Women's preferences for facial masculinity are not related to their hormonal status

Benedict C Jones[1], Amanda C Hahn[2], Claire I Fisher[1], Hongyi Wang[1], Michal Kandrik[1], Chengyang Han[1], Vanessa Fasolt[1], Danielle Morrison[1], Anthony Lee[1], Iris Holzleitner[1], Craig Roberts[3], Anthony Little[4] & Lisa DeBruine[1]

1. Institute of Neuroscience & Psychology, University of Glasgow, UK.
2. Department of Psychology, Humboldt State University, USA.
3. Department of Psychology, University of Stirling, UK.
4. Department of Psychology, University of Bath, UK.

Corresponding author

Benedict C Jones (ben.jones@glasgow.ac.uk), Institute of Neuroscience & Psychology, University of Glasgow, UK.

Women's preferences for facial masculinity are not related to their hormonal status

Abstract

Although widely cited as strong evidence that sexual selection has shaped human facial attractiveness judgments, evidence that preferences for masculine characteristics in men's faces are related to women's hormonal status is equivocal and controversial. Consequently, we conducted the largest ever longitudinal study of women's preferences for facial masculinity (N=584). Analyses showed no evidence that preferences for facial masculinity were related to changes in women's salivary steroid hormone levels. Furthermore, both within-subject and between-subject comparisons showed no evidence that oral contraceptive use decreased masculinity preferences. However, women generally preferred masculinized over feminized versions of men's faces, particularly when assessing men's attractiveness for short-term, rather than long-term, relationships. Our results do not support the hypothesized link between women's preferences for facial masculinity and their hormonal status.

Introduction

Exaggerated male sex-typical (i.e., masculine) characteristics in men have been proposed as cues of a strong immune system that would be inherited by offspring, but also linked to reduced willingness to invest time and other resources in personal relationships (Perrett et al., 1998; Penton-Voak et al., 1999; Little et al., 2011; Gildersleeve et al., 2014; Gangestad et al., 2004). Given this proposed trade off between the benefits and costs of choosing a masculine mate, researchers have hypothesized that women could maximize the benefits of their mate choices by mating with masculine men when fertile, while forming long-term relationships with relatively feminine men (Penton-Voak et al., 1999; Little et al., 2011; Gildersleeve et al., 2014; Gangestad et al., 2004).

Consistent with this hypothesis, some studies have reported that women show stronger preferences for masculine characteristics in men's faces when in hormonal states associated with high fertility (e.g., during the ovulatory phase of the menstrual cycle and/or when not using hormonal contraceptives, Ditzen et al., 2017; Penton-Voak et al., 1999; Little & Jones, 2012; Penton-Voak & Perrett, 2000; Johnston et al., 2001; Roney & Simmons, 2008; Roney et al., 2011; Welling et al., 2007; Vaughn et al., 2010; Little et al., 2002; Little et al., 2013). These effects are widely cited as evidence that sexual selection has shaped women's judgments of men's facial attractiveness (Gangestad & Simpson, 2000; Grammer et al., 2003; Thornhill & Gangestad, 1999; Fink & Penton-Voak, 2002).

The claim that women’s preferences for facial masculinity are related to their hormonal status has been influential (Gangestad & Simpson, 2000; Grammer et al., 2003; Thornhill & Gangestad, 1999; Fink & Penton-Voak, 2002). However, recent work has highlighted four potentially serious problems with this research.

First, sample sizes are usually small, meaning that studies are badly

underpowered (Gangestad et al., 2016). For example, the mean sample size of within-subject studies reporting significant effects of hormonal status on facial masculinity preferences is only 40 women (median = 34). Consequently, results from previous studies are difficult to interpret (Gangestad et al., 2016; Blake et al., 2016).

Second, hormonal status is typically assessed using self-reported menstrual cycle data (e.g., number of days since onset of last menses or number of days until expected date of next menses, Penton-Voak et al., 1999; Little & Jones, 2012; Penton-Voak & Perrett, 2000; Johnston et al., 2001; Harris, 2013; Zietsch et al., 2015; Scott et al., 2014; Munoz-Reyes et al., 2014). This method is imprecise and prone to bias (Blake et al., 2016; Harris, 2013; Gangestad et al., 2016).

Third, some recent studies have reported null results (Harris, 2013; Zietsch et al., 2015; Scott et al., 2014; Marcinkowska et al., 2016; Munoz-Reyes et al., 2014). However, all of these studies used between-subject designs. This could be problematic because, even with large samples, the substantial genetic contribution to individual differences in facial masculinity preferences (Zietsch et al., 2015) could obscure subtle effects of hormonal status when between-subject designs are employed.

Fourth, studies using within-subject designs typically test women on only two occasions (Penton-Voak et al., 1999; Little & Jones, 2012; Johnston et al., 2001; Roney et al., 2011; Little et al., 2013). This limited approach may not adequately capture complex changes in hormonal status.

The current study directly addressed all of these potentially serious methodological problems by recruiting 584 heterosexual women for a longitudinal (i.e., within-subject) study in which both women's hormonal status and preferences for masculinity in men's faces were repeatedly assessed (519 women completed at least 5 test sessions, 176 women completed at

least 10 test sessions). Changes in women's hormonal status were assessed by measuring steroid hormones from saliva samples and also by tracking within-subject changes in hormonal contraceptive use.

Preferences for facial masculinity were measured using well-established methods (Penton-Voak et al., 1999; Little & Jones, 2012; Penton-Voak & Perrett, 2000; Vaughn et al., 2010; Ditzen et al., 2017; Harris, 2013; Zietsch et al., 2015; Marcinkowska et al., 2016; Munoz-Reyes et al., 2014; Little et al., 2002; Little et al., 2013) in which women chose between images of male faces in which sex-typical aspects of facial morphology had been increased (i.e., face shape was masculinized) or decreased (i.e., face shape was feminized) using computer graphics. Examples of these face stimuli are shown in Figure 1.

Figure 1. Examples of masculinized (left) and feminized (right) versions of men's faces used to assess facial masculinity preferences in our study.

Hormonal status is thought to influence women's preferences for masculinity when women assess men's attractiveness for short-term, but not long-term, relationships (Penton-Voak et al., 1999; Little & Jones, 2012). To address this

possibility, attractiveness of men for short-term relationships and long-term relationships were measured separately.

We tested four main hypotheses. Full model specifications and full results for these analyses are given in our Supplemental Materials (see osf.io/9b4y7). Importantly, our analyses showed no evidence that preferences for facial masculinity were related to changes in women's salivary steroid hormone levels. Our analyses also showed no evidence that oral contraceptive use decreased masculinity preferences.

Our Supplemental Materials (see osf.io/9b4y7) also report versions of each of the analyses reported below that controlled for hypothesized effects of women's partnership status (i.e., whether or not they had a romantic partner) on the magnitude of hormone-linked changes in women's masculinity preferences (Penton-Voak et al., 1999). These additional analyses also showed no evidence that women's salivary steroid hormone levels were related to their facial masculinity preferences or that oral contraceptive use decreased masculinity preferences.

Hypothesis 1. Do facial masculinity preferences track changes in measured steroid hormone levels in women not using hormonal contraceptives?

The fertile phase of the menstrual cycle is characterized by the combination of high estradiol and low progesterone (Gangestad & Haselton, 2015; Puts et al., 2013). Additionally, some previous studies have suggested that changes in women's masculinity preferences are positively correlated with changes in estradiol (Roney & Simmons, 2008; Roney et al., 2010) and negatively correlated with changes in progesterone (Jones et al., 2005; Puts, 2006). We therefore used linear mixed models to test for possible effects of estradiol, progesterone, and their interaction on women's facial masculinity preferences. Masculinity preference scores could range from -3.5 to 3.5 (0 indicated no preference) and higher scores indicated stronger masculinity preferences.

This analysis included all women who were not using any form of hormonal contraceptive when tested (N=351).

The significant intercept in our analysis (beta=0.35, SE=0.03, t=13.47, p<.001) indicated that these women generally judged masculinized versions of men's faces to be more attractive than feminized versions (M=0.35, SEM=0.03). The significant effect of relationship context in this analysis (beta=0.05, SE=0.01, t=4.10, p<.001) also indicated that these women generally showed stronger preferences for masculinized versions when judging men's attractiveness for short-term (M=0.37, SEM=0.03) than long-term (M=0.32, SEM=0.03) relationships. No effects involving hormone levels were significant (all ts<0.88, all ps>.38), suggesting that women's preferences for facial masculinity are not related to their hormonal status. This pattern of results did not change when partnership status was included in the model, although women with romantic partners reported stronger masculinity preferences (M=0.45, SEM=0.05) than did unpartnered women (M=0.31, SEM=0.03).

We conducted additional analyses to test for previously reported effects of testosterone (Welling et al., 2007) and cortisol (Ditzen et al./, 2017) on masculinity preferences, and for hypothesized effects of estradiol-to-progesterone ratio on mating-related behavior (Eisenbruch et al., 2015). These analyses also showed no evidence that women's preferences for masculine men were related to their hormone levels (see Supplemental Materials, osf.io/9b4y7).

Hypothesis 2. Do women not using hormonal contraceptives show stronger facial masculinity preferences than women using the combined oral contraceptive pill?

Studies reporting that women not using hormonal contraceptives show stronger facial masculinity preferences than do women using hormonal contraceptives have been interpreted as converging evidence that women's

hormonal status influences their facial masculinity preferences (Little et al., 2013). To investigate this issue in our data set, we first used linear mixed models to compare the facial masculinity preferences of women using the combined oral contraceptive pill (N=212) and women not using any form of hormonal contraceptive (N=326). This analysis included all women who had reported either no use of hormonal contraceptives throughout the study or use of the combined oral contraceptive pill throughout the study (responses from women who changed contraceptive status during the study are reported under Hypothesis 4).

The significant intercept (beta=0.41, SE=0.02, t=19.22, p<.001) indicated that the women generally judged masculinized versions of men's faces to be more attractive than feminized versions (M=0.40, SEM=0.02). The significant effect of relationship context (beta=0.05, SE=0.02, t=2.95, p=.003) indicated that masculinity preferences were again generally stronger when judging men's attractiveness for short-term (M=0.42, SEM=0.02) than long-term (M=0.38, SEM=0.02) relationships. Although there was a significant effect of oral contraceptive use (beta=0.12, SE=0.04, t=2.75, p=.006), the effect was such that women using the combined oral contraceptive pill showed *stronger* masculinity preferences (M=0.47, SEM=0.03) than did women not using any form of hormonal contraceptive (M=0.35, SEM=0.03). Note that stronger masculinity preferences in women using the combined oral contraceptive pill is the opposite pattern of results to what would be expected if fertility had the hypothesized positive effect on women's masculinity preferences. Stronger masculinity preferences in women using hormonal contraceptives have been reported in one other study (Cobey et al., 2015). We suggest that these between-group differences reflect effects of lifestyle and/or personality factors that are correlated with contraceptive use, rather than hormonal effects.

Hypothesis 3. Do facial masculinity preferences of women using the combined oral contraceptive pill change when they are taking inactive pills?

In women using the combined oral contraceptive pill, fertility-linked hormone levels are affected when women are not taking active pills (i.e., the scheduled ‘hormone-free interval’ or ‘break’) during their monthly cycle of oral contraceptive use (van Heusden & Fauser, 2002). If women’s masculinity preferences are influenced by their hormonal status, one would then expect women’s facial masculinity preferences to change during this scheduled break. To investigate this possibility, we used linear mixed models to compare the facial masculinity preferences of women (N=173) using the combined oral contraceptive pill when they were taking active pills versus when they were taking a scheduled break from taking active pills. Note that not all women using the combined oral contraceptive pill were tested during a scheduled break.

Consistent with our previous analyses, the significant intercept (beta=0.44, SE=0.03, t=12.66, p<.001) and effect of relationship context (beta=0.06, SE=0.02, t=2.73, p=.007) showed that women generally preferred masculinized faces (M=0.44, SEM=0.03) and that this masculinity preference was stronger when women judged men’s attractiveness for short-term (M=0.47, SEM=0.04) than long-term (M=0.41, SEM=0.04) relationships. No effects involving the scheduled break were significant (both absolute ts<0.64, both ps>.52).

Hypothesis 4. Do facial masculinity preferences change when women start or stop using the combined oral contraceptive pill?

During the course of the current study, 45 women changed their hormonal contraceptive use by either switching from using no hormonal contraceptive to using the combined oral contraceptive pill, or vice versa. There was a mean time of 360 days (SD=282 days, range=56 to 1113 days) between test sessions where women were using no hormonal contraceptives and those where they were using the combined oral contraceptive pill. A previous study of 18 women’s facial masculinity preferences reported that women’s preferences for masculinity in men’s faces decreased when women started using oral contraceptives (Little et al., 2013). We therefore used linear mixed

models to compare the facial masculinity preferences of these women when they were using the combined oral contraceptive pill and when they were using no form of hormonal contraceptive. Our analysis controlled for the direction of change in women's oral contraceptive use (i.e., whether they changed from using no form of hormonal contraceptive to using the combined oral contraceptive pill, N=30; or vice versa, N=15).

The significant intercept in this analysis (beta=0.39, SE=0.07, t=5.83, p<.001) indicated that these women generally judged masculinized versions of men's faces to be more attractive than feminized versions (M=0.36, SEM=0.06). As in our previous analyses, women's facial masculinity preferences were generally stronger when judging men's attractiveness for short-term (M=0.40, SEM=0.06) than long-term (M=0.34, SEM=0.07) relationships, although the effect of relationship context was not significant in this smaller subset of participants (beta=0.06, SE=0.03, t=1.81, p=.073). The effect of oral contraceptive use was not significant (beta=0.08, SE=0.05, t=1.57, p=.12). Note that women's masculinity preferences tended to be stronger when they were using the combined oral contraceptive pill (although not significantly so), suggesting that a lack of power did not prevent detection of the hypothesized weaker masculinity preferences when women are using the combined oral contraceptive pill.

Because changes in oral contraceptive use could be associated with a change in partnership status, we repeated this analysis controlling for possible effects of changes in women's partnership status (see Supplemental Materials, osf.io/9b4y7). This additional analysis also did not show any evidence that using the combined oral contraceptive pill weakened women's masculinity preferences.

Conclusions

Collectively, our analyses show no evidence that changes in women's salivary hormone levels are associated with their facial masculinity preferences or that the combined oral contraceptive pill decreases women's masculinity

preferences. This was despite having a much larger sample size, having tested participants more often, and having used more reliable measures of hormonal status (e.g., measurements of multiple steroid hormones from saliva samples) than previous studies. Thus, the current study presents strong evidence against the popular and influential hypothesis that women's facial masculinity preferences increase when women are in hormonal conditions associated with fertility.

Our analyses do, however, present clear evidence that women show stronger preferences for masculine facial characteristics when assessing men's attractiveness for short-term relationships than when assessing men's attractiveness for long-term relationships. This pattern of results is consistent with the proposal that perceived costs associated with choosing a masculine mate cause women's preferences for masculinity in long-term partners to be weaker than preferences for masculinity in short-term partners (Little et al., 2011). Thus, our data suggest that differences in the temporal context of the relationship sought, rather than differences in hormonal status, contribute to variation in women’s attraction to masculine men.

Methods

Participants

Five hundred and ninety-eight heterosexual white women who reported that they were either not using any form of hormonal contraceptive (i.e., had natural menstrual cycles) or were using the combined oral contraceptive pill were recruited for the study. Data from 14 of these women were excluded from the dataset because they reported hormonal contraceptive use inconsistently within a single block of test sessions. Thus, the final data set was 584 women (mean age=21.46 years, SD=3.09 years). Participants completed up to three blocks of test sessions (mean time between Block 1 and Block 2 = 230 days; mean time between Block 2 and Block 3 = 487 days). Each of the three blocks of test sessions consisted of five weekly test sessions. Table 1 shows how many women completed one, two, three, four, or five test sessions in Block 1, Block 2, and Block 3.

Table 1. The number of women who completed five, four, three, two, or one weekly test sessions in Block 1, Block 2, and Block 3.

	5 sessions	**4 sessions**	**3 sessions**	**2 sessions**	**1 session**
Block 1	508	22	6	14	26
Block 2	184	3	3	1	4
Block 3	18	0	0	0	0

Forty-five women reported changing their hormonal contraceptive status between blocks during the study. Fifteen women reported changing from using the combined oral contraceptive pill to not using the combined oral contraceptive pill and 30 women reported changing from not using the combined oral contraceptive pill to using the combined oral contraceptive pill.

Stimuli

The methods we used to manufacture stimuli to test women's preferences for facial masculinity have been used in many previous studies (e.g., Penton-Voak et al., 1999; Little & Jones, 2012; Penton-Voak & Perrett, 2000; Johnston et al., 2001; Welling et al., 2007; Harris, 2013; Zietsch et al., 2015; Scott et al., 2014; Marcinkowska et al., 2016; Munoz-Reyes et al., 2014). Responses to stimuli manufactured using these methods predict women's actual partner choices have been shown to be very similar to responses to stimuli manufactured using other methods for manipulating sexually dimorphic characteristics in face images (DeBruine et al., 2006). We have made the stimuli from this study publicly available at osf.io/9b4y7.

First, we manufactured a female prototype (i.e., average) face by using specialist software (Tiddeman et al., 2001) to average the shape, color, and texture information from images of 50 young white women's faces. A male prototype face was also manufactured in this way by averaging the shape, color, and texture information from images of 50 young white men's faces.

Next, we randomly selected 10 images from the set of 50 individual male faces. We then created a feminized and a masculinized version of each of these 10 male images by adding or subtracting 50% of the linear (i.e., vector) differences in 2D shape between symmetrized versions of the female and male prototypes to (or from) each individual image. This process created 10 pairs of face images in total, with each pair consisting of a feminized and a masculinized version of one of the individual face images. Examples of these stimuli are shown in Figure 1. Note that our feminized and masculinized versions of faces differed in sexually dimorphic shape characteristics only (i.e., were matched in other regards, such as identity, color, and texture, Tiddeman et al., 2001).

Procedure

In each test session, women reported their current romantic partnership status (partnered or unpartnered), reported their hormonal contraceptive use status (using the combined oral contraceptive pill, not using any form of hormonal contraceptive), reported whether they were currently taking a scheduled break from the pill (and, if so, how many days into this scheduled break they were), provided a saliva sample, and completed two face preference tests (one assessing men's attractiveness for a short-term relationship, the other assessing men's attractiveness for a long-term relationship).

In the two face preference tests, women were shown the 10 pairs of male faces, each pair consisting of a masculinized and feminized version of a given individual. Women were instructed to select the more attractive face in each pair and to indicate the strength of that preference by choosing from the options "slightly more attractive", "somewhat more attractive", more attractive", and "much more attractive". This procedure has been used to assess masculinity preferences in previous studies (e.g., Zietsch et al., 2015).

In the short-term attractiveness test, women were told: "You are looking for the type of person who would be attractive in a short-term relationship. This implies that the relationship may not last a long time. Examples of this type of

relationship would include a single date accepted on the spur of the moment, an affair within a long-term relationship, and possibility of a one-night stand."

In the long-term attractiveness test, women were told: "You are looking for the type of person who would be attractive in a long-term relationship. Examples of this type of relationship would include someone you may want to move in with, someone you may consider leaving a current partner to be with, and someone you may, at some point, wish to marry (or enter into a relationship on similar grounds as marriage)."

Trial order within each test was fully randomized and the order in which the two face preference tests were completed in each test session was also fully randomized. Definitions of short-term and long-term relationships were taken from previous studies (Little & Jones, 2012; Penton-Voak et al., 2003).

Responses on the face preference test were coded using the following scale (higher scores indicate stronger masculinity preferences and the scale is centered on chance, i.e., zero):

0.5 to 3.5: masculinized face rated 'slightly more attractive' (=0.5), 'somewhat more attractive' (=1.5), 'more attractive' (=2.5) or 'much more attractive' (=3.5) than feminized face.

-0.5 to -3.5: feminized face rated 'slightly more attractive' (=-0.5), 'somewhat more attractive' (=-1.5), 'more attractive' (=-2.5) or 'much more attractive' (=-3.5) than masculinized face.

Each woman's average masculinity preference score was calculated separately for the short-term and long-term judgments for each test session. Higher scores indicate stronger masculinity preferences.

In each face preference test, the 10 trials assessing preferences for sexually dimorphic shape characteristics were interspersed among 30 filler trials assessing preferences for other facial traits.

Saliva samples

Participants 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=3.30 pg/mL, SD=1.27 pg/mL, sensitivity=0.1 pg/mL, intra-assay CV=7.13%, inter-assay CV=7.45%), Salivary Progesterone Enzyme Immunoassay Kit 1-1502 (M=148.55 pg/mL, SD=96.13 pg/mL, sensitivity=5 pg/mL, intra-assay CV=6.20%, inter-assay CV=7.55%), Salivary Testosterone Enzyme Immunoassay Kit 1-2402 (M=87.66 pg/mL, SD=27.19 pg/mL, sensitivity<1.0 pg/mL, intra-assay CV=4.60%, inter-assay CV=9.83%), and Salivary Cortisol Enzyme Immunoassay Kit 1-3002 (M=0.23 µg/dL, SD=0.16 µg/dL, sensitivity<0.003 µg/dL, intra-assay CV=3.50%, inter-assay CV=5.08%). Only hormone levels from women not using hormonal contraceptives were used in analyses (values given above are for these women only).

Hormone levels more than three standard deviations from the sample mean for that hormone or where Salimetrics indicated levels were outside their sensitivity range were excluded from the dataset (~1% of hormone measures were excluded for these reasons). The descriptive statistics given above do not include these excluded values. Values for each hormone were centered on their subject-specific means to isolate effects of within-subject changes in hormones. They were then scaled so the majority of the distribution for each hormone varied from -.5 to .5 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 analyses considering hormone levels.

Analyses

Linear mixed models were used to test for possible effects of hormonal status on women's facial masculinity preferences. Analyses were conducted using R version 3.3.2 (R Core Team, 2016), with lme4 version 1.1-13 (Bates et al., 2014) and lmerTest version 2.0-33 (Kuznetsova et al., 2013). The dependent variable was masculinity preference score, which was centered on chance. The relationship context for which women had judged men's attractiveness was effect-coded (short-term=+0.5 and long-term=-0.5) and included as an independent variable in all analyses. Random slopes were specified maximally following Barr et al. (2013) and Barr (2013). Full model specifications and full results for each analysis are given in our Supplemental Materials (see osf.io/9b4y7). Data files and analysis scripts are also available at osf.io/9b4y7.

References

Barr, D. J. (2013) Random effects structure for testing interactions in linear mixed-effects models. *Frontiers in Psychology, 4*, 328.

Barr, D. J., Levy, R., Scheepers, C., & Tily, H. J. (2013) Random effects structure for confirmatory hypothesis testing: Keep it maximal. *Journal of Memory and Language, 68*, 255 – 278.

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2014). lme4: Linear mixed-effects models using Eigen and S4. R package version, 1.1-13.

Bao, A. -M., Liu, R. -Y., Van Someren, E., Hofman, M. A., Cao, Y. -X., & Zhou, J. -N. (2003). Diurnal rhythm of free estradiol during the menstrual cycle. *European Journal of Endocrinology, 148,* 227 – 232.

Blake, K. R., Dixson, B. J. W., O'Dean, S. M., & Denson, T. F. (2016). Standardized protocols for characterizing women's fertility: A data-driven approach. *Hormones and Behavior, 81,* 74 – 83.

Cobey, K. D., Little, A. C., & Roberts, S. C. (2015). Hormonal effects on women's facial masculinity preferences: The influence of pregnancy,

post-partum and hormonal contraceptive use. *Biological Psychology, 104,* 35 – 40.

DeBruine, L. M., et al. (2006). Correlated preferences for facial masculinity and ideal or actual partner's masculinity. *Proceedings of the Royal Society B, 273,* 1355 –1360.

Ditzen, B., Palm-Fischbacher, S., Gossweiler, L., Stucky, L., & Ehlert, U. (2017). Effects of stress on women's preference for male facial masculinity and their endocrine correlates. Psychoneuroendocrinology, in press.

Eisenbruch, A. B., Simmons, Z. L., & Roney, J. R. (2015). Lady in red. *Psychological Science, 26,* 1332 – 1338.

Fink, B. & Penton-Voak, I. S. (2002). Evolutionary psychology of facial attractiveness. *Current Directions in Psychological Science, 11,* 154 – 158.

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

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

Gangestad, S. W. & Haselton, M. G. (2015). Human estrus: Implications for relationship science. *Current Opinion in Psychology, 1,* 45 – 51.

Gangestad, S. W., et al. (2016). How valid are assessments of conception probability in ovulatory cycle research? Evaluations, recommendations, and theoretical implications. *Evolution and Human Behavior, 37,* 85 – 96.

Gildersleeve, K., Haselton, M. G., & Fales, M. (2014). Do women's mate preferences change across the ovulatory cycle? A meta-analytic review. *Psychological Bulletin, 140,* 1205 – 1259.

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

Harris, C. R. (2013). Shifts in masculinity preferences across the menstrual cycle: Still not there. *Sex Roles, 69*, 507 – 515.

Johnston, V. S., Hagel, R., Franklin, M., Fink, B., & Grammer, K. (2001). Male facial attractiveness: Evidence for hormone-mediated adaptive design. *Evolution and Human Behavior, 22,* 251 – 267.

Jones, B. C., et al. (2005). Commitment to relationships and preferences for femininity and apparent health in faces are strongest on days of the menstrual cycle when progesterone level is high. *Hormones and Behavior, 48*, 283 – 290.

Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2013). lmerTest: Tests for random and fixed effects for linear mixed effect models (lmer objects of lme4 package). R package version 2.0-33.

Little, A. C., Jones, B. C., & DeBruine, L. M. (2011). Facial attractiveness: Evolutionary based research. *Philosophical Transactions of the Royal Society B, 366,* 1638 – 1659.

Little, A. C. & Jones, B. C. (2012). Variation in facial masculinity and symmetry preferences across the menstrual cycle is moderated by relationship context. *Psychoneuroendocrinology, 37,* 999 – 1008.

Little, A. C., Jones, B. C., Penton-Voak, I. S., Burt, D. M., & Perrett, D. I. (2002). Partnership status and the temporal context of relationships influence human female preferences for sexual dimorphism in male face shape. *Proceedings of the Royal Society B*, *269*, 1095 – 1103.

Little, A. C., Burriss, R. P., Petrie, M., Jones, B. C., & Roberts, S. C. (2013). Oral contraceptive use in women changes preferences for male facial masculinity and is associated with partner facial masculinity. *Psychoneuroendocrinology, 38,* 1777 – 1785.

Marcinkowska, U. M., et al., (2016). Lack of support for relation between woman's masculinity preference, estradiol level and mating context. *Hormones and Behavior, 78,* 1 – 7.

Muñoz-Reyes, J. A., Iglesias-Julios, M., Martín-Elola, C., Losada-Perez, M., Monedero, I., Pita, M., & Turiégano, E. (2014). Changes in preference for male faces during the menstrual cycle in a Spanish population. *Anales de Psicología, 30*, 667 – 675.

Papacosta, E., & Nassis, G. P. (2011). Saliva as a tool for monitoring steroid, peptide and immune markers in sport and exercise science. *Journal of Science and Medicine in Sport, 14*, 424 – 434.

Penton-Voak, I. S., et al. (1999). Menstrual cycle alters face preference. *Nature, 399*, 741 – 742.

Penton-Voak, I. S. & Perrett, D. I. (2000). Female preference for male faces changes cyclically: Further evidence. *Evolution and Human Behavior, 21*, 39 – 48.

Penton-Voak, I. S., Little, A. C., Jones, B. C., Burt, D. M., Tiddeman, B. P., & Perrett, D. I. (2003). Female condition influences preferences for sexual dimorphism in faces of male humans (Homo sapiens). *Journal of Comparative Psychology, 117*, 264 – 271.

Perrett, D. I., et al. (1998). Effects of sexual dimorphism on facial attractiveness. *Nature, 394*, 884 – 887.

Puts, D. A. (2006). Cyclic variation in women's preferences for masculine traits: Potential hormonal causes. *Human Nature: An Interdisciplinary Biosocial Perspective, 17*, 114 – 127.

Puts, D. A., et al., (2013). Women's attractiveness changes with estradiol and progesterone across the ovulatory cycle. *Hormones and Behavior, 63*. 13 – 19.

Roney, J. R., Simmons, Z. L., & Gray, P. B. (2011). Changes in estradiol predict within-women shifts in attraction to facial cues of men's testosterone. *Psychoneuroendocrinology, 36*, 742 –749.

Roney, J. R. & Simmons, Z. L. (2008). Women's estradiol predicts preference for facial cues of men's testosterone. *Hormones and Behavior, 53,* 14 – 19.

R Core Team (2016). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Scott, I. M., et al. (2014). Human preferences for sexually dimorphic faces may be evolutionarily novel. *Proceedings of the National Academy of Sciences, 111*, 14388 – 14393.

Thornhill, R. & Gangestad, S. W. (1999). Facial Attractiveness. *Trends in Cognitive Sciences, 3,* 452 – 460

Tiddeman, B., Burt, M., & Perrett, D. I. (2001). Prototyping and transforming facial textures for perception research. *IEEE computer graphics and applications, 21*, 42 – 50.

van Heusden, A. M. & Fauser, B. C. J. M. (2002). Residual ovarian activity during oral steroid contraception. *Human Reproduction Update, 8,* 345 – 358.

Vaughn, J. E., Bradley, K. I., Byrd-Craven, J., & Kennison, S. M. (2010). The effect of mortality salience on women's judgments of male faces. *Evolutionary Psychology, 8*, 477 – 491.

Veldhuis, J. D., Christiansen, E., Evans, W. S., Kolp, L. A., Rogol, A. D., & Johnson, M. L. (1988). Physiological profiles of episodic progesterone release during the midluteal phase of the human menstrual cycle: Analysis of circadian and ultradian rhythms, discrete pulse properties, and correlations with simultaneous luteinizing hormone release. *Journal of Clinical Endocrinology and Metabolism, 66*, 414 – 421.

Welling, L. L. M., et al. (2007). Raised salivary testosterone in women is associated with increased attraction to masculine faces. *Hormones and Behavior, 52*, 156 – 161.

Zietsch, B. P., Lee, A. J., Sherlock, J. M., & Jern, P. (2015). Variation in women's preferences regarding male facial masculinity is better explained by genetic differences than by previously identified context-dependent effects. *Psychological Science, 26,* 1440 – 1448.