avoidance weaken following induced sexual arousal in women. *PLoS One, 7*(9), e44111.

Borg, C., De Jong, P. J., & Schultz, W. W. (2010). Vaginismus and dyspareunia: Automatic vs. deliberate disgust responsivity. *The Journal of Sexual Medicine, 7*(6), 2149–2157. doi:10.1111/j.1743-6109.2010.01800.x.

Bouman, A., Moes, H., Heineman, M. J., De Leij, L., & Faas, M. (2001). The immune response during the luteal phase of the ovarian cycle: Increasing sensitivity of human monocytes to endotoxin. *Fertility and Sterility, 76*(3), 555–559.

Brauer, M., van Leeuwen, M., Janssen, E., Newhouse, S. K., Heiman, J. R., & Laan, E. (2012). Attentional and affective processing of sexual stimuli in women with hypoactive sexual desire disorder. *Archives of Sexual Behavior, 41*(4), 891–905. doi:10.1007/s10508-011-9820-7.

Burns, G. L., Keortge, S. G., Formea, G. M., & Sternberger, L. G. (1996). Revision of the Padua Inventory of obsessive compulsive disorder symptoms: Distinctions between worry, obsessions, and compulsions. *Behaviour Research and Therapy, 34*(2), 163–173.

Buyon, J. P. (1996). Oral contraceptives in women with systemic lupus erythematosus. In *Annales De Médecine Interne* (Vol. 147, pp. 259–264). Retrieved from http://cat.inist.fr/?aModele=afficheN&cpsidt=3233753

Calder, A. J., Beaver, J. D., Davis, M. H., Van Ditzhuijzen, J., Keane, J., & Lawrence, A. D. (2007). Disgust sensitivity predicts the insula and pallidal response to pictures of disgusting foods. *European Journal of Neuroscience, 25*(11), 3422–3428. doi:10.1111/j.1460-9568.2007.05604.x.

Carnes, P. J. (1998). The case for sexual anorexia: An interim report on 144 patients with sexual disorders. *Sexual Addiction & Compulsivity, 5*(4), 293–309. doi:10.1080/10720169808402338.

Carrigan, M. (2011). There's more to life than sex? Difference and commonality within the asexual community. *Sexualities, 14*(4), 462–478. doi:10.1177/1363460711406462.

Chavanne, T. J., & Gallup, G. G. J. (1998). Variations in risk taking behavior among female college students as a function of the menstrual cycle. *Evolution and Human Behavior, 19*(1), 27–32. doi:10.1016/S1090-5138(98)00016-6.

Clark, W. R. (2007). *In defense of self: How the immune system really works in managing health and disease*. Oxford, USA: Oxford University Press.

Clark, R. D., & Hatfield, E. (1989). Gender differences in receptivity to sexual offers. *Journal of Psychology & Human Sexuality, 2*(1), 39–55.

Conway, C. A., Jones, B. C., DeBruine, L. M., Welling, L. L. M., Law Smith, M. J., Perrett, D. I., et al. (2007). Salience of emotional displays of danger and contagion in faces is enhanced when progesterone levels are raised. *Hormones and Behavior, 51*(2), 202–206.

Curtis, V., Aunger, R., & Rabie, T. (2004). Evidence that disgust evolved to protect from risk of disease. *Proceedings: Biological Sciences, 271*, 131–133.

Darwin, C. (1872/1965). *The expression of the emotions in man and animals*. London, UK: John Murray.

Dawkins, R. (2006). *The selfish gene*. New York: Oxford University Press.

De Jong, P. J., Peters, M., & Vanderhallen, I. (2002). Disgust and disgust sensitivity in spider phobia: Facial EMG in response to spider and oral disgust imagery. *Journal of Anxiety Disorders, 16*(5), 477–493. doi:10.1016/S0887-6185(02)00167-6.

De Jong, P. J., Van Overveld, M., Weijmar Schultz, W., Peters, M. L., & Buwalda, F. M. (2009). Disgust and contamination sensitivity in vaginismus and dyspareunia. *Archives of Sexual Behavior, 38*(2), 244–252.

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 by moral or sexual disgust. *Evolution and Human Behavior, 31*(1), 69–74.

DeBruine, L. M., Jones, B. C., Crawford, J. R., Welling, L. L. M., & Little, A. C. (2010). The health of a nation predicts their mate preferences: cross-cultural variation in women's preferences for masculinized male faces. *Proceedings of the Royal Society B: Biological Sciences, 277*(1692), 2405–2410. doi:10.1098/rspb.2009.2184.

Diamond, J. (1999). *Guns, steel and germs: The fate of human societies*. New York: WW Norton.

Dillon, K. M., & Brooks, D. (1992). Unusual cleaning behavior in the luteal phase. *Psychological Reports, 70*(1), 35.

Drife, J. O. (1996). *The benefits and risks of oral contraceptives today* (1st ed.). London: Informa HealthCare.

Duncan, L. A., Schaller, M., & Park, J. H. (2009). Perceived vulnerability to disease: Development and validation of a 15-item self-report instrument. *Personality and Individual Differences, 47*(6), 541–546.

Ekman, P., & Friesen, W. V. (1971). Constants across cultures in the face and emotion. *Journal of Personality and Social Psychology, 17*(2), 124.

Ekman, P., Friesen, W. V., & Hager, J. C. (2002). Facial action coding system. *A Human Face*. Retrieved from http://library.wur.nl/WebQuery/clc/1810828

Faas, M., Bouman, A., Moesa, H., Heineman, M. J., De Leij, L., & Schuiling, G. (2000). The immune response during the luteal phase of the ovarian cycle: A Th2-type response? *Fertility and Sterility, 74*(5), 1008–1013.

Faulkner, J., Schaller, M., Park, J. H., & Duncan, L. A. (2004). Evolved disease-avoidance mechanisms and contemporary xenophobic attitudes. *Group Processes & Intergroup Relations, 7*(4), 333–353. doi:10.1177/1368430204046142.

Fessler, D. M. (2001). Luteal phase immunosuppression and meat eating. *Rivista di Biologia Biology Forum, 94*(3), 403–426.

Fessler, D. M. T. (2002). Reproductive immunosuppression and diet. An evolutionary perspective on pregnancy sickness and meat consumption. *Current Anthropology, 43*(1), 19–61.

Fessler, D. M. T., Arguello, A. P., Mekdara, J. M., & Macias, R. (2003). Disgust sensitivity and meat consumption: A test of an emotivist account of moral vegetarianism. *Appetite, 41*(1), 31–41.

Fessler, D. M. T., Eng, S. J., & Navarrete, C. D. (2005). Elevated disgust sensitivity in the first trimester of pregnancy: Evidence supporting the compensatory prophylaxis hypothesis. *Evolution and Human Behavior, 26*(4), 344–351.

Fessler, D. M. T., & Fleischman, D. S. (2011). Progesterone's effects on the psychology of disease avoidance: Support for the compensatory behavioral prophylaxis hypothesis. *Hormones and Behavior, 59*(2), 271–275.

Fessler, D. M. T., & Haley, K. (2006). Guarding the perimeter: The outside-inside dichotomy in disgust and bodily experience. *Cognition & Emotion, 20*(1), 3–19. doi:10.1080/02699930500215181.

Fessler, D. M. T., & Navarrete, C. D. (2003a). 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), 1–40. doi:10.1163/156853703321598563.

Fessler, D. M. T., & Navarrete, C. D. (2003b). Domain-specific variation in disgust sensitivity across the menstrual cycle. *Evolution and Human Behavior, 24*(6), 406–417. doi:10.1016/S1090-5138(03)00054-0.

Fessler, D. M. T., & Navarrete, C. D. (2005). The effect of age on death disgust: Challenges to terror management perspectives. *Evolutionary Psychology*. Retrieved from http://psycnet.apa.org/psycinfo/2006-23138-019

Fessler, D. M. T., Pillsworth, E. G., & Flamson, T. J. (2004). Angry men and disgusted women: An evolutionary approach to the influence of emotions on risk taking. *Organizational Behavior and Human Decision Processes, 95*(1), 107–123.

Flaxman, S. M., & Sherman, P. W. (2000). Morning sickness: A mechanism for protecting mother and embryo. *Quarterly Review of Biology, 75*(2), 113–148.

Fleischman, D. S., & Fessler, D. M. T. (2007). Differences in dietary intake as a function of sexual activity and hormonal contraception. *Evolutionary Psychology, 5*(1), 642–652.

Fleischman, D. S., & Fessler, D. M. T. (2009). *Progesterone effects on women's psychology: Support for the compensatory prophylaxis hypothesis*. Paper presented at the 21st Annual Human Behavior and Evolution Society Conference, Fullerton, CA.

Fleischman, D. S., Hamiltion, L. D., Fessler, D. M. T., & Meston, C. (2014). *Disgust versus lust: Exploring the reciprocal interaction of disgust and fear on sexual arousal in women*. Manuscript submitted for publication.

Haake, P., Krueger, T. H. C., Goebel, M. U., Heberling, K. M., Hartmann, U., & Schedlowski, M. (2004). Effects of sexual arousal on lymphocyte subset circulation and cytokine production in man. *Neuroimmunomodulation, 11*(5), 293–298.

Haidt, J. (2006). *The happiness hypothesis*. New York: Basic Books.

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*(5), 701–713.

Hart, B. L. (1990). Behavioral adaptations to pathogens and parasites: Five strategies. *Neuroscience & Biobehavioral Reviews, 14*(3), 273–294.

Haselton, M. G., & Buss, D. M. (2000). Error management theory: A new perspective on biases in cross-sex mind reading. *Journal of Personality and Social Psychology, 78*(1), 81.

Hatcher, R. A., & Namnoum, A. B. (2004). The menstrual cycle. *Contraceptive Technology, 18*, 63–72.

Jones, B. C., DeBruine, L. M., Perrett, D. I., Little, A. C., Feinberg, D. R., & Law Smith, M. J. (2008). Effects of menstrual cycle phase on face preferences. *Archives of Sexual Behavior, 37*(1), 78–84.

Jones, B. C., Perrett, D. I., Little, A. C., Boothroyd, L., Cornwell, R. E., Feinberg, D. R., et al. (2005). Menstrual cycle, pregnancy and oral contraceptive use alter attraction to apparent health in faces. *Proceedings of the Royal Society B: Biological Sciences, 272*(1561), 347.

Kelly, D. (2011). *Yuck!: The nature and moral significance of disgust*. MIT Press. Retrieved from http://books.google.co.uk/books?hl=en&lr=&id=j-VGSQPE40oC&oi=fnd&pg=PP1&dq=yuck+kelly&ots=WdzpPXPAKr&sig=S-z80IvvuMRnrgOnijDb0BD9vKM

Keuthen, N. J., O'Sullivan, R. L., Hayday, C. F., Peets, K. E., Jenike, M. A., & Baer, L. (1997). The relationship of menstrual cycle and pregnancy to compulsive hairpulling. *Psychotherapy and Psychosomatics, 66*(1), 33–37.

Koukounas, E., & McCabe, M. (1997). Sexual and emotional variables influencing sexual response to erotica. *Behaviour Research and Therapy*. Retrieved from http://psycnet.apa.org/psycinfo/1997-08057-005

Kozlowski, P. A., Williams, S. B., Lynch, R. M., Flanigan, T. P., Patterson, R. R., Cu-Uvin, S., et al. (2002). Differential induction of mucosal and systemic antibody responses in women after nasal, rectal, or vaginal immunization: Influence of the menstrual cycle. *Journal of Immunology (Baltimore, Md.: 1950), 169*(1), 566–574.

Kurzban, R., Dukes, A., & Weeden, J. (2010). Sex, drugs and moral goals: Reproductive strategies and views about recreational drugs. *Proceedings of the Royal Society B: Biological Sciences, 277*(1699), 3501–3508.

Labad, J., Menchon, J. M., Alonso, P., Segalạs, C., Jimenez, S., & Vallejo, J. (2005). Female reproductive cycle and obsessive-compulsive disorder. *The Journal of Clinical Psychiatry, 66*(4), 428.

Laland, K. N., & Brown, G. R. (2011). *Sense and nonsense: Evolutionary perspectives on human behaviour*. Oxford: Oxford University Press.

Lang, P. J., Bradley, M. M., & Cuthbert, B. N. (1999). *International affective picture system (IAPS): Instruction manual and affective ratings*. Gainesville, FL: The Center for Research in Psychophysiology, University of Florida.

Leakey, R. (1994). *The origin of humankind*. London: Weidenfeld and Nicolson.

Lieberman, D., Pillsworth, E. G., & Haselton, M. G. (2011). Kin affiliation across the ovulatory cycle females avoid fathers when fertile. *Psychological Science, 22*(1), 13–18.

Little, A. C., DeBruine, L. M., & Jones, B. C. (2011). Exposure to visual cues of pathogen contagion changes preferences for masculinity and symmetry in opposite-sex faces. *Proceedings of the Royal Society B: Biological Sciences, 278*(1714), 2032–2039.

Lochmiller, R. L., & Deerenberg, C. (2000). Trade-offs in evolutionary immunology: Just what is the cost of immunity? *Oikos, 88*(1), 87–98.

Lohse, A. (2012, January 25). Lohse: Telling the truth. *The Dartmouth*. Retrieved from http://thedartmouth.com/2012/01/25/opinion/lohse

Madkan, V. K., Giancola, A. A., Sra, K. K., & Tyring, S. K. (2006). Sex differences in the transmission, prevention, and disease manifestations of sexually transmitted diseases. *Archives of Dermatology, 142*(3), 365.

Malamuth, N. M., & Check, J. V. (1980). Sexual arousal to rape and consenting depictions: The importance of the woman's arousal. *Journal of Abnormal Psychology, 89*(6), 763.

Mancini, F., Gragnani, A., & D'Olimpio, F. (2001). The connection between disgust and obsessions and compulsions in a non-clinical sample. *Personality and Individual Differences, 31*(7), 1173–1180.

Mancini, F., Gragnani, A., Orazi, F., & Grazia Pietrangeli, M. (1999). Obsessions and compulsions: Normative data on the Padua Inventory from an Italian non-clinical adolescent sample. *Behaviour Research and Therapy, 37*(10), 919–925.

Miller, S. L., & Maner, J. K. (2011). Sick body, vigilant mind the biological immune system activates the behavioral immune system. *Psychological Science, 22*(12), 1467–1471.

Miller, S. L., & Maner, J. K. (2012). Overperceiving disease cues: The basic cognition of the behavioral immune system. *Journal of Personality and Social Psychology, 102*(6), 1198.

Miller, G., Tybur, J. M., & Jordan, B. D. (2007). Ovulatory cycle effects on tip earnings by lap dancers: Economic evidence for human estrus? *Evolution and Human Behavior, 28*(6), 375–381.

Moore, F. R., Cornwell, R. E., Smith, M. J. L., Al Dujaili, E. A. S., Sharp, M., & Perrett, D. I. (2011). Evidence for the stress-linked immunocompetence handicap hypothesis in human male faces. *Proceedings of the Royal Society B: Biological Sciences, 278*(1706), 774–780.

Navarette, C. D., Fessler, D. M. T., & Eng, S. J. (2007). Elevated ethnocentrism in the first trimester of pregnancy. *Evolution and Human Behavior, 28*(1), 60–65. doi:10.1016/j.evolhumbehav.2006.06.002.

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*(4), 270–282. doi:10.1016/j.evolhumbehav.2005.12.001.

Nesse, R. M. (2005). Natural selection and the regulation of defenses: A signal detection analysis of the smoke detector principle. *Evolution and Human Behavior, 26*(1), 88–105.

Neumark-Sztainer, D., Story, M., Resnick, M. D., & Blum, R. W. (1997). Adolescent vegetarians: A behavioral profile of a school-based population in Minnesota. *Archives of Pediatrics and Adolescent Medicine, 151*(8), 833.

Oaten, M., Stevenson, R. J., & Case, T. I. (2009). Disgust as a disease-avoidance mechanism. *Psychological Bulletin, 135*(2), 303.

Olatunji, B. O., Haidt, J., McKay, D., & David, B. (2008). Core, animal reminder, and contamination disgust: Three kinds of disgust with distinct personality, behavioral, physiological, and clinical correlates. *Journal of Research in Personality, 42*(5), 1243–1259.

Olatunji, B. O., Moretz, M. W., McKay, D., Bjorklund, F., De Jong, P. J., Haidt, J., et al. (2009). Confirming the three-factor structure of the Disgust Scale—Revised in eight countries. *Journal of Cross-Cultural Psychology, 40*(2), 234–255.

Quigley, J. F., Sherman, M. F., & Sherman, N. C. (1997). Personality disorder symptoms, gender, and age as predictors of adolescent disgust sensitivity. *Personality and Individual Differences, 22*(5), 661–667. doi:10.1016/S0191-8869(96)00255-3.

Rohrmann, S., & Hopp, H. (2008). Cardiovascular indicators of disgust. *International Journal of Psychophysiology*. Retrieved from http://psycnet.apa.org/psycinfo/2008-05424-006

Rozin, P., & Fallon, A. E. (1987). A perspective on disgust. *Psychological Review, 94*(1), 23–41.

Rozin, P., Haidt, J., & McCauley, C. R. (2008). *Disgust*. Retrieved from http://doi.apa.org/?uid=2008-07784-047

Rozin, P., Haidt, J., McCauley, C., Dunlop, L., & Ashmore, M. (1999). Individual differences in disgust sensitivity: Comparisons and evaluations of paper-and-pencil versus behavioral measures. *Journal of Research in Personality, 33*(3), 330–351.

Ryan, S., Oaten, M., Stevenson, R. J., & Case, T. I. (2012). Facial disfigurement is treated like an infectious disease. *Evolution and Human Behavior, 33*(6), 639–646. doi:10.1016/j.evolhumbehav.2012.04.001.

Scanlan, J. M., Werner, J. J., Legg, R. L., & Laudenslager, M. L. (1995). Natural killer cell activity is reduced in association with oral contraceptive use. *Psychoneuroendocrinology, 20*(3), 281–287. doi:10.1016/0306-4530(94)00059-J.

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* (pp. 293–307). New York: 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*(5), 649.

Schaller, M., & Park, J. H. (2011). The behavioral immune system (and why it matters). *Current Directions in Psychological Science, 20*(2), 99–103.

Schaller, M., Park, J., & Faulkner, J. (2003). Prehistoric dangers and contemporary prejudices. *European Review of Social Psychology, 14*(1), 105–137.

Schienle, A., Stark, R., Walter, B., & Vaitl, D. (2003). The connection between disgust sensitivity and blood related fears, faintness symptoms, and obsessive compulsiveness in a non clinical sample. *Anxiety, Stress & Coping, 16*(2), 185–193. doi:10.1080/10615806.2003.10382972.

Shapira, N. A., Liu, Y., He, A. G., Bradley, M. M., Lessig, M. C., James, G. A., et al. (2003). Brain activation by disgust-inducing pictures in obsessive-compulsive disorder. *Biological Psychiatry, 54*(7), 751–756.

Sintchak, G., & Geer, J. H. (1975). A vaginal plethysmograph system. *Psychophysiology, 12*(1), 113–115.

Stark, R., Schienle, A., Walter, B., Kirsch, P., Sammer, G., Ott, U., et al. (2003). Hemodynamic responses to fear and disgust-inducing pictures: an fMRI study. *International Journal of Psychophysiology, 50*(3), 225–234.

Stark, R., Zimmermann, M., Kagerer, S., Schienle, A., Walter, B., Weygandt, M., et al. (2007). Hemodynamic brain correlates of disgust and fear ratings. *NeuroImage, 37*(2), 663–673. doi:10.1016/j.neuroimage.2007.05.005.

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*(1), 79–85.

Stevenson, R. J., Oaten, M. J., Case, T. I., Repacholi, B. M., & Wagland, P. (2010). Children's response to adult disgust elicitors: Development and acquisition. *Developmental Psychology, 46*(1), 165.

Thorneycroft, I. H., & Stone, S. C. (1972). Radioimmunoassay of serum progesterone in women receiving oral contraceptive steroids. *Contraception, 5*(2), 129–146.

Thornhill, R., & Gangestad, S. W. (2006). Facial sexual dimorphism, developmental stability, and susceptibility to disease in men and women. *Evolution and Human Behavior, 27*(2), 131–144.

Trivers, R. L. (1996). Parental investment and sexual selection. In L. D. Houck & L.C. Drickamer (Eds.), *Foundations of animal behavior: Classic papers with commentaries* (pp. 795–838). Chicago, USA: University of Chicago Press.

Trzonkowski, P., Myśliwska, J., Tukaszuk, K., Szmit, E., Bryl, E., & Myśliwski, A. (2001). Luteal phase of the menstrual cycle in young healthy women is associated with decline in interleukin 2 levels. *Hormone and Metabolic Research, 33*(6), 348–353. doi:10.1055/s-2001-15420.

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*(3), 343–348.

Tybur, J. M., & Gangestad, S. W. (2011). Mate preferences and infectious disease: Theoretical considerations and evidence in humans. *Philosophical*

Transactions of the Royal Society, B: Biological Sciences, 366(1583), 3375–3388.

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*(1), 103–122.

Tybur, J. M., Bryan, A. D., Magnan, R. E., & Hooper, A. E. C. (2011). Smells like safe sex olfactory pathogen primes increase intentions to use condoms. *Psychological Science, 22*(4), 478–480.

Tybur, J. M., Lieberman, D., Kurzban, R., & DeScioli, P. (2012). Disgust: Evolved function and structure. *Psychological Review*. doi:10.1037/a0030778.

Van Oppen, P. (1992). Obsessions and compulsions: Dimensional structure, reliability, convergent and divergent validity of the Padua Inventory. *Behaviour Research and Therapy, 30*(6), 631–637.

Van Overveld, M., De Jong, P. J., Peters, M. L., & Schouten, E. (2011). The Disgust Scale-R: A valid and reliable index to investigate separate disgust domains? *Personality and Individual Differences, 51*(3), 325–330.

Vonderheide, S. G., & Mosher, D. L. (1988). Should I put in my diaphragm? *Journal of Psychology & Human Sexuality, 1*(1), 97–111.

Vulink, N. C., Denys, D., Bus, L., & Westenberg, H. G. (2006). Female hormones affect symptom severity in obsessive-compulsive disorder. *International Clinical Psychopharmacology, 21*(3), 171.

Wedekind, C., Seebeck, T., Bettens, F., & Paepke, A. J. (1995). MHC-dependent mate preferences in humans. *Proceedings: Biological Sciences, 260*(1359), 245–249.

Weissman, M. M., Bland, R. C., Canino, G. J., & Greenwald, S. (1994). The cross national epidemiology of obsessive compulsive disorder: The Cross National Collaborative Group. *Journal of Clinical Psychiatry*. Retrieved from http://psycnet.apa.org/psycinfo/1994-37618-001

Wilder, R. L. (2006). Hormones, pregnancy, and autoimmune diseases. *Annals of the New York Academy of Sciences, 840*(Neuroimmunomodulation: Molecular aspects, integrative systems, and clinical advances), 45–50.

Williams, K. E., & Koran, L. M. (1997). Obsessive-compulsive disorder in pregnancy, the puerperium, and the premenstruum. *The Journal of Clinical Psychiatry, 58*(7), 330.

Wright, P., He, G., Shapira, N. A., Goodman, W. K., & Liu, Y. (2004). Disgust and the insula: fMRI responses to pictures of mutilation and contamination. *Neuroreport, 15*(15), 2347.

Zohar, A. H. (1999). The epidemiology of obsessive-compulsive disorder in children and adolescents. *Child and Adolescent Psychiatric Clinics of North America*. Retrieved from http://psycnet.apa.org/psycinfo/1999-03673-001

Zohar, A. H., & Bruno, R. (2006). Normative and pathological obsessive-compulsive behavior and ideation in childhood: A question of timing. *Journal of Child Psychology and Psychiatry, 38*(8), 993–999.