No evidence that inbreeding avoidance is up-regulated during the ovulatory phase of the menstrual cycle

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This research was supported by European Research Council grants awarded to LMD (KINSHIP) and BCJ (OCMATE).

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Abstract

Mate preferences and mating-related behaviors are hypothesized to change over the menstrual cycle in ways that function to increase reproductive fitness. Results of recent large-scale studies suggest that many of these hormone-linked behavioral changes are less robust than was previously thought. One hypothesis that has not yet been subject to a large-scale test is the proposal that women's preference for associating with male kin is down-regulated during the ovulatory (high-fertility) phase of the menstrual cycle. Consequently, we used a longitudinal design to investigate the relationship between changes in women's steroid hormone levels and their perceptions of faces experimentally manipulated to possess kinship cues. Analyses suggested that women viewed men's faces displaying kinship cues more positively (i.e., more attractive and trustworthy) when estradiol-to-progesterone ratio was high. Since estradiol-to-progesterone ratio is positively associated with conception risk during the menstrual cycle, these results directly contradict the hypothesis that women's preference for associating with male kin is down-regulated during the ovulatory (high-fertility) phase of the menstrual cycle. Data and code are publicly available at https://osf.io/wnhma/.

Keywords: kinship; endocrinology; inbreeding avoidance; fertility; kin affiliation

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Many researchers have proposed that during the ovulatory (i.e., high-fertility) phase of the menstrual cycle, women's preferences for potential mates who will increase their reproductive fitness will strengthen and/or that women's aversions to potential mates who will decrease their reproductive fitness will strengthen (see Gildersleeve et al., 2014; Gangestad & Thornhill 2008; Jones et al., 2008 for reviews). Increased attraction to men displaying putative good-fitness cues (Gangestad et al., 2004; Gangestad et al., 2007; Penton-Voak et al., 1999; Penton-Voak & Perrett, 2000) during the ovulatory phase of the menstrual cycle are particularly high-profile (but not the only) examples of evidence that is widely cited for this claim.

Recently, however, the robustness of the evidence for ovulatory shifts in women's mate preferences has been called into question. For example, two different meta-analyses of this literature drew very different conclusions about the robustness of the evidence for ovulatory shifts in women's mate preferences (Gildersleeve et al., 2014; Wood et al., 2004). Researchers have also highlighted several potentially important methodological limitations of studies on this topic (Blake et al., 2016; Gangestad et al., 2016; Jones et al., 2018a).

First, many researchers have emphasized that the majority of studies reporting significant ovulatory shifts in these behaviors are badly underpowered (Gangestad et al., 2016; Jones et al., 2018a). In combination with publication bias, this issue means that many of the published effects are likely to be false positives.

Second, many studies in this literature have employed between-subjects (i.e., cross-sectional) designs, which are ill-suited for testing subtle ovulatory shifts in behaviors that have substantial between-subject variance (Gangestad et al., 2016; Jones et al., 2018a). Importantly, large-scale within-subject (i.e., longitudinal) studies that used more objective methods to assess women's hormonal status (e.g., measuring sex hormones from saliva) have generally not replicated previously reported findings for ovulatory shifts in mate preferences (Jones et al., 2018a; Jünger et al., 2018a; Jünger et al., 2018b; Marcinkowska et al., 2018).

Third, studies have typically used self-report methods to assess position in the menstrual cycle (e.g., self-reported number of days since last period of menstrual bleeding at time of testing). Empirical studies suggest these are imprecise and prone to bias (Blake et al., 2016), although this may not be a problem in longitudinal studies with very large samples (e.g., Arslan et al., 2018).

Behaviors aimed at reducing opportunities for inbreeding to occur are predicted to increase around ovulation (Lieberman et al., 2011) but have yet to be the focus of large-scale, rigorous tests. To date, the best evidence for ovulatory shifts in inbreeding-avoidance comes from Lieberman et al. (2011). In a longitudinal study of 48 women's mobile phone records from one menstrual cycle, Lieberman et al. reported that women called their fathers less frequently (and spoke to them for less time when they did call them) during the high-fertility phase of the menstrual cycle than when fertility was low. Because Lieberman et al. observed no such change in women's frequency or duration of calls to their mothers, they interpreted these results as evidence for adaptations that function to reduce opportunities for inbreeding to occur around ovulation. Consistent with Lieberman et al.'s findings, DeBruine et al. (2005) found that women showed stronger preferences for faces manipulated to

possess kinship cues during the luteal (low-fertility) phase of the menstrual cycle than during the ovulatory phase in a cross-sectional study of 71 women. However DeBruine et al. (2005) also found that preferences for cues of kinship in women's, but not men's, faces were related to women's progesterone level, but not estimated fertility. Both progesterone and fertility were estimated by converting reported menstrual cycle day to progesterone and conception risk values using actuarial tables.

Researchers have recently emphasized the importance of replicating cyclic shifts in behaviors that have not yet been the target of large-scale replications, including inbreeding avoidance (Jones et al., in press). Thus, we revisited the claim of hormonal regulation of inbreeding-avoidance behaviors in a large-scale longitudinal study of the relationship between women's (N=199) salivary hormone levels and their responses to kinship cues in faces. Following previous studies of responses to facial kinship cues (DeBruine, 2002, 2004, 2005; DeBruine et al., 2005), we experimentally manipulated male and female face images to be more or less similar in shape to our participants and assessed the effects of this manipulation on perceptions of attractiveness and trustworthiness. Previous research has shown that this image manipulation can reliably tap inbreeding-avoidance behaviors. For example, women show aversions to opposite-sex faces with similar shape characteristics to their own when assessing men for exclusively sexual relationships, such as one-night stands, but not when assessing their trustworthiness (DeBruine, 2005). Further evidence that people respond to this image manipulation in ways consistent with it functioning as a kinship cue comes from studies showing that people are more likely to cooperate with people with similar face-shape characteristics (DeBruine, 2002) and perceive them to be more trustworthy (DeBruine, 2005).

The ovulatory phase of the menstrual cycle is characterized by the combination of high estradiol and low progesterone (Gangestad & Haselton, 2015). Thus, if Lieberman et al. (2011) are correct that ovulation increases inbreeding-avoidance behaviors, we would expect preferences for self-resembling male, but not self-resembling female, faces to decrease when estradiol is high and progesterone is simultaneously low.

Methods

Participants

We tested 205 heterosexual women (mean age=21.5 years, SD=3.3 years) who reported that they were not using any form of hormonal contraceptive (i.e., reported having natural menstrual cycles). Participants completed up to three blocks of test sessions. Each of the three blocks of test sessions consisted of five weekly test sessions. Women participated as part of a large study of possible effects of steroid hormones on women's behavior (Jones et al., 2018a, 2018b, 2018c). The data analyzed here are all responses from blocks of test sessions where women were not using any form of hormonal contraceptive and completed the face-judgment task in at least one test session. One hundred and seventy-two women had completed four or more test sessions and 41 of these women completed nine test sessions. Thirty-three women completed fewer than five test sessions.

Procedure

In the first test session, a full-face photograph of each woman was taken under standardized photographic conditions. Camera-to-head distance was held constant. These photographs were used to manufacture self-resembling faces using the same

methods as previous research (DeBruine, 2002, 2004, 2005; DeBruine et al., 2005). Self-resembling faces were created by applying 50% of the shape difference between each participant's face and a same-sex (i.e. female) prototype face to same-sex and opposite-sex prototypes, to produce same-sex and opposite-sex self-resembling faces. Importantly, this method for manipulating self-resemblance in opposite-sex faces avoids the feminization of male stimulus faces that occurs when simply blending self and opposite-sex faces (DeBruine, 2004). Male and female comparison stimuli that resembled none of the participants were manufactured in the same way using images of ten women who did not participate in the study. As in previous research on responses to self-resembling faces (DeBruine, 2002, 2004), image manipulations were carried out using specialist computer graphic software (DeBruine, 2018; Tiddeman et al., 2001). Example stimuli are shown in Figure 1.

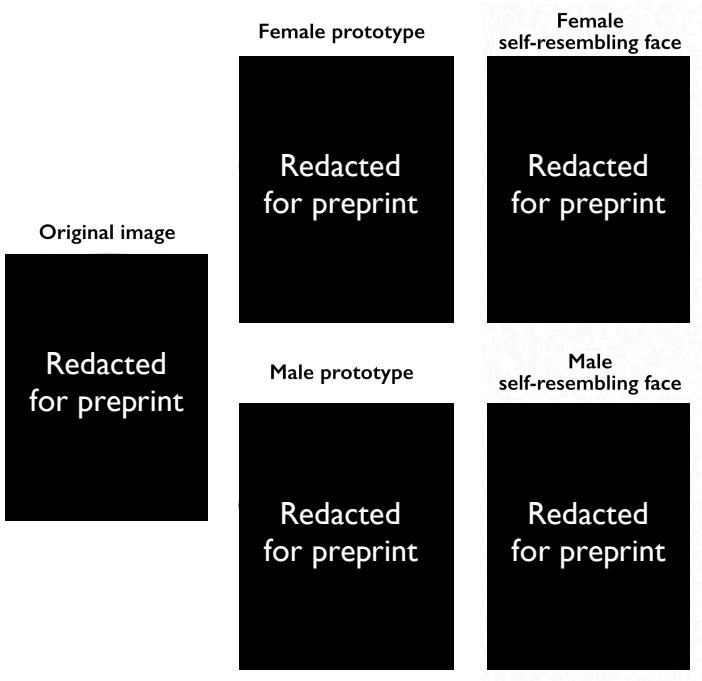

Figure 1. Self-resembling stimulus faces were created by applying 50% of the difference in shape between an individual's face and the female prototype to both female and male prototype faces.

In all subsequent test sessions (all test sessions after the first), each woman completed a face-judgment task in which they were presented 20 pairs of faces. Ten of these pairs consisted of a self-resembling face and a comparison face. The other ten pairs consisted of a non-resembling face (constructed from another randomly selected age-matched woman participating in the study) and the same comparison faces. This method allows us to compare judgments of self-resembling faces to judgments of non-resembling faces, while keeping equal the number of times self- and non-resembling faces are presented.

Participants were instructed to click on the face in each pair that they thought looked more attractive or, in a separate block of trials, more trustworthy. Trial order and the side of the screen on which any given image was presented were fully randomized. In each test session, each woman completed the face-judgment task four times. In the first version, they were presented female faces and judged attractiveness. In the second version, they were presented female faces and judged trustworthiness. In the third version, they were presented male faces and judged attractiveness. In the fourth version, they were presented male faces and judged trustworthiness. The order in which participants completed these versions of the face-judgment task was fully randomized.

For each version of the face-judgment task, we calculated a self-resemblance bias score by subtracting the number of times the non-resembling faces were chosen (out of 10) from the number of times the self-resembling faces were chosen (out of 10). These four scores were calculated separately for each participant in each test session. Positive scores indicated a bias towards self-resembling (versus non-resembling) faces and higher scores indicated self-resembling faces were perceived as more attractive or trustworthy than control faces.

Saliva samples

Participants also provided a saliva sample via passive drool (Papacosta & Nassis, 2011) in each test session. Participants were instructed to avoid consuming alcohol and coffee in the 12 hours prior to participation and avoid eating, smoking, drinking, chewing gum, or brushing their teeth in the 60 minutes prior to participation. Each woman's test sessions took place at approximately the same time of day to minimize effects of diurnal changes in hormone levels (Veldhuis et al., 1988; Bao et al., 2003).

Saliva samples were frozen immediately and stored at −32°C until being shipped, on dry ice, to the Salimetrics Lab (Suffolk, UK) for analysis, where they were assayed using the Salivary 17β-Estradiol Enzyme Immunoassay Kit 1-3702 (M=2.82 pg/mL, SD=1.03 pg/mL, sensitivity=0.1 pg/mL, intra-assay CV=7.13%, inter-assay CV=7.45%) and Salivary Progesterone Enzyme Immunoassay Kit 1-1502 (M=157.2 pg/mL, SD=104.9 pg/mL, sensitivity=5 pg/mL, intra-assay CV=6.20%, inter-assay CV=7.55%). Hormone levels more than three standard deviations from the sample mean for that hormone or where Salimetrics indicated levels were outside the sensitivity range of their relevant ELISA were excluded from the dataset (~0.1% of hormone measures were excluded for these reasons). The descriptive statistics given above do not include these excluded values and do not include statistics for the first test session where women did not complete the face-judgment task. Values for each hormone were centered on their subject-specific means to isolate effects of within-subject changes in hormones and were scaled so the majority of the distribution for each hormone varied from −.5 to .5. This was done simply to facilitate calculations in the linear mixed models. Since hormone levels were centered on their subject-specific

means, women with only one value for a hormone could not be included in these analyses.

Analyses

Linear mixed models were used to test for possible effects of hormonal status on responses on the face-judgment task. Analyses were conducted using R version 3.5.1 (R Core Team, 2018), with lme4 version 1.1-18-1 (Bates et al., 2014) and lmerTest version 3.0-1 (Kuznetsova et al., 2017). Random slopes were specified maximally following Barr et al. (2013) and Barr (2013). Data files and analysis scripts are publicly available at https://osf.io/wnhma/.

The models we used to investigate hormonal regulation of responses to kinship cues in faces are identical to those we have used previously to test for hormonal regulation of women's masculinity preferences (Jones et al., 2018a), disgust sensitivity (Jones et al., 2018b), and sexual desire (Jones et al., 2018c). Face sex was effect coded (−.5 = female, +.5 = male), as was judgment type (−.5 = attractiveness, +.5 = trustworthiness). Self-resemblance bias scores (−10 to +10) were the dependent variable. Note that women with only a single test session where they completed the face-judgment task and had valid estradiol and progesterone levels cannot be included in these longitudinal analyses (N=6). Thus, data from 199 women were included in these analyses.

The first model (Model 1) we tested included estradiol (scaled and centered), progesterone (scaled and centered), estradiol-to-progesterone ratio (scaled and centered), face sex, and judgment type as predictors, as well as all possible two-way and three-way interactions among these predictors. Full results for this analysis are shown in Table 1. The intercept was positive and significant (estimate=0.43, 95% CI

= [0.15, 0.72], p=.003), indicating that women chose self-resembling faces more often than would be predicted by chance. There was a significant positive effect of progesterone (estimate=0.63, 95% CI = [0.13, 1.13], p=.015) and a significant negative effect of estradiol (estimate=−0.76, 95% CI = [−1.31, −0.2], p=.008), indicating that self-resemblance-bias scores tracked changes in both progesterone and estradiol. Although self-resemblance bias scores tended to be higher for judgments of female faces than male faces, this effect of face sex was not significant (estimate=−0.21, 95% CI = [−0.43, 0.01], p=.068). The main effect of estradiol-to-progesterone ratio (estimate=0.34, 95% CI = [−0.11, 0.78], p=.159) was not significant, but the interaction between face sex and estradiol-to-progesterone ratio was significant (estimate=0.71, 95% CI = [0.02, 1.4], p=.044). However, self-resemblance bias scores for male faces were higher when estradiol-to-progesterone ratio was high (see Figure 2), which is in the opposite direction to the prediction that self-resemblance bias scores for male faces will decrease when conception risk is high. Self-resemblance bias scores for female faces did not appear to be related to estradiol-to-progesterone ratio (see Figure 2). No other effects were significant or close to being significant.

Table 1

The effect of estradiol, progesterone and estradiol-to-progesterone ratio on self-resemblance bias scores (Model 1)

Effect	Estimate	2.5%	97.5%	SE	df	t	p value
Intercept	0.43	0.15	0.72	0.14	198.33	2.99	.003
Estradiol (E)	-0.76	-1.31	-0.20	0.28	622.16	-2.67	.008
Progesterone (P)	0.63	0.13	1.13	0.26	125.44	2.46	.015

EP ratio	0.34	-0.11	0.78	0.23	15.17	1.48	.159
Judgment type	-0.16	-0.42	0.10	0.13	200.74	-1.23	.222
Face sex	-0.21	-0.43	0.01	0.11	170.57	-1.84	.068
E x judgment	-0.08	-1.00	0.84	0.47	800.28	-0.17	.865
E x face sex	0.06	-0.92	1.03	0.50	751.47	0.12	.908
P x judgment	-0.11	-0.96	0.74	0.43	158.68	-0.25	.804
P x face sex	-0.35	-1.20	0.50	0.43	96.02	-0.80	.424
Judgment x face sex	0.15	-0.12	0.41	0.14	172.87	1.06	.290
EP ratio x judgment	0.03	-0.62	0.69	0.33	753.03	0.10	.918
EP ratio x face sex	0.71	0.02	1.40	0.35	665.32	2.02	.044
E x judgment x face sex	-0.20	-2.03	1.64	0.94	813.66	-0.21	.833
P x judgment x face sex	-0.09	-1.77	1.59	0.86	104.65	-0.11	.915
EP ratio x judgment x face sex	0.67	-0.64	1.98	0.67	704.71	1.01	.314

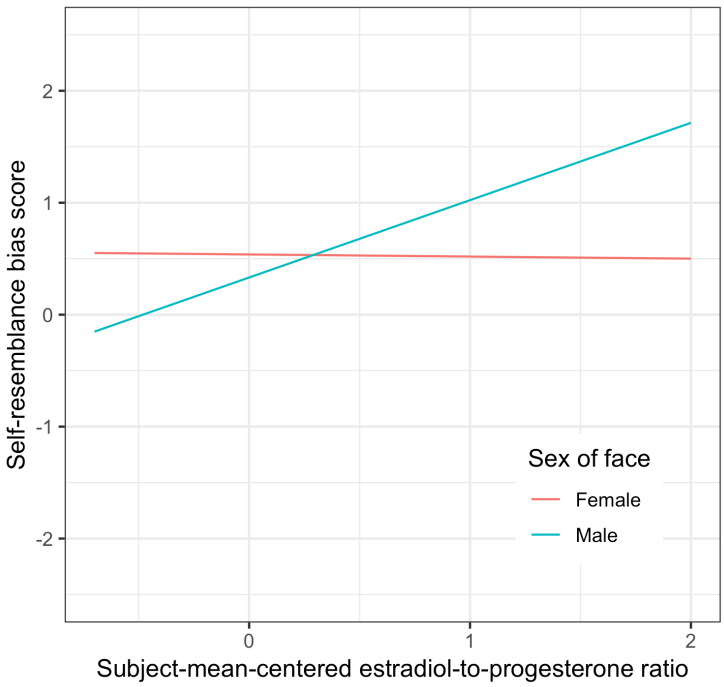

Figure 2. The effect of estradiol-to-progesterone ratio on self-resemblance bias scores. Self-resemblance bias scores for male faces were higher when estradiol-to-

progesterone ratio was high, while self-resemblance bias scores for female faces appeared to be unrelated to estradiol-to-progesterone ratio.

The second model (Model 2) we tested included estradiol (scaled and centered), progesterone (scaled and centered), face sex, and judgment type as predictors, as well as all possible two-way, three-way, and four-way interactions among these predictors. This model did not converge with either the bobyqa or Nelder-Mead optimizers (see https://osf.io/wnhma/). To facilitate convergence, we ran a simplified model, in which only random slopes for the highest-order interaction and the interaction among face sex, estradiol, and progesterone were included. This model produced identical results when run with bobyqa and Nelder-Mead optimizers (see https://osf.io/wnhma/). Full results for this analysis are shown in Table 2. Replicating the results reported for Model 1, the intercept was significant (estimate=0.44, 95% CI = [0.15, 0.72], p=.003), there was a significant positive effect of progesterone (estimate=0.43, 95% CI = [0.03, 0.83], p=.033), and a significant negative effect of estradiol (estimate=−0.63, 95% CI = [−1.17, −0.08], p=.024). Self-resemblance bias scores were higher for judgments of female faces than male faces and this effect of face sex was significant in this analysis (estimate=−0.22, 95% CI = [−0.36, −0.08], p=.003). The effect of judgment type was significant in this analysis (estimate=−0.18, 95% CI = [−0.33, −0.04], p=.012), indicating that self-resemblance bias scores were greater for attractiveness judgments than trustworthiness judgments. In this analysis, the interaction between progesterone and face sex was significant (estimate=−0.84, 95% CI = [−1.63, −0.06], p=.035) and showed that the positive effect of progesterone on self-resemblance scores was greater for female than male faces (see Figure 3). No other effects were significant or close to being significant. Of note, neither the three-

way interaction of progesterone, estradiol and sex of face (estimate=1.79, 95% CI = [−2.83, 6.42], p=.447), nor the two-way interaction of progesterone and estradiol (estimate=−0.77, 95% CI = [−3.43, 1.9], p=.573) were significant. The pattern of results observed for the simplified model are very similar to those observed in the full models that did not converge (see https://osf.io/wnhma/).

Table 2

The effect of estradiol, progesterone and the interaction of estradiol and progesterone on self-resemblance bias scores (Model 2)

Effect	Estimate	2.5%	97.5%	SE	df	t	p value
Intercept	0.44	0.15	0.72	0.14	199.80	3.02	.003
Estradiol (E)	-0.63	-1.17	-0.08	0.28	2729.38	-2.26	.024
Progesterone (P)	0.43	0.03	0.83	0.20	3416.23	2.13	.033
Judgment type	-0.18	-0.33	-0.04	0.07	3761.04	-2.51	.012
Face sex	-0.22	-0.36	-0.08	0.07	3761.04	-3.00	.003
E x P	-0.77	-3.43	1.90	1.36	3286.64	-0.56	.573
E x judgment	-0.11	-1.18	0.95	0.54	3761.03	-0.21	.834
P x judgment	-0.14	-0.92	0.64	0.40	3761.02	-0.35	.726
E x face sex	0.28	-0.79	1.34	0.54	3761.03	0.51	.610
P x face sex	-0.84	-1.63	-0.06	0.40	3761.02	-2.11	.035
Judgment x face sex	0.15	-0.14	0.43	0.15	3761.04	1.02	.310
E x P x judgment	-2.07	-6.69	2.55	2.36	3761.02	-0.88	.380
E x P x face sex	1.79	-2.83	6.42	2.36	3761.02	0.76	.447
E x judgment x face sex	0.16	-1.97	2.29	1.09	3761.03	0.15	.882
P x judgment x face sex	-0.76	-2.32	0.81	0.80	3761.02	-0.94	.345
E x P x judgment x face sex	0.09	-9.16	9.33	4.72	3761.02	0.02	.985

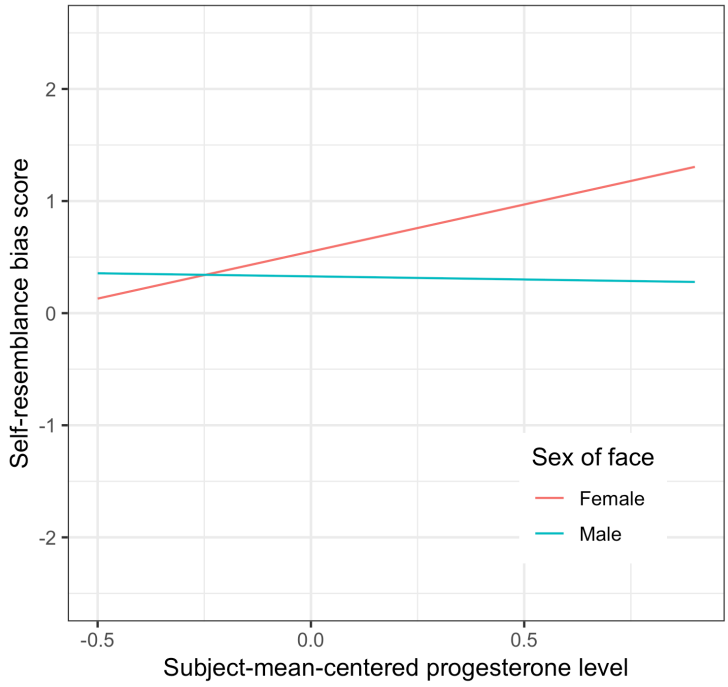

Figure 3. Model 2 showed a significant interaction between progesterone and face sex. The positive effect of progesterone on self-resemblance scores was greater for female than male faces.

Discussion

We tested for evidence of hormonally regulated inbreeding avoidance in a longitudinal study of women's responses to faces possessing kinship cues (i.e., self-resembling faces). By contrast with our predictions, we found no evidence that self-resemblance bias (i.e., the tendency to perceive self-resembling faces to be more attractive or trustworthy) decreased when fertility was high. In fact, in our analyses, self-resemblance bias when assessing men's faces was *greater* when estradiol-to-progesterone ratio was higher (see Model 1). Since estradiol-to-progesterone ratio is positively correlated with conception risk during the menstrual cycle (Gangestad & Haselton, 2015; Puts et al., 2013), the observed positive effect of estradiol-to-progesterone ratio on self-resemblance bias when judging male faces is then in the

opposite direction to what would be expected if inbreeding avoidance increased when fertility is high. Thus, our data do not support Lieberman et al.'s (2011) suggestion that inbreeding avoidance increases with conception risk during the menstrual cycle.

Although we found no evidence that self-resemblance bias was weaker when fertility was high, women did (on average) judge self-resembling faces to be more trustworthy and attractive than non-self-resembling faces. This tendency to perceive self-resembling faces more positively than would be expected by chance alone replicates results from previous research (DeBruine, 2002, 2004, 2005). We also found that women's self-resemblance bias tended to be greater when judging women's faces than when judging men's faces, although this effect of sex of face was only significant in one analysis[1]. Nonetheless, in both analyses, the direction of the effect of face sex is consistent with both previous research (DeBruine, 2004) and the proposal that inbreeding avoidance acts as a brake on the self-resemblance bias in social judgments of faces (DeBruine et al., 2008).

In a cross-sectional study, DeBruine et al. (2005) reported that self-resemblance bias increased when progesterone levels were relatively high when assessing women's, but not men's, faces. Evidence for such an effect in our sample was mixed. Both of our analyses found that the self-resemblance bias was stronger when progesterone was higher. Results from Model 2, but not Model 1, suggested that this positive effect of progesterone on self-resemblance bias scores was driven by responses to female faces. DeBruine et al. (2005) suggested that stronger self-resemblance bias for women's faces when progesterone is high could function to increase bonding with female kin when raised progesterone prepares the body for

[1] In Model 1, the estimate for the effect of face sex was −0.21 (p=.068). The corresponding effect in Model 2 was −0.22 (p=.003).

pregnancy and support from kin may be particularly beneficial. However, in the current study, we also found that self-resemblance bias was weaker when estradiol was higher. Both estradiol and progesterone are elevated during pregnancy (Johnson, 2007). Thus, that progesterone and estradiol have opposite effects on self-resemblance bias does not straightforwardly support DeBruine et al.'s (2005) proposal that stronger self-resemblance bias when progesterone is high reflects hormonal regulation of responses to kinship cues that evolved to increase bonding with kin during pregnancy.

In summary, the main finding from this study is that self-resemblance bias scores for male faces were positively (rather than negatively) related to estradiol-to-progesterone ratio (a well-validated proxy measure of conception risk). This pattern of results directly contradicts (i.e., is in the opposite direction to what would be predicted by) Lieberman et al.'s (2011) hypothesis that inbreeding-avoidance behaviors increase during ovulation. Further work is needed to establish whether this negative result is specific to responses to kinship cues in faces, reflects low replicability of hormone-linked inbreeding avoidance behaviors more generally, or is evidence that factors affecting kinship-linked behaviors in one domain (frequency of telephone interaction with opposite-sex parent, Lieberman et al., 2011) do not necessarily affect kinship-linked behaviors in another domain (perceptions of unfamiliar individuals displaying facial cues of kinship) in the same way. Resolving this issue would provide important insight into the viability of existing models of kin recognition, which typically suggest that a single "kinship estimator" cognitive module guides kinship-linked behaviors (Lieberman et al., 2007).

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