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RESEARCH ARTICLE

Disgust, Sexual Cues, and the Prophylaxis Hypothesis

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Abstract Women's susceptibility to infection has been found to vary across the menstrual cycle. During the luteal phase of the menstrual cycle, when progesterone levels are at their peak, women experience a downregulation in inflammatory immune responses to tolerate the presence of foreign paternal genetic material. The prophylaxis hypothesis holds that, during such periods of physiological immune vulnerability, women will engage in increased prophylactic behavior in response to cues associated with pathogen transmission (like sexual cues) to guard against infection. The current study examined disgust and other proposed prophylactic responses (i.e., attention and desire for solitary and dyadic sexual activity) in response to sexual and nonsexual films among naturally cycling women ($N = 21$) during the follicular and luteal phases of their menstrual cycles. No significant differences were found during the follicular and luteal phase on disgust, attention, or desire for solitary or dyadic sexual activity. Strong negative associations were found between feelings of disgust to sexual stimuli and proposed prophylactic behaviors (attention, desire for sexual activity with a partner) that were most prominent during the luteal phase of women's menstrual cycles, suggesting that they may have served as a prophylactic mechanism, protecting women's bodies from infection during a period of immune vulnerability. However, contrary to hypothesis, no significant associations were found between progesterone (the hormone that regulates changes in immune functioning) and proposed prophylactic responses. Further research examining prophylactic effects in response to sexual stimuli is warranted.

Keywords Disgust · Menstrual cycle · Progesterone · Sex · Prophylaxis

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Disgust and Sex

In the past few decades, an empirical link between sexual cues and feelings of disgust has been emerging: The idea of coming into contact with another's bodily orifices (even indirectly) is a very unpleasant one for most people, with the vagina, penis, mouth, and anus consistently rated as the most unpleasant apertures to come into contact with (Rozin et al. 1995) and sex-related secretions and odors being among the strongest disgust elicitors (Rozin and Fallon 1987). Likewise, in neuroimaging studies, stimuli known to induce disgust, such as rotten food items, have been found to evoke similar patterns of brain activity as stimuli depicting sexual (penile-vaginal) penetration (Borg et al. 2014; Karama et al. 2011). Despite this empirically supported aversion to sexual orifices and activities, however, the average person is estimated to engage in sexual activity anywhere from 30 to 80 times a year (dependent upon their age; Twenge et al. 2017). It remains unclear how disgust to sexual cues may or may not interfere with the mechanisms underlying sexual motivation and behavior. Indeed, much of the research literature examining sexuality and sexual functioning has largely overlooked disgust as a relevant contributing factor to sexual response and behaviors (see de Jong et al. 2013), though research in this area is beginning to expand (e.g., Fleischman et al. 2015).

Disgust has been identified as a basic emotion (e.g., Darwin 1965; Plutchik 1962; Kelly 2011) that is reported to have a unique, culturally universal facial expression (the "gape face"; Ekman and Friesen 1971, 1986; Kelly 2011) and characteristic physiological response, including activation of the autonomic nervous system (Ekman et al. 1983; Rohrmann and Hopp 2008), nausea and vomiting (to expel possible pathogens; Rozin and Fallon 1987), and increased salivation (preventing damage to tooth enamel during vomiting; Angyal 1941). Given the cross-cultural consistency that has been found in the expression of disgust, the clear relationship between disgust elicitors and threats for pathogen transmission and infectious disease (e.g., Curtis et al. 2004), and the known selective pressures that pathogens have imposed on the evolution of most organisms (e.g., Fumagalli et al. 2011), contemporary disgust researchers agree that an evolutionary perspective is needed to understand and conceptualize disgust (e.g., Kelly 2011; Oaten et al. 2009; Tybur et al. 2009).

Using this evolutionary conceptual framework, Tybur et al. (2009) have argued that selection has favored the evolution of three distinct domains of disgust: pathogen disgust (i.e., as a mechanism protecting against infectious microorganisms), disgust related to mate choice (e.g., incest avoidance), and moral disgust (relating to social transgressions). While sexuality can be implicated in all three disgust domains (see de Jong et al. 2013), the concept of pathogen disgust holds particular relevance to sexual behaviors. Body apertures (like the vagina, penis, anus, and mouth) and sex-related secretions (such as saliva, sweat, semen, and vaginal fluids) elicit strong feelings of disgust (Rozin and Fallon 1987; Rozin et al. 1995). It is perhaps not coincidental that these very cues are recognized to provide a potent threat for the transmission of disease, infection, and foreign genetic material (e.g., Alexander 1990; Chakraborty et al. 2001; Fessler et al. 2005). In this way, disgust has been proposed to be an evolved behavioral solution to adaptive problems. More specifically, disgust is posited to promote the avoidance of substances associated with pathogen transmission (like body apertures and secretions) to guard against disease (e.g., Curtis et al. 2004; Oaten et al. 2009).

The concept of disgust as an avoidance mechanism is one that has been built into the very subjective experience of the emotion: Research suggests that disgust is typically experienced as a feeling of revulsion alongside a strong desire to withdraw from the eliciting stimulus (Rozin et al. 2000). In the context of disgust-related psychopathologies (e.g., washing compulsions, spider phobias), a great deal of laboratory evidence substantiates the idea that feelings of disgust are strongly related to avoidance behaviors (e.g., de Jong and Peters 2007; Oaten et al. 2009; Olatunji et al. 2011; Woody et al. 2005). Similarly, unlike other threat-related emotions (e.g., fear, anger) that tend to be associated with increased attentional resources toward the eliciting stimulus (in case of a need to approach and fight; e.g., Vuilleumier et al. 2001), disgust has been found to suppress attention and/or direct it away from the eliciting stimulus (e.g., Liu et al. 2014). In this way, disgust is proposed to guard against the transmission of disease by minimizing the duration, intensity, and/or impact of the physical contact with disgust-eliciting stimuli (e.g., Woody et al. 2005; de Jong et al. 2013).

Pathogen disgust has been posited to be selected for as a low-cost first line of defense against threats (i.e., "behavioral immune system") to offset the relatively high costs of a full immune system response (Clark 2007; Laskin et al. 2011; Lochmiller and Deerenberg 2000). However, pathogen disgust is not without its own trade-offs. In particular, pathogen disgust in response to sexual fluids or bodily apertures may work to inhibit sexual response, avoid sexual stimuli, and consequently, sexual behaviors that provide some evolutionary benefits (like the successful propagation of one's own genes). Indeed, disgust has been found to be negatively associated with sexual arousal (e.g., Koukounas and McCabe 1997). Two recent studies found that participants experimentally primed with disgust-eliciting stimuli experienced less sexual arousal in response to subsequent explicit sexual images than those exposed to neutral priming stimuli (Andrews et al. 2015; Fleischman et al. 2015). In this way, the mechanisms of sex and disgust present a unique evolutionary challenge; sexual responses and behaviors must represent a complex negotiation between conflicting processes aiming to avoid risk (e.g., infection, disease) and achieve benefit (e.g., reproductive success; Bancroft et al. 2009; Gangestad 2007).

Women's Immune Vulnerability and the Prophylaxis Hypothesis

Women consistently report higher overall disgust sensitivity (e.g., Haidt et al. 1994; Fessler et al. 2004; Quigley et al. 1997) and greater pathogen disgust (Tybur et al. 2011) than do men. This finding is, perhaps, unsurprising, when one considers that women may have experienced unique selective pressures (particularly with regard to sexuality) for which heightened disgust sensitivity would be an adaptive characteristic. For instance, due to the potential for vaginal tissue damage during penetrative sexual activity, women are at an increased risk of contracting sexually transmitted infections (Madkan et al. 2006). During gestation, childbirth, or nursing, an untreated infection may lead to more severe consequences for women's reproductive fitness than men (Madkan et al. 2006). As such, disgust sensitivity as a disease-avoidance mechanism may have served to protect against women's heightened vulnerability to infections.

Though greater disgust sensitivity may serve as an adaptive feature for women overall, consistent hypervigilance to pathogens would be a taxing and costly enterprise; recall the importance of negotiating between avoiding risk and achieving reproductive benefit. Consequently, variations in disgust sensitivity would be expected at times when pathogen transmission may be most detrimental to a woman. Indeed, women's bodies have been found to show phasic changes in immunosuppression across the menstrual cycle and during pregnancy, in accordance with threats to the body due to sexual intercourse (i.e., conception; Critchley et al. 2001). That is, women experience a downregulation in inflammatory immune responses during the latter, or "luteal," stage of the menstrual cycle and during pregnancy to tolerate the presence of a potential fetal allograft (i.e., foreign paternal genetic material; Critchley et al. 2001). Following ovulation, increased levels of progesterone induce changes that make the uterus receptive to implantation (Corner and Allen 1929; Hyde et al. 2004). Progesterone also suppresses the influx of inflammatory cells into the uterus to tolerate the presence of foreign (paternal) genetic material; this immunosuppression continues throughout pregnancy, if an embryo implants on the uterine wall (Critchley et al. 2001). Thus, the luteal phase and pregnancy mark periods in a woman's menstrual cycle when she may be particularly vulnerable to infection.

The compensatory behavioral prophylaxis hypothesis holds that, during such periods of physiological immune vulnerability (i.e., the luteal phase/pregnancy), women will engage in increased prophylactic behavior to avoid infection (Fleischman and Fessler 2011). In support of this hypothesis, researchers have found that during the first trimester of pregnancy, women experience heightened disgust sensitivity (particularly to food), increased nausea, vomiting, and changes in their dietary habits away from foods that are thought to be associated with risk for pathogen transmission (Fessler 2001, 2002; Fessler et al. 2005; Flaxman and Sherman 2000). With respect to menstrual cycle shifts in prophylaxis, during the luteal phase, women avoid threats of contagion by engaging in more cleaning behaviors (Dillon and Brooks 1992); may prefer healthy over unhealthy faces (Jones et al. 2005, though this finding later failed to replicate; Jones et al. 2017); show heightened sensitivity to fearful and disgusted faces with averted gazes (Conway et al. 2007); and have greater disgust reactivity and sensitivity (Fleischman 2014; Żelaźniewicz et al. 2016). Further, hormonal indicators of downregulated immune responses (i.e., progesterone) correlate positively with the degree to which women report disgust sensitivity, thoughts, and behaviors (Fleischman and Fessler 2011).

Current Study

Despite the strong pathogenic disgust relevance of sexual cues (e.g., Rozin and Fallon 1987), to our knowledge, no one has examined menstrual cycle shifts in prophylaxis in response to films of sexual activity. Sexual cues (e.g., erect penises, exposed vulvas, vaginal secretions) are unique in that they represent a potent threat for the transmission of disease and signal the possibility of intercourse and subsequent reproduction simultaneously (see Spape et al. 2014). Thus, it would be adaptive if women's prophylactic responses to these cues were reserved for periods of increased immune vulnerability. We, therefore, hypothesized that greater prophylactic response to sexual cues would be an adaptive feature during the luteal phase, but not the follicular phase, when (a) the likelihood of conception is low (e.g., Wilcox et al. 2001) and (b) when progesterone levels are high (i.e., immune functioning is downregulated; Critchley et al. 2001). Prophylactic responses were operationalized as increased disgust, decreased attention, and increased desire for solitary as opposed to dyadic sexual activity.

Hypothesis 1: Disgust

Given that disgust has been proposed to be a prophylactic, disease-avoidant emotion (e.g., Oaten et al. 2009) and that overall disgust sensitivity has been found to fluctuate with immune changes due to hormone shifts in women's menstrual cycles (e.g., Fleischman and Fessler 2011), we expected that women would report greater disgust in response to sexual films during the luteal than follicular phase of their menstrual cycle.

Hypothesis 2: Attention

One mechanism by which disgust has been found to lead to the avoidance of possible pathogens is through the suppression of attention to disgust-eliciting stimuli (e.g., Liu et al. 2014). Thus, we expected that disgust would be negatively associated with attention and that women would report decreased attention to sexual stimuli during the luteal than follicular phase.

Hypothesis 3: Desire for Solitary Vs. Dyadic Sexual Activity

Sexual stimuli have been found to elicit sexual desire (e.g., Dawson and Chivers 2014; Timmers et al. under review). Desire is thought to be a multidimensional construct (e.g., Spector et al. 1996), with solitary desire (i.e., desire to masturbate) and desire for sexual activity with a partner (referred to as "dyadic desire") representing two independent desire dimensions. Given that excitatory (e.g., desire) and inhibitory (e.g., disgust) mechanisms of sexual response have been noted to conflict (e.g., Bancroft et al. 2009), we expected that disgust would be negatively associated with desire to engage in solitary and dyadic sexual activity. In keeping with the prophylaxis hypothesis, we also hypothesized that, in response to sexual videos, women would report less desire to engage in high-risk disease transmission sexual behavior (i.e., partnered/dyadic sexual activity) than to engage in low-risk sexual behavior (i.e., solitary behavior, or masturbation) during the luteal phase (relative to the follicular phase).

Hypothesis 4: Progesterone

We expected that progesterone would be associated with women's levels of disgust (e.g., Fleischman and Fessler 2011), attention, and interest in dyadic and solitary sexual activity.

Method

Participants

Data for 37 heterosexual women were acquired from an archival dataset collected by Bossio et al. (2014). Women were originally recruited through advertisements posted on Queen's University campus and the surrounding Kingston community and were screened via telephone to determine their eligibility for the study. Women were eligible for the study if they (1) were between 18 and 40 years of age; (2) were able to read, write, and understand English; (3) did not have a history of mental illness or substance abuse; (4) had no history of sexual dysfunction (including no history of pain during vaginal penetration); (5) did not have an active sexually transmitted infection; (6) were not taking any medications that are known to interfere with sexual responding (Meston and Frohlich 2000); and (7) reported predominant or exclusive heterosexual attractions (i.e., scores of 0 to 2 on the Kinsey Sexual Attraction Scale; Kinsey et al. 1953). Additionally, women were ineligible to participate in the study if they had never experienced vaginal penetration (during sexual activity, tampon insertion, or a pelvic examination); were pregnant, or nursing, or had been pregnant in the last 6 months; did not have a regular menstrual cycle (between 27 and 33 days; Chiazze et al. 1968); or were currently taking hormonal contraceptives or similar medications.

Of the original 37 participants, data for 21 women were included in final data analyses. Data were excluded from analyses for the following reasons: women did not attend the second testing session ($n = 6$), cycle phase could not be accurately confirmed by hormonal analysis ($n = 7$), difficulties were encountered with freezing salivary samples ($n = 1$), loss of self-report ratings during one cycle phase ($n = 1$), and equipment problems occurred affecting data during relevant stimulus trials ($n = 1$). Among the remaining 21 women, testing order was counter-balanced (10 women participated in their luteal phase first and 11 women began their first session in their follicular phase). The mean age of our participants was 22.14 years ($SD = 4.93$) with a range of 18 to 36 years. The majority of the women were single at the time of testing (61%, $n = 13$). Twenty-nine percent ($n = 6$) of the sample reported being in a dating relationship at the time of testing, with a median relationship length of 21 months ($M = 38.88$ months, $SD = 42.98$). The remainder of the women were either married (5%; $n = 1$) or in a common-law relationship (5%, $n = 1$). The women were of European (57%, $n = 12$), Asian (33%, $n = 7$), African (5%, $n = 1$), and Middle Eastern (5%, $n = 1$) heritage. All participants were either currently attending or had attended college (5%, $n = 1$), university (for an undergraduate degree; 81%, $n = 17$), or graduate/professional school (14%, $n = 3$).

Measures

Personal Information Participants completed a questionnaire assessing age, relationship status, sexual identity, education level, and ethnicity. No significant difference on demographic variables were observed between women who started testing in the luteal phase compared to women who started testing in the follicular phase.

Sexual Attraction Only those women who had exclusively or predominantly heterosexual attractions on a modified Kinsey Sexual Attraction Scale (KSAS; Kinsey et al. 1953) were included in the data analysis. The majority of women (71%, $n = 15$) reported experiencing sexual attractions toward "men only" (Kinsey 0), 24% of women ($n = 5$) reported sexual attraction to "men mostly but women occasionally too" (Kinsey 1), and 5% ($n = 1$) reported sexual attraction to "men mostly but women frequently" (Kinsey 2). On a related measure, women were asked to identify how disgusted they felt with the idea of having sex with a man. The scale ranged from 1 (*not at all*) to 5 (*extremely*). Generally, women reported low levels of disgust to sexual activity with a man ($M = 1.14$, $SD = 0.48$). An identical question asking about the idea of having sex with a woman met with slightly greater ratings of disgust ($M = 3.10$, $SD = 1.14$). All 21 women self-identified as "heterosexual."

Salivary Assays Salivary hormone assays were collected prior to each testing session. Two saliva samples (approximately 1 mL each) were collected in 2-mL polypropylene vials via passive drool 30 min apart, pooled together, and frozen at − 80 °C after collection until assay. All samples were assayed for salivary progesterone using a highly sensitive enzyme immunoassay (cat. no. 1-1502, Salimetrics LLC, State Colleve, PA); the assay plate was coated with rabbit anti-progesterone antibodies. The test used 50 μL of saliva per determination, had a lower limit of sensitivity of 5.0 pg/mL, standard curve range from 10 to 2430 pg/mL, an average intra-assay coefficient of variation of 6.2%, and an inter-assay coefficient variation of 7.6%. Method accuracy determined by spike recovery averaged 99.6% and linearity determined by serial dilution averaged 91.8%. Previous research shows that progesterone assayed from saliva using these methods correlates highly ($r = 0.87$) with serum assays in young women (Nallanathan et al. 2007). Menstrual cycle phase was verified by progesterone levels; among our remaining sample of 21 women, progesterone was higher in the luteal ($M = 216.90$ pg/mL, $SD =$

173.69) relative to the follicular phase ($M = 82.67$ pg/mL, $SD = 42.79$), $t(20) = 4.16$, $p < .001$, $d = 2.20$). Cycle phase progesterone difference ranged between 0.87 and 593.11 pg/mL, with a median change of 67.51 pg/mL; $SD = 147.84$.

Experimental Stimuli Audiovisual stimuli were comprised of two nonsexual videos of landscapes and two sexual videos of male-female sexual activity (one featuring penile-vaginal intercourse and the other featuring cunnilingus). Participants also viewed a series of other films that were part of the larger study by Bossio et al. (2014). Each video was 90 s in length and was presented in a pre-determined, randomized order for each participant. Because participants viewed two different videos for each stimulus category (sexual, nonsexual), paired-samples *t* tests were conducted to confirm no significant differences in participant ratings between the two videos for all dependent variables (disgust, attention, desire for solitary and dyadic sexual activity). Data were averaged across the two exemplars of each film type to create one score for each stimulus category, for each dependent variable. The sexual videos presented in the current study have previously been proven to be sexually competent stimuli—eliciting sexual response—in heterosexual women (e.g., Chivers et al. 2007).

Change in Self-Reported Disgust Participants completed pre-stimulus ("How disgusted do you feel?") and post-stimulus ("How disgusted did you feel during the video?") items, rated on a 10-point, Likert-type scale ranging from 0 (*no disgust*) to 9 (*extremely disgusted/most disgust ever felt*). Change in self-reported disgust was calculated as the difference between post- and pre-stimulus disgust ratings.

Self-Reported Attention After each stimulus presentation, participants responded to the question: "How much attention did you pay to the video?" Self-reported attention was rated on a 10-point, Likert-type scale ranging from 0 (*did not pay any attention to the video*) to 9 (*paid 100% attention to the video*).

Self-Reported Desire for Solitary Sexual Activity Before and after each stimulus presentation, participants responded to the question: "How strong is your desire to masturbate?" Responses were rated on a 10-point scale ranging from 0 (*no desire*) to 9 (*most desire I have ever felt*). Self-reported desire for solitary sexual activity was calculated as the difference between post- and pre-stimulus solitary desire ratings.

Self-Reported Desire for Dyadic Sexual Activity Before and after each stimulus presentation, participants responded to the question: "How strong is your desire for sex with a partner?" Responses were rated on a 10-point scale ranging from 0 (*no desire*) to 9 (*most desire I've ever felt*). Self-reported desire for dyadic sexual activity was calculated as the difference between post- and pre-stimulus dyadic desire ratings.

Self-Reported Desire for Solitary Vs. Dyadic Sexual Activity A contrast score was computed, where change in desire for a partner was subtracted from change in solitary desire. Possible contrast scores ranged from −9 to 9. Positive scores indicate greater desire for solitary than dyadic sexual activity, and negative scores indicate the reverse.

Procedure

Procedures are identical to that reported in Bossio and colleagues (2014). Participants were randomly assigned to attend their first session during the luteal or follicular phase of their menstrual cycle. The second laboratory session took place during the opposite phase of the menstrual cycle from which they were originally tested, approximately 2 weeks after their first session. Menstrual cycle phase was determined during eligibility screening using Puts' (2006) forward-backward counting technique; the onset of women's next menstrual bleeding was estimated (forward-counting) and then an approximation of the participant's number of days from ovulation was determined (backward counting − ovulation typically occurs about 14 days prior to next menstruation; Bakos et al. 1994). Women's menstrual cycles were transformed to a 28-day equivalent, as per previous hormone literature (e.g., Regan 1996; Puts 2006). Women who were 6 to 0 days prior to their expected ovulation in a standardized 28-day menstrual cycle were categorized as high-probability conception, or in the follicular phase of their menstrual cycle. Women who were 6 to 11days after expected ovulation were categorized as low probability of conception, or in the luteal phase of the menstrual cycle. Cycle phase was confirmed using progesterone salivary assays (described above).

During each testing session, participants completed questionnaires assessing demographic and other variables of interest, followed by a sexual psychophysiological assessment using vaginal photoplethysmography in a private testing room (see Bossio et al. 2014 for procedures and data pertaining to genital and self-reported sexual arousal). The participants were seated in a private room and watched the experimental stimuli presented on a computer monitor with audio delivered through headphones. There was an inter-stimulus period of approximately 1 min, during which time participants were asked to relax, to allow their genital arousal to return to its pre-trial level. Before and after every stimulus, participants responded to the experimental questions on a keypad. The second testing session's procedure was identical to the first, except that the questionnaire provided to participants was significantly shorter (excluding variables that were not expected to change between testing sessions). Monetary compensation was provided at the end of each testing session. Study procedures were approved by the Health Sciences Research Ethics Board at Queen's University.

Results

Change in Self-Reported Disgust Following Sexual Stimuli

Change in self-reported disgust ratings were submitted to a 2 (testing order: luteal phase first, follicular phase first) × 2 (cycle phase: luteal, follicular) × 2 (film type: sexual, nonsexual) mixed-model ANOVA. The ANOVA revealed no significant three- or two-way interactions, all Wilks' λs = 0.99, all *F*s < 0.21, all *p*s > 0.65, all η_p^2s < 0.01. Similarly, no significant effect of cycle phase was found on participants' disgust ratings, Wilks' $\lambda = 0.99$, $F(1, 19) = 0.60$, $p = 0.81$, $\eta_p^2 < .01$ (see Fig. 1).

Change in self-reported disgust following sexual stimuli ($M = 0.14$, $SD = 0.84$) was greater than disgust to nonsexual stimuli ($M = -0.45$, $SD = 1.00$) at a level that approached statistical significance, Wilks' $\lambda = 0.82$, $F(1, 19) = 4.07$, $p = 0.06$, $\eta_p^2 = 0.18$. It is unclear if the differences between post- and pre-stimulus levels of disgust are small due to high or low ratings of both pre- and post-stimulus disgust. Therefore, mean post-stimulus ratings of disgust were calculated and found to be relatively small for sexual ($M = 1.05$, $SD = 1.31$) and nonsexual ($M = 0.37$, $SD = 0.59$) stimuli alike.

Self-Reported Attention

Self-reported attention ratings were submitted to a 2 (testing order: luteal phase first, follicular phase first) × 2 (cycle phase: luteal, follicular) × 2 (film type: sexual, nonsexual) mixed-model ANOVA. The ANOVA revealed no significant three- or two-way interactions; all Wilks' λs > 0.88, all *F*s < 2.58, all *p*s > .13, all η_p^2 s < 0.12. Similarly, no significant effect of cycle phase was found on participants' attention ratings; Wilks' $\lambda = 0.96$, $F(1, 19) = 0.71$, $p = 0.41$, $\eta_p^2 = 0.04$ (see Fig. 2). However, a main effect of film type was found, such that women reported paying significantly greater attention to sexual ($M = 7.20$, $SD = 1.57$) than nonsexual ($M = 5.38$, $SD = 2.06$) stimuli; Wilks' $\lambda = 0.44$, $F(1, 19) = 24.64$, $p < .001$, $\eta_p^2 = 0.57$.

Pearson's correlations found that self-reported change in disgust ratings in response to sexual stimuli was negatively associated with the level of attention paid to the sexual films (at a level that approached statistical significance), during the luteal phase, $r(19) = -0.41$, $p = 0.07$, but were not associated during the follicular phase, $r(19) = -0.13$, $p = 0.57$.

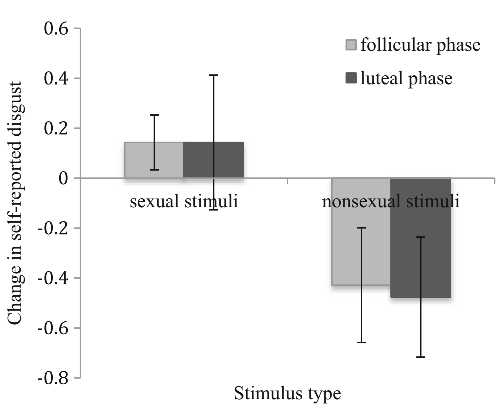

Fig. 1 Women's change in self-reported disgust ratings (pre-stimulus disgust ratings subtracted from post-stimulus disgust ratings) for sexual and nonsexual stimuli. Error bars represent the standard error of the mean. Figure represents means for $n = 21$

Self-Reported Desire for Solitary Vs. Dyadic Sexual Activity

Solitary vs. dyadic desire contrast scores (i.e., difference between the two change scores) were submitted to a 2 (testing order: luteal phase first, follicular phase first) × 2 (cycle phase: luteal, follicular) × 2 (film type: sexual, nonsexual) mixed-model ANOVA. The ANOVA revealed no significant three- or two-way interactions; all Wilks' λs > 0.94, all *F*s < 1.33, all *p*s > 0.41, all η_p^2 s < 0.04. Similarly, no significant effect of cycle phase was found; Wilks' $\lambda = 0.96$, $F(1, 19) = 0.71$, $p = 0.41$, $\eta_p^2 = 0.04$ (see Fig. 3). However, a main effect of film type was found (Wilks' $\lambda = 0.96$, $F(1, 19) = 28.14$, $p < .001$, $\eta_p^2 = 0.60$), such that contrast scores were significantly greater to nonsexual ($M = 0.70$, $SD = 0.98$) than sexual ($M = -1.04$, $SD = 1.27$) stimuli, indicating that women reported greater desire for dyadic versus solitary sexual activity during sexual compared to nonsexual films.

Pearson's correlations revealed that, during the luteal phase, self-reported change in disgust ratings in response to sexual stimuli was significantly negatively associated with change in dyadic desire, $r(19) = -0.50$, $p = 0.02$, but not change in solitary desire, $r(19) = -0.34$, $p = 0.13$. During the follicular phase, self-reported change in disgust ratings in response to sexual stimuli were not significantly associated with change in dyadic ($r(19) = -0.21$, $p = 0.35$) or solitary desire ($r(19) = -0.36$, $p = 0.11$).

Progesterone

Associations among progesterone and disgust, attention, and desire for dyadic and solitary sexual activity[1] ratings in response to sexual films were examined. Contrast scores were created such that progesterone and self-reported disgust, attention, and solitary and dyadic desire in the follicular phase were subtracted from progesterone levels and self-reported ratings

[1] Desire for dyadic sexual activity and solitary sexual activity were analyzed as distinct constructs in lieu of a contrast score for ease of interpretation.

during the luteal phase. Positive scores indicate greater progesterone or self-reported ratings during the luteal phase, and negative scores indicate the reverse. Contrary to our hypothesis, change in progesterone was not significantly associated with change in disgust, $r(19) = 0.09$, $p = 0.71$; attention, $r(19) = -0.06$, $p = 0.79$; solitary desire, $r(19) = -0.35$, $p = 0.12$; or dyadic desire, $r(19) = 0.31$, $p = 0.18$.[2]

Discussion

This study is the first to test the compensatory behavioral prophylaxis hypothesis by examining prophylactic responses (increased disgust, decreased attention, reduced desire for dyadic relative to solitary sexual activity) to sexual films across the menstrual cycle.

Disgust

Our first hypothesis, in which women would report greater disgust to sexual cues during the luteal phase of their menstrual cycle as a compensatory, prophylactic mechanism, was unsupported. Although women reported greater disgust to sexual than nonsexual films at a level that approached statistical significance (and a medium to large effect size), no significant differences in disgust ratings were found between the luteal and follicular phases of women's menstrual cycles. It is plausible that the inconsistency between the current study's findings and those of previous literature (e.g., Fleischman and Fessler 2011) may be due to the fact that, unlike previous research which has relied on images of unwashed bodies, infected wounds, etc. (Curtis et al. 2004; Fleischman and Fessler 2011), the stimuli used in the present study were sexually potent (Bossio et al. 2014; Chivers et al. 2007). Thus, it is possible that sexual arousal elicited by the sexual stimuli interfered with women's disgust ratings, thereby attenuating our ability to detect phasic changes in disgust across the menstrual cycle. Findings on the relationship between arousal and disgust have been mixed, with one study finding that sexual arousal inhibits disgust (Borg and de Jong 2012), another finding that sexual arousal inhibits sexual disgust but not pathogen disgust (Lee et al. 2014), one study finding arousal and disgust effects may depend on one's underlying trait-levels of disgust (Fleischman et al. 2015), and still others finding no effects (van Overveld and Borg 2015; Zsok et al. 2017). As sexual arousal data was collected in the current sample as part of a larger study (Bossio et al. 2014), we ran post hoc analyses on the association between genital and self-reported sexual arousal and disgust. Sexual arousal was generally negatively (though non-significantly) associated with disgust in both the luteal and follicular phases (all Pearson's rs < -0.31 and > -0.11; all ps > 0.16), lending some support to the hypothesis that sexual arousal interacted with disgust ratings.

It is also possible that our sexual films triggered not only pathogen disgust but also disgust related to mate choice (often referred to as "sexual disgust"). Indeed, as previously mentioned, sexual cues are implicated in all three domains of disgust (de Jong et al. 2013). Unlike pathogen disgust, however, sexual disgust has actually been found to increase during the follicular, relative to the luteal phase, to protect against possible reproduction with suboptimal sexual partners (Fessler and Navarrete 2003). That is, women may be more selective about potential sexual partners during their fertile, relative to non-fertile periods of their menstrual cycle (see Gildersleeve et al. 2014), which may lead to women experiencing greater levels of disgust to sexual targets that are deemed as undesirable reproductive partners. Since our study did not assess specific domains of disgust (instead asking about feelings of "disgust" generally), it is possible that increased pathogen disgust in the luteal phase was offset by increased sexual disgust to our sexual films in the follicular phase. Future research examining multifaceted aspects of disgust to sexual cues across the menstrual cycle is needed to disentangle this question.

Interestingly, on a ten-point Likert-type scale ranging from 0 (*no disgust*) to 9 (*most disgust ever felt*), women's mean disgust ratings in response to sexual films were quite low ($M = 1.05$, $SD = 1.31$), despite previous literature suggesting that sexual cues, including bodily fluids and body apertures, are among the strongest cues of disgust (Rozin et al. 1995; Rozin and Fallon 1987). It is possible that if our stimuli had included more salient cues of potential pathogen transmission (e.g., infected and inflamed genitals, visibly ill sexual actors) that a larger disgust effect and possible prophylactic response may have been observed. Notably, however, women's disgust ratings (though low overall) were still greater than disgust ratings to nonsexual stimuli—indicating that even if arousal may have dampened disgust to the sexual stimuli, disgust responses were robust enough that they were not eliminated completely. Though comparisons between disgust ratings in response to sexual and nonsexual stimuli did not reach statistical significance, a medium to large effect size was found, and a retrospective power analysis suggests our study may have been underpowered. In this way, the current study's results are not inconsistent with those of previous literature that have found significant disgust responses to sexual cues (Rozin et al. 1995; Rozin and Fallon 1987) and, as such, our data may reflect a true lack of variability of disgust responses between cycle phases. Indeed, the effect size for our analysis examining cyclic variations in women's disgust to sexual and nonsexual

[2] A similar pattern emerged when z- and log-transformed values were used instead of raw progesterone data.

films was quite small ($\eta_p^2 = .009$), suggesting that the prophylaxis hypothesis may not hold true for women's disgust responses to sexual films.

Attention

Contrary to our second hypothesis, in which attention to sexual stimuli would decrease in the luteal phase, women reported more attention to the sexual stimuli than to the nonsexual stimuli, irrespective of menstrual cycle phase. Though we did not anticipate this effect, it is, perhaps, unsurprising, when one considers previous research that has found that more attention is paid (particularly by women) to stimuli that are sexual as compared to nonsexual in nature (Geer and Bellard 1996; Spiering et al. 2004). Indeed, due to their evolutionary salience, cues that are appraised as being sexual in nature (such as those including aroused genitals, as in the current study; see Spape et al. 2014) are thought to automatically draw implicit attentional resources (Janssen et al. 2000). Subsequent sexual responses resulting from attentional adhesion to these sexual cues may have then increased attention to the sexual stimuli, thus using more attentional resources during the sexual than nonsexual videos. Given that women did not report a great deal of disgust to the videos, it is unsurprising that the mechanisms of arousal would have led to an approach rather than avoidance-driven attentional process.

It is interesting that during the luteal phase of women's menstrual cycles, our participants' self-reported attention was negatively correlated with their disgust ratings ($r = -0.41$). Indeed, the strong (but not statistically significant) negative correlation suggests that, during the luteal phase (when progesterone was greater and, subsequently, women experienced a downregulation in inflammatory immune response), women paid less attention to the video as they felt more disgusted. Though a negative association was also found between attention and disgust during the follicular phase of the menstrual cycle (suggesting an avoidant response), the effect was much smaller than during the luteal phase ($r = -0.12$). Together, these findings hint at the presence of a prophylactic mechanism, whereby women's attempts to avoid cues associated with pathogen transmission (i.e., sexual cues) by withdrawing attentional resources was more marked during periods of susceptibility to infection (i.e., the luteal phase of the menstrual cycle). It is important to note, however, that participants tended to report relatively low levels of disgust and high levels of attention to both sexual and nonsexual films overall.

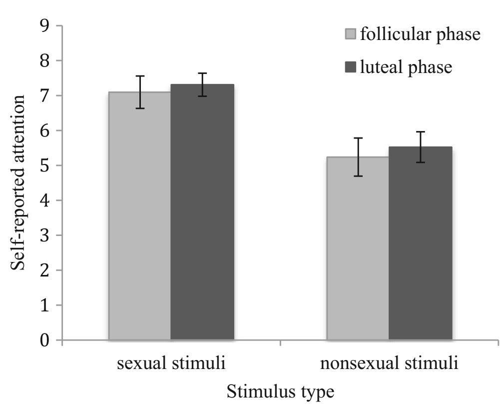

Fig. 2 Women's self-reported attention ratings for sexual and nonsexual stimuli. Attention was rated on a 0 (*did not pay any attention to the video*) to 9 (*paid 100% attention to the video*) scale. Error bars represent the standard error of the mean. Figure represents means for $n = 21$

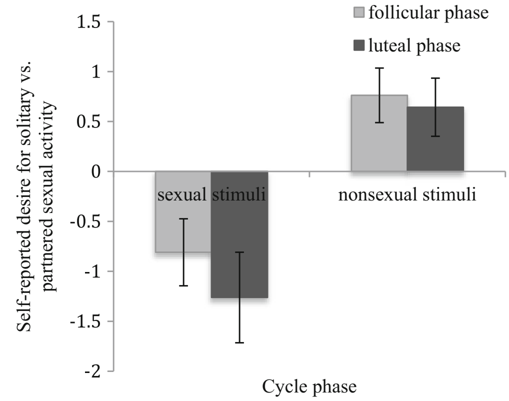

Fig. 3 Women's self-reported desire for solitary vs. dyadic sexual activity. Positive scores indicate greater desire for solitary than dyadic sexual activity, and negative scores indicate the reverse. Error bars represent the standard error of the mean. Figure represents means for $n = 21$

Desire for Dyadic Vs. Solitary Sexual Activity

We posited that participants would experience decreased desire to engage in sexual behaviors that could be associated with the transmission of disease (i.e., dyadic, rather than solitary desire) in response to sexual stimuli during the luteal more than the follicular phase of their menstrual cycles. This hypothesis was unsupported; women's desires for dyadic and solitary activity did not vary by menstrual cycle phase. Indeed, it is possible that dyadic sexual desire may persist among women during the luteal phase, even when the possibility of reproduction is low, due to other evolutionary advantages (such as affiliative pair-bonding benefits; e.g., Gangestad and Haselton 2015).

A main effect of film type was found, such that participants' desires tended to favor dyadic over solitary sexual activity more in response to sexual, as opposed to nonsexual, films. Participants' increased dyadic desire in response to sexual films may be related to an increase in arousal to the sexual films, as sexual desire emerges from sexual arousal (Both et al. 2007). As to why dyadic desire was greater than solitary desire, it is possible that dyadic desire (more than solitary desire) was elicited by the films since they featured dyadic (and not solitary) sexual activity (see Dawson and Chivers 2014).

Importantly, though disgust to sexual stimuli was negatively correlated with solitary and dyadic desire in both the luteal and follicular phases, the strongest correlation we observed was between disgust and desire for sexual activity with a partner during the luteal phase. Thus, during the point in the menstrual cycle when women's immune system is most compromised, increases in women's disgust to sexual stimuli were strongly ($r = -0.50$) associated with less desire to engage in dyadic sexual activity, a potentially prophylactic response in that dyadic sexual activity may facilitate disease transmission. This is consistent with the prophylaxis hypothesis, which holds that, during periods of immune vulnerability, women will engage in prophylactic responses to cues of pathogen transmission. It should be noted, however, that relatively strong negative correlations were also found between disgust and dyadic desire during the follicular phase, as well as between disgust and solitary desire during both the luteal and follicular phases. The failure of these strong effects to reach statistical significance may be related to our small sample size. Thus, the possibility that decreased solitary and dyadic desire may simply be related to increased disgust ratings inhibiting subsequent sexual arousal (e.g., Andrews et al. 2015) and subsequently desire (incentive motivation model; Both et al. 2007), irrespective of cycle phase, cannot be ruled out.

Progesterone

Increasing levels of progesterone during the luteal phase of the menstrual cycle have been found to lead to a downregulation in inflammatory immune response (Critchley et al. 2001). Thus, central to our test of the compensatory behavioral prophylaxis hypothesis was the prediction that changes in progesterone between the follicular and luteal phases would be associated with increases in prophylactic responses (i.e., changes in disgust, attention, and desire for dyadic and solitary sexual activity). Surprisingly, progesterone was not significantly related to any of the dependent variables in the current study, contrary to previous research reporting significant associations between progesterone and emotions, thoughts, and behaviors consonant with enhanced prophylaxis (Fleischman and Fessler 2011; Żelaźniewicz et al. 2016). However, new research using a large sample of naturally cycling women found no correlated changes between progesterone and pathogen disgust across the menstrual cycle (Jones et al. 2017). Thus, our failure to detect an effect of progesterone on prophylactic emotions and behaviors may be indicative of a true lack of a relationship between progesterone and prophylaxis in response to sexual cues.

Limitations and Future Directions

Contrary to our hypothesis, disgust, attention, and desire for dyadic and solitary sexual activities in response to sexual and nonsexual stimuli were not found to differ in the luteal and follicular phases. Future examination of the complex relationship between sexual arousal and prophylaxis emotions and responses (e.g., disgust) across the menstrual cycle may be warranted. An examination of sexual arousal and disgust concurrently in response to a wide range of stimuli, differing in their level of sexual competence (ability to elicit sexual arousal) and utilizing a superior measure of pathogen disgust, may improve the study design significantly. Indeed, it is unclear from our one-item question assessing disgust what domains of disgust participants may have experienced in response to the films (i.e., sexual, moral, pathogen; Tybur et al. 2009). Thus, it is possible that participants' disgust ratings in the current study may not be indicative of an aversion to cues of pathogens per se.

Though, to our knowledge, there is no definitive threshold for salivary progesterone, below which ovulation can be said not to occur (Ellison 1988; Vitzthum et al. 2002), we acknowledge that the change in progesterone (between the follicular and luteal phases) among our participants ranged widely. Consequently, we conducted our analyses again, excluding two participants for whom at least one observed luteal progesterone value that was not greater than 2 SDs above the average follicular progesterone levels (e.g., Ellison 1988; Panter-Brick et al. 1993). These analyses revealed the same general pattern of results to those reported above.

Volunteers for sexual psychophysiology studies have been found to differ from non-volunteers in various ways (e.g., Strassberg and Lowe 1995; Morokoff 1986). Though research suggests that many of the factors that differentiate volunteers from non-volunteers do not affect patterns of sexual arousal (Chivers et al. 2004), to our knowledge, no one has tested for differences in disgust sensitivity among those who do and do not participate in studies of sexual psychophysiology. It remains possible that the current sample (who participated in a study of sexual psychophysiology as part of the larger study paradigm) had decreased disgust sensitivity relative to the general population, and that this decreased disgust sensitivity affected our ability to test for changes in prophylactic responses (including disgust) across the menstrual cycle. Future research testing for differences in disgust sensitivity among volunteers and non-volunteers in studies of sexual psychophysiology would, therefore, lend important information about the generalizability of our results.

As previously noted, the sample size for the current study was quite small ($n = 21$, with the majority of analyses based on 21 women due to issues with missing data). Post hoc power analyses generally found that we lacked statistical power to detect significant effects. Consequently, results from the current study must be interpreted cautiously. However, it should be noted that despite these small sample sizes, large effect sizes were found for some of our analyses. As such, further investigation of the current hypotheses with a larger sample of women is warranted. Similarly, given the largely exploratory nature of our analyses surrounding attention and desire for dyadic vs. solitary desire, future research may wish to more directly examine the prophylactic relevance of these constructs.

The current study would have benefitted from the inclusion of a wider range of disgust and other prophylactic measures. For instance, disgust ratings for the current study were restricted to a one-item question: "How disgusted do you feel during the video?" Participant ratings on a previously validated multi-item disgust measure (see Fleischman 2014 for a discussion of the most widely used measures) after viewing sexual stimuli may have improved the validity and specificity of our construct. It is also worth considering that constructs other than disgust may be underlying the phasic changes in prophylactic responses found in previous literature (see Fleischman 2014). For instance, during periods of immunosuppression, such as the luteal phase of their menstrual cycles and pregnancy, women may experience an increase in general "worry" about/fear of contracting illness/disease. Though such a construct might be expected to be strongly associated with overall disgust (given, as mentioned previously, that disgust is posited to be an evolved mechanism that works to identify and avoid pathogens that may cause illness/disease), to our knowledge, no one has examined this directly. Future research may wish to examine the construct of general worry about/fear of contracting illness and its relevance to the prophylaxis hypothesis and disgust responses directly.

Concluding Statements

The current study examined the effects of menstrual cycle phase and subsequent changes in immune vulnerability on proposed prophylactic responses to sexual films among heterosexual women. Contrary to our hypotheses, we did not find any significant phasic changes in differences in disgust, attention, or desire for dyadic and solitary sexual activity in response to sexual and nonsexual videos. Interestingly, we did discover strong negative associations between feelings of disgust to sexual stimuli and subsequent proposed prophylactic behaviors (attention, desire for sexual activity with a partner) that were most prominent during the luteal phase of women's menstrual cycles, suggesting that they may have served as a prophylactic mechanism, protecting women's bodies from infection during a period of immune vulnerability. However, contrary to hypothesis, no significant associations were found between progesterone (the hormone that regulates changes in immune functioning) and proposed prophylactic responses. Further research examining prophylactic effects in response to sexual stimuli is warranted.

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Compliance with Ethical Standards Study procedures were approved by our Health Sciences and Affiliated Teaching Hospitals Research Ethics Board. All procedures performed in studies involving human participants were in accordance with the ethical standards of the institutional and/or national research committee and with the 1964 Helsinki Declaration and its later amendments or comparable ethical standards. Informed consent was obtained from all individual participants included in the study.

Conflict of Interest The authors declare that they have no conflicts of interest.

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