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SHORT REPORT

Women's Short-Term Mating Goals Elicit Avoidance of Faces Whose Eyes Lack Limbal Rings

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Limbal rings are dark rings around the eye's iris and their presence represents a good genes cue, which augments facial attractiveness. This communicative function implicates limbal rings as especially desirable in short-term mating contexts, suggesting a stronger motivation to approach prospective mates with limbal rings relative to those without. To assess approach and avoidance tendencies more directly, the current study adopted a line bisection task capable of assessing cortical activity. Whereas a right visual-field bias is associated with approach motivation, a left visual-field (LVF) bias is associated with avoidance motivation. In this study, we activated women's short-term mating motives (vs. a general positive affect control state) and presented a series of male and female faces with and without limbal rings over centrally bisected lines. Participants indicated which side of each line was longer to determine potential activation of consonant cortical areas. Mating-primed women demonstrated LVF bias when presented with targets lacking limbal rings, suggesting an avoidance response, relative to targets with limbal rings. No differences in behavioral tendencies between targets with and without limbal rings emerged for control-primed women. Results indicate the importance of limbal rings in short-term mating decisions by demonstrating a behavioral aversion to prospective mates lacking this health cue.

Public Significance Statement

When thinking about acquiring a short-term mate (e.g., a partner for a single sexual experience), women were motivated to avoid faces without limbal rings, whereas women did not appear motivated to approach faces with limbal rings. These results suggest women's preference for limbal rings may reflect an aversion to individuals who appear unhealthy.

Keywords: limbal rings, approach/avoidance, evolutionary psychology, short-term mating, bad genes

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Conventional logic suggests that selecting physically attractive short-term mates is in the

service of acquiring mates possessing heritable fitness. Conversely, aversion to conspecifics lacking good genes cues aids in avoiding low-quality mates, thus preventing costly mating mistakes (Zebrowitz & Rhodes, 2004). A reliance on eye contact throughout human evolution suggests individuals have evolved a concomitant ability to detect prospective mates' overall quality through cues contained in features of the eyes connoting health, thus facilitating approach toward desirable mates and avoidance of undesirable mates. Limbal rings, dark rings around the iris, augment facial

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attractiveness and are implicated as fitness cues (Peshek, Semmaknejad, Hoffman, & Foley, 2011). Although limbal rings augment facial attractiveness, short-term mating (STM) motives foster an aversion to faces without limbal rings, suggesting that attraction to such good gene cues may ultimately be rooted in aversion to lowquality prospective mates (Brown & Sacco, 2018). Given sensitivity to limbal ring presence, and the fact eyes possessing limbal rings appear healthier, prospective mates with limbal rings may activate approach motivation, whereas those without may trigger behavioral avoidance.

Asymmetric Cortical Activity in Approach/Avoidance

Cortical asymmetries influence approach/ avoidance motives. Left frontal cortical activation elicits approach, whereas right cortical activation elicits avoidance (Fetterman, Ode, & Robinson, 2013; Harmon-Jones, Gable, & Peterson, 2010). Respective cortical activations operate hydraulically to minimize competing neural messages and ensure appropriate responses for appetitive/ aversive stimuli. Such activations differentially elicit visual biases in respective contralateral visual fields. Approach-related activity elicits right visual field bias (RVF bias) and avoidance-related activity elicits left visual field bias (LVF bias), commonly measured through responses in line bisection tasks (Drake & Myers, 2006; Nash, McGregor, & Inzlicht, 2010). Participants in this task judge the relative lengths of the right side of a centrally bisected line versus the left. Because line segments are of equal length, consistently reporting one segment in a visual field as longer than the other indicates visual field bias. Perceiving the left side as longer indicates LVF bias, whereas perceiving the right side as longer indicates RVF bias. Visual field biases assessed through bisection tasks are perceptual proxies for motivational states implicated in approach/ avoidance.

Activation of goals related to survival and reproduction adaptively influence visual field biases indicative of approach/avoidance motives. These motives serve to identify social opportunities (e.g., mates) that would facilitate goal acquisition as well as threats that would impede goal satisfaction (e.g., exploitative conspecifics). For example, attractive prospective mates evoke approach motivation among individuals with unsatisfied mate-acquisition needs to maximize reproductive opportunities (Miller, Prokosch, & Maner, 2012). Conversely, those with satisfied mating motives (i.e., in committed relationships) perceive such targets as threatening to their current pair bond, prompting avoidance motivation to protect oneself from infidelity. Priming physical safety threats further elicits right hemispheric activation implicated in avoidance (Friedman & Förster, 2005), which serves to mitigate contact with threats. An intersection between face perception and approach/avoidance indicates trustworthy faces heighten RVF biases, suggesting willingness to engage benevolent conspecifics, with untrustworthy faces reducing RVF biases to minimize contact with exploitative conspecifics (Slepian, Young, & Harmon-Jones, 2017). Good gene cues may similarly elicit approach responses toward healthy mates and avoidance responses toward unhealthy mates.

Limbal Rings as Mating Cues

Humans infer health through information gleaned from characteristics in another's eyes. Bright sclerata and contrasts afforded by surrounding facial features augment scleral brightness, which subsequently augments perceptions of health and attractiveness (Russell et al., 2016; Russell, Sweda, Porcheron, & Mauger, 2014). Limbal rings afford vibrant contrasts as dark annuli encircling the iris, accentuating scleral brightness by "whitening" the sclerata (Shyu & Wyatt, 2009). Visibility of limbal rings decreases with declining chronic health and accumulation of phospholipids in the bloodstream, precursors to cardiovascular health complications (Ang et al., 2011; Sangwan, 2001). This contrast implicates limbal rings as health cues, as the contrast augments attractiveness (Peshek et al., 2011).

Eyes with limbal rings are perceived as healthier than those without, specifically when considering women's evaluation of prospective short-term mates (Brown & Sacco, 2018). Women's sensitivity seems adaptive, given their emphasis on selecting men based on facial features connoting good genes and greater level of selectivity in STM compared with men (Confer, Perilloux, & Buss, 2010; Kenrick, Groth, Trost, & Sadalla, 1993). Women prefer limbal rings, but such favorability appears rooted in derogation of individuals without limbal rings. STM-primed women perceive male faces without limbal rings as unhealthy compared with control-primed women, a potential avoidance response when presented with low-quality mates (Brown & Sacco, 2018). Conversely, STM- and control-primed women did not differ in ratings of faces with limbal rings. This avoidant response is consonant with the "bad gene aversion" hypotheses, suggesting that mate selection relies more on avoiding lowquality mates than on selecting high-quality mates (Zebrowitz & Rhodes, 2004). Because limbal ring visibility decreases with chronic health issues (Ang et al., 2011), activating STM motives may heighten women's sensitivity to cues indicating compromised health to detect low-quality mates or unhealthy conspecifics, subsequently eliciting avoidance.

Limbal rings may elicit approach motives with salient STM goals to increase contact with high-quality mates. Indeed, activated mating motives heighten attentional adhesion toward physically attractive individuals (Maner, Gailliot, Rouby, & Miller, 2007; Maner, Miller, Rouby, & Gailliot, 2009). In fact, opposite- and same-sex targets elicit visual adhesion, suggesting interest in prospective mates and hypervigilance toward rivals, both eliciting approach motives serving different functions (Maner, Miller, Coyle, & Kaschak, 2014). This could suggest that approach responses could be in the service of mate acquisition (i.e., opposite sex conspecifics) and confronting intrasexual rivals (i.e., same sex conspecifics).

Current Research

This study proposed complementary hypotheses to determine the extent to which limbal rings' favorability is rooted in selecting good genes and avoiding bad genes through approach/avoidance tendencies. Participants viewed bisected lines presented under faces with or without limbal rings to determine visual biases. If good gene selection explains limbal rings' favorability, women should report heightened approach motivation (RVF bias) toward faces with limbal rings. Conversely, if bad gene aversion explains favorability (Zebrowitz & Rhodes, 2004), women should report avoidance motives (LVF bias) toward faces *without* limbal rings. Given both the prioritization of good genes in STM (Li & Kenrick, 2006) and women's utilization of limbal rings to infer another's mate value (Brown & Sacco, 2018), we predicted these responses would be especially strong for mating-motivated women with heightened perceptual acuity toward highquality mates and intrasexual competition (approach) or low-quality mates and unhealthy individuals (avoidance).

Method

Participants

Consistent with standards in previous research on assessing laterality (Jewell & Mc-Court, 2000), we recruited 257 right-handed undergraduate participants in exchange for course credit. We exclusively recruited women, because they are especially sensitive to limbal rings as health cues (Brown & Sacco, 2018). Although 200 participants sufficed to detect small effects (Cohen's f = 0.10, $\beta = 0.80$), we oversampled to account for possible exclusions. We excluded 23 participants for reporting nonheterosexual attraction or not being a conventional reproductive age (41+ years). The final sample included 234 women ($M_{age} = 20.34$, SD = 3.42; 57.1% White).

Materials and Procedure

Mating prime. Participants read one of two immersive narratives eliciting either STM desire or general positive affect as a control (Griskevicius et al., 2007). Primes activated either STM goals or an equally positive state, unrelated to mating or sexual arousal. The mating prime instructed participants to imagine themselves as having a one-night stand with an attractive man on vacation. The control prime instructed participants to imagine themselves going to a concert with a same-sex friend. Participants then indicated sexual arousal (four items; 1 = not at all, 7 = very much; $\alpha = .92$) and general affect (-3 = very negative, 3 = very positive).

Target stimuli. Participants completed a line bisection task by judging whether horizontal lines were longer on either the left or right side of a perpendicularly bisecting line (Miller et al., 2012). In randomized order, participants viewed 20 filler trials with asymmetrically bisected lines and 20 critical trials featuring centrally bisected lines. Above each line was a facial image (Slepian et al., 2017). Critical lines accompanied 20 unique faces (10 male, 10 female) altered for limbal ring presence (five with and five without for both sexes; Peshek et al., 2011). Faces were altered by superimposing irises cropped from other eyes over targets' original eyes to ensure that no properties of the targets' original irises could be seen in the stimuli. Limbal ring versions of faces had radial gradients imposed over the superimposed irises at 50% opacity to create a natural appearance (Peshek, 2013); versions without limbal rings had no gradient. Unique identities in the critical trials were counterbalanced for limbal ring presence. Filler lines accompanied 10 male and 10 female faces not altered for ring presence. Participants viewed each unique identity once.

We coded trials in which participants indicated the left side of centrally bisected lines as longer (i.e., LVF bias) as "0" and trials in which participants indicated the right side as longer as "1" (RVF bias). For each participant, we computed proportions for responses on critical trials for male and female faces with and without limbal rings separately by computing the sum of the number of RVF bias response trials divided the total number of trials. Scores below 0.5 indicated LVF bias (i.e., heightened right frontal activation) and above RVF bias (left frontal activation).

Consenting participants were randomly primed with either STM motives or a control state before performing the bisection task. This was followed by demographics and debriefing.

Results

Manipulation Check

Mating-primed participants (M = 3.85, SD = 1.71) reported greater arousal than control participants (M = 1.65, SD = 1.70), t(192.65) = 11.77, p < .001, d = 1.54, 95% confidence interval [CI] [1.83, 2.57]. Positive affect was equivocal across mating-primed (M = 1.52, SD = 1.22) and control conditions (M = 1.31, SD = 1.37), t(232) = 1.20, p = .22, d = 0.15, 95% CI [-0.13, 0.54].

Primary Analysis

We conducted a 2 (condition: mating vs. control) × 2 (limbal rings: present vs. absent) × 2 (target sex: male vs. female) mixed-model ANOVA with repeated factors over the latter two factors. In this model, our dependent measure was VF-bias. A Condition × Limbal Rings interaction emerged, F(1, 232) = 7.95, p < .01, $\eta_p^2 = 0.03$. No other main effects or interactions emerged (Fs < 2.90, ps > 0.06).

Simple effects tests revealed mating-primed women reported greater LVF bias toward faces without limbal rings (M = 0.41, SE = 0.02) than faces with limbal rings (M = 0.48, SE =0.02), F(1, 232) = 10.11, p < .01, $\eta_p^2 = 0.04$, 95% CI [0.02, 0.10] (Figure 1). Conversely, control women did not differ in LVF bias for faces with (M = 0.47, SE = 0.02) and without limbal rings (M = 0.49, SE = 0.02), F(1,232) = 0.64, p = .42, η_p^2 = 0.00, 95% CI [-0.02, 0.05]. LVF bias did not differ for faces with limbal rings for either condition, F(1,232) = 0.01, p = .94, η_p^2 = 0.00, 95% CI [-0.06, 0.06]. LVF bias was greater for faces without limbal rings among mating-primed women than control, F(1, 232) = 6.77, p = .01, $\eta_p^2 = 0.03, 95\%$ CI [-0.14, -0.02].

One-sample *t* tests weighted against the midpoint (0.5) indicate control women demonstrated no visual field biases (ts < 1.10, ps > 0.270). Mating-primed women demonstrated LVF bias for faces without limbal rings, t(115) = -4.08, p < .01, d = 0.62, 95% [-0.13, -0.04], but no VF bias for faces with limbal rings, t(115) = -0.98, p = .33, d = 0.18, 95% CI [-0.06, 0.02].¹

Discussion

Results clarified previous findings demonstrating limbal rings' augmentative properties in attractiveness. Supporting bad genes hypotheses (Zebrowitz & Rhodes, 2004), mating-motivated women demonstrated LVF bias toward faces

¹ Although there were only five critical trials containing a male and female target with or without limbal rings, we computed proportions associated with participants selecting one line segment as longer than the other. These analyses were identical when we instead tested our hypotheses using a series of ordinal regressions (see the online supplemental materials).

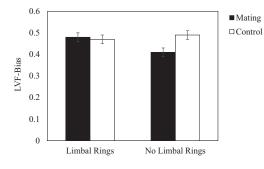


Figure 1. Women's left visual field (LVF) bias toward faces with and without limbal rings as a function of prime (with error bars). Lower numbers indicate greater LVF bias.

without limbal rings to avoid prospective mates whose physical appearance communicates reduced health. This avoidance bias aligns with previous findings indicating mating-primed women perceive faces lacking limbal rings as unhealthy (Brown & Sacco, 2018). Considering women's more judicious selection criteria, relative to men, in STM to avoid costly mating mistakes (Haselton & Buss, 2000; Kenrick et al., 1993), aversion to demonstrably low-quality mates is adaptive.

Perhaps surprisingly, we did not find comparable evidence for a good-genes hypothesis. The STM prime, relative to the control, did not elicit an approach-related RVF bias for targets possessing limbal rings. Although approaching high-quality mates would enhance offspring's heritable fitness, the costs of selecting lowquality mates could be greater, thereby eliciting aversion to faces lacking good genes indicators (Zebrowitz, Fellous, Mignault, & Andreoletti, 2003). Limbal rings may be desirable in STM (Brown & Sacco, 2018), but their role as health cues may be more accurately understood as their absence cuing poor health, thus eliciting avoidance. This aversion seems plausible considering humans' sensitivity to pathogenic conspecifics (Neuberg, Kenrick, & Schaller, 2011). Costs of associating with diseased conspecifics, compared with healthy, would be greater, necessitating aversion to unhealthy individuals (Young, Sacco, & Hugenberg, 2011). Avoiding mates without limbal rings would prevent transmission of low-quality genes to offspring and increasing vulnerability to chronic health issues (Ang et al., 2011).

Aversion to the absence of limbal rings was equivocal for male and female faces. Although aversion to ostensibly low-quality male faces seems sensible, the aversion to such female faces may suggest general avoidance of unhealthy conspecifics (Young et al., 2011; Zebrowitz & Rhodes, 2004). However, this aversion was primarily apparent upon activating STM goals. This could suggest women's avoidance is for specific reasons. Aversion to lowquality men would serve to mitigate contact, women's avoidance of low-quality female targets could be rooted in perceiving them as intrasexually nonthreatening, with avoidance being akin to disregard. Indeed, women are vigilant toward attractive female targets to monitor intrasexual competition (Maner et al., 2007, 2009). Because women without limbal rings may be perceived as unhealthy, and therefore nonideal mates, STM-motivated women may disengage from nonthreatening women.

Aversion to faces without limbal rings may serve to mitigate contact with unhealthy mates and conspecifics. Indeed, limbal rings' visibility decreases at the onset of chronic health declines (Ang et al., 2011; Sangwan, 2001), suggesting that they reliably connote chronic health. However, inflammatory responses to infectious disease often precede chronic health issues (e.g., cardiovascular disease; Roivainen et al., 2000; Sessa, Pietro, Filardo, & Turriziani, 2014). Limbal ring presence may also communicate previous exposure to infections, with decreased visibility indicating greater history of infection and therefore a compromised immune system. Given humans' aversion to bad gene cues when pathogenic concerns are salient (Young et al., 2011), it would seem sensible to predict aversion to limbal rings could be in the service of limiting contact with infectious disease. Future research would benefit from teasing apart whether such aversion serves to mitigate contact with those in chronically poor health or a greater infection risk (or a combination of both).

Limitations, Future Directions, and Conclusions

Despite identifying potential neural underpinnings for approach/avoidance toward faces, certain limitations emerge. Approach/avoidance responses indicate willingness to engage but not necessarily the impetus behind engagement for both target sexes. Although women's perceptions of men seem obvious for mate acquisition, ambiguity exists for other women. Because attractive female targets elicit hypervigilance and negative attitudes among mating-motivated women (Maner et al., 2009), perhaps the basis of VF bias toward women is perceiving the target's intrasexual threat, which would require commensurate attention for the threat. One way to tease apart sex-differentiated LVF bias would be priming women with intrasexual threat. Activation of such concerns should elicit similar approach motives toward female faces with limbal rings, given women's heightened alertness to intrasexually threatening cues (Ein-Dor, Perry-Paldi, Hirschberger, Birnbaum, & Deutsch, 2015).

These results suggest interplays between social motives and visual perception, which could ultimately predict discrete behaviors. Future research would benefit from considering specific approach/avoidance behavior. For example, the avoidance motivation elicited from limbal ring absence may elicit distal responses to aversive stimuli, such as arm extensions to foster distance between oneself and stimuli (Cacioppo, Priester, & Berntson, 1993). Mating-motivated women may seek distance between themselves and low-quality mates to mitigate contact with diseased individuals (Mortensen, Becker, Ackerman, Neuberg, & Kenrick, 2010).

Future research should consider how other facial features provide complementary cues for optimum STM in bisection tasks. Facial symmetry's ubiquity in communicating heritable fitness implicates it as one such cue that may elicit approach (Thornhill & Gangestad, 2006). Mating-motivated individuals especially prefer symmetry (Sacco, Hugenberg, & Sefcek, 2009), suggesting approach motivation and potentially RVF bias. Further, STM-focused women similarly prefer facial extraversion, whereas longterm-focused women prefer introversion (Brown & Sacco, 2017). STM-primed women may demonstrate RVF bias for approaching extraverted faces, with long-term mating-primed women demonstrating LVF bias.

Along with identifying optimum mates, avoidance of mates not possessing heritable fitness is paramount for reproductive success (Zebrowitz et al., 2003). This study demonstrated that such prioritization heightens sensitivity toward fitness indicators through perceptual biases. Importantly, this study provided a neural basis for perceptions of a subtle facial feature, which aids in the identification of unhealthy mates.

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