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Women's estradiol predicts preference for facial cues of men's testosterone

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Abstract

A growing body of research has shown that women express stronger attraction to more masculine traits when they are tested near ovulation than when tested during other times in the menstrual cycle. Although these effects have been interpreted as increased preferences for markers of elevated testosterone during times in the cycle when conception is most likely, no previous studies have directly demonstrated that women express stronger attraction to higher testosterone men at different times in the cycle. In addition, little research has addressed which hormonal or other physiological mechanisms may regulate temporal shifts in women's attractiveness judgments. In this research, we demonstrate that women with higher estradiol concentrations exhibit stronger preferences for the faces of men with higher testosterone concentrations, and that women's testosterone preference and estradiol curves track one another across days of the cycle. The findings are the first direct demonstration in humans that hormone concentrations in one sex are associated with attraction to cues of hormonal status in the opposite sex. The results support a functional role for estradiol in calibrating women's mating psychology to indices of their current fertility, analogous to similar processes that have been documented in nonhuman species. A strong correlation between estradiol and testosterone preference specifically during the luteal phase further suggests that women's mate preferences may track their fertility between different cycles in addition to being calibrated to the timing of ovulation within individual cycles.

Keywords: Menstrual cycle; Mate preferences; Estradiol; Testosterone; Attractiveness

Introduction

An expanding research literature has provided evidence that menstrual cycle phase is associated with shifts in women's mate preferences: the time near ovulation is associated with stronger preferences for facial masculinity (Johnston et al., 2001; Penton-Voak et al., 1999; Penton-Voak and Perrett, 2000), deeper voice pitch (Feinberg et al., 2006; Puts, 2005), more masculine body shape (Little et al., 2007), and olfactory cues associated with body symmetry (Gangestad and Thornhill, 1998; Thornhill and Gangestad, 1999). These effects have been widely interpreted as products of mechanisms that are designed to increase attraction to good genes markers during days of the cycle when conception is possible (for a review, see Gangestad et al., 2005). Traits such as facial masculinity are alleged to indicate genetic quality because they are markers of higher testosterone concentrations (e.g., Penton-Voak et al., 1999; for evidence that higher testosterone men do possess more masculine faces, see Penton-Voak and Chen, 2004; Roney et al., 2006), with high testosterone in turn being sustainable only by healthier men due to the hormone's immunosuppressive effects (Folstad and Karter, 1992). Despite the central role played by testosterone in such arguments, though, no cycle shifts studies have measured the actual testosterone concentrations of the men whose stimuli were rated by women.

There is likewise little direct evidence regarding which physiological mechanisms in women may regulate cycle phase shifts in attractiveness judgments. Studies that have estimated women's hormone concentrations by assigning population averages to specific cycle days have reported null effects of estradiol and negative effects of progesterone on preferences for artificially masculinized traits (Jones et al., 2005; Puts, 2006); given variability in the shape of hormone curves around population averages (e.g., Alliende, 2002), though, direct measurements of women's hormone concentrations may be more informative. A recent study (Welling et al., 2007) found that women chose artificially masculinized faces as more attractive

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than artificially feminized faces at higher rates during test sessions when women's salivary testosterone was higher. Although that study suggests testosterone may be the important physiological regulator of cycle phase shifts, it is not clear whether the computer morphing techniques used to artificially masculinize faces may accurately represent natural cues of men's sex hormone concentrations. Our goal in the present research is to test whether sex hormone concentrations in women predict differential attraction to the unmanipulated faces of higher testosterone men.

Determination of the physiological signals that regulate temporal shifts in women's mate preferences is important because it may shed light on the evolved functions of such shifts. Extant studies (Jones et al., 2005; Puts, 2006; Welling et al., 2007) have all proposed hormonal signals that may demarcate the fertile days within a given menstrual cycle but it is potentially important to point out that hormone concentrations also vary considerably between different cycles within the same women. Ovarian hormones undergo suppression in response to negative energy balance (for reviews, see Ellison, 1994, 2001), for instance, and evidence suggests that women are more likely to conceive during cycles with higher estradiol concentrations (Lipson and Ellison, 1996; Venners et al., 2006). Brain mechanisms could therefore use estradiol as an index of the fertility of a given menstrual cycle, and increase attraction to more masculine traits across cycle days in more vs. less fertile cycles. Since estradiol also reaches a maximum near ovulation within individual cycles, though, such a mechanism might generate within-cycle preference shifts even if it was primarily designed to change psychology across different cycles. In summary, we propose that hormonal mechanisms might be designed to adjust mating psychology between different cycles instead of or in addition to calibrating preferences to the timing of ovulation within individual cycles.

A mechanism designed to adjust mating psychology across different cycles seems plausible on functional grounds. Women in ancestral environments likely experienced long periods of suppressed fertility associated with events such as lactation or energetic stress, much like women in modern, natural fertility populations (e.g., Strassmann, 1997). Attraction to good genes markers would have been less important during stretches of the life-cycle when conception was unlikely, and reduced attention to men's sexual attractiveness at such times may have facilitated an adjustment of motivational priorities toward tasks such as foraging or care of young children. Upon re-experiencing more fertile menstrual cycles characterized by higher estradiol concentrations, though, increased weight placed on good genes markers may have increased the probability of mate choice leading to the production of healthier offspring. On this account, estradiol could act as a signal that couples the activation of mate preference mechanisms to the conditions under which mating effort is most adaptive.

Evidence supports a similar functional role for estradiol in various nonhuman species. Ovariectomized female rodents exhibit no preferences for associating with intact over castrated males, but ovariectomized females administered estradiol and progesterone exhibit clear preferences for intact males (e.g., Edwards and Pfeifle, 1983; Xiao et al., 2004). Other evidence further suggests that intact, cycling females exhibit preferences for the odors of higher testosterone males (e.g., Ferkin et al., 1994; Litvinova et al., 2005). These studies support a role for estradiol in promoting attraction to androgen-dependent cues in males. A similar role for estradiol in humans has not yet been directly tested.

In the present research, we directly measured men's testosterone concentrations and women's estradiol, progesterone, and testosterone concentrations; photographed the men's faces; and asked the women to rate the face photographs for physical attractiveness. Based on the positive relationships between estradiol and both within- and between-cycle fertility, and based on the nonhuman literature, we hypothesized that women's estradiol concentrations would positively predict their preferences for the faces of men with higher testosterone concentrations. As a preliminary test of whether attractiveness judgments may fluctuate with indices of between-cycle fertility, we tested the secondary hypothesis that estradiol will predict testosterone preferences when analyses are restricted to women tested during the luteal phase. Conception is not possible during the luteal phase, but estradiol will clearly be higher during luteal phase days of fertile ovulatory cycles vs. during, say, amenorrheic cycles with suppressed ovarian hormones. As such, elevated luteal estradiol can indicate that a woman is currently experiencing higher fertility cycles, and a positive correlation between estradiol and testosterone preference during the luteal phase would therefore be consistent with the operation of a mechanism that adjusts attractiveness judgments between different cycles.

Methods

Subjects

The subjects who provided the stimulus photos were male students at the University of California, Santa Barbara (UCSB). Data from one man were excluded due to insufficient saliva for testosterone assay and from another man whose testosterone concentration was over four SD above the mean. The final sample of 37 faces included 23 men who self-identified as Caucasian, 5 as Hispanic, 4 as Asian, and 5 as mixed ethnicity. Mean age of the men was 19.69± 0.28 years.

Women raters were UCSB students who were recruited conditional on not using hormonal contraceptives. Complete rating data were available from 75 women, though correlations between preferences and specific hormone concentrations were based on slighter smaller samples due to missing hormone data and the exclusion of extreme outliers for hormone concentrations (see Hormonal analyses). Forty-three women self-identified as Caucasian, 10 as Hispanic, 14 as Asian, 7 as mixed ethnicity, and 1 as African American. Mean age of the women was 18.36±0.10 years.

Procedures

Upon arrival, male subjects provided a saliva sample via passive drool into polypropylene vials. They were next photographed at a standard distance using a digital camera and were instructed to assume a neutral facial expression for the photos.

Women rated the photos for 'physical attractiveness' on a 1–7 scale with the faces presented in random order by a computer program. Ovals were placed around the faces to obscure information about hairstyles. The women raters also provided saliva samples at the beginning and end of the testing session, and completed a number of other measures. Of relevance to the present report, one of these measures was a survey in which the women indicated the first day of their last menses.

Table 1
Correlates of women's testosterone preference

	Estradiol	Progesterone	Testosterone	Conception risk
Testosterone Preference	0.351 $p=0.003$	0.057 $p=0.629$	0.059 $p=0.625$	0.224 $p=0.053$

Note. Spearman's rank-order correlations appear in the table. Degrees of freedom = 73 for conception risk, 71 for progesterone, and 70 for estradiol and testosterone.

Hormonal analyses

Saliva samples were stored at −80 °C before being shipped on dry ice to the Mendoza Endocrine Core Lab of the California National Primate Research Center, University of California, Davis. Hormone concentrations were estimated in duplicate using commercial radioimmunoassay kits (estradiol and testosterone from Diagnostics Systems Laboratories, Webster, TX; progesterone from Diagnostic Products Corporation, Los Angeles, CA) modified for use with saliva. The assay for men's testosterone had a sensitivity of 1.956 pg/ml and intra- and inter-assay coefficients of variation (CV) of 6.06 and 4.21, respectively. Sensitivities of women's progesterone, estradiol, and testosterone assays were 0.009 ng/ml, 0.62 pg/ml, and 0.97 pg/ml, respectively. Intra- and inter-assay CVs, respectively, were 4.17 and 10.58 for progesterone, 6.88 and 8.71 for estradiol, and 4.33 and 5.51 for testosterone. The two saliva samples collected from each woman produced assay concentrations that were highly correlated with one another (rs > 0.75) and thus means of the two sample values for each hormone were used in data analyses. For each hormone, outliers more than three standard deviations from the mean were dropped from data analyses, though results were similar with outliers included. Combined with missing assay data from one woman for estradiol, this produced sample sizes of $n=72$ for estradiol and testosterone, and $n=73$ for progesterone.

Statistical analyses

Men's testosterone concentrations were correlated with time of day at which samples were collected, r (37) = −0.35, $p=0.033$. To remove the influence of time, testosterone concentrations were regressed onto the time of day variable and the standardized residuals were employed in subsequent analyses. Testosterone concentrations were marginally associated with ethnic group membership, $F(3,33)=2.19$, $p=0.11$; to remove a possible confound between preference for testosterone and preference for specific ethnic groups, we standardized the time-corrected testosterone concentrations within ethnic group categories to produce values relative to other members of the same group. These values were highly correlated with those that were not standardized within ethnic groups ($r=0.89$) and no statistical conclusions were changed via this transformation. Both the raw and transformed testosterone variables were normally distributed as determined by the Shapiro–Wilk test ($p>0.40$).

To measure each woman's preference for testosterone, we regressed her attractiveness ratings of the faces onto the transformed testosterone concentrations of the men depicted in the photos; the resulting regression coefficients indicate how much variance in a woman's preferences is accounted for by men's testosterone. Following convention in other cycle shift studies, we used women's reports of the first day of their last menses to assign 'conception risk' values based on published estimates of the probability of unprotected intercourse producing a conception on that day of the cycle (Wilcox et al., 2001). In addition, we assigned estimated estradiol values to the cycle days on which women were tested based on published estimates of the median population values of estradiol associated with those days (Stricker et al., 2006). Women's hormone concentrations were not normally distributed, and therefore associations between raters' hormone values and their preferences for testosterone were tested using nonparametric, rank-order correlations. Descriptive statistics appear as mean ± SEM. Reported significance levels are all two-tailed.

Results and discussion

Our primary hypothesis predicted that women's testosterone preferences would be calibrated to their estradiol concentrations. Results depicted in Table 1 demonstrate that the women in our sample with higher estradiol concentrations did in fact exhibit stronger preferences for the faces of men with greater testosterone concentrations. Women's progesterone and testosterone were unrelated to such preferences. Women tested on days of the cycle with higher estimated conception risk also exhibited stronger preferences for facial cues of men's testosterone, a result that extends the demonstration of menstrual phase shifts in preferences for artificially masculinized stimuli to direct preferences for testosterone in natural stimuli.

The correlation between estradiol and testosterone preference depicted in Table 1 was computed from women who were tested across diverse cycle days, and, as such, it is ambiguous to what extent the relationship was driven by stronger testosterone preferences among women tested on higher estradiol days of the cycle, or by women with higher estradiol for a given cycle day also exhibiting stronger preferences for testosterone. To help address this, Fig. 1 plots women's testosterone preferences and estradiol concentrations by day of the menstrual cycle (values represent three day moving averages computed as a means of smoothing the two curves). Notice that women in our sample should be randomly distributed across cycle days and thus a high trait estradiol woman should be just as likely to appear on day 18 (a testosterone preference nadir) as on day 14 (a preference peak). The similar peaks in the estradiol and testosterone preference curves seen in Fig. 1 therefore entail that individual women's testosterone preferences are tracking changes in their estradiol concentrations across days of the cycle. Further supporting this argument, our subjects' testosterone preference scores were also positively correlated with estimates of the median population values of estradiol associated with the cycle days on which women were tested, r (65) = 0.31, $p=0.011$ (sample size is reduced because estimated values were not available for all cycle days).

The estradiol and testosterone preference curves in Fig. 1 move in concert across most regions of the cycle, with a notable exception in the early to mid-follicular phase. This is interesting in light of our theory that women's attractiveness judgments are calibrated to indices of current cycle fertility, as estradiol is a

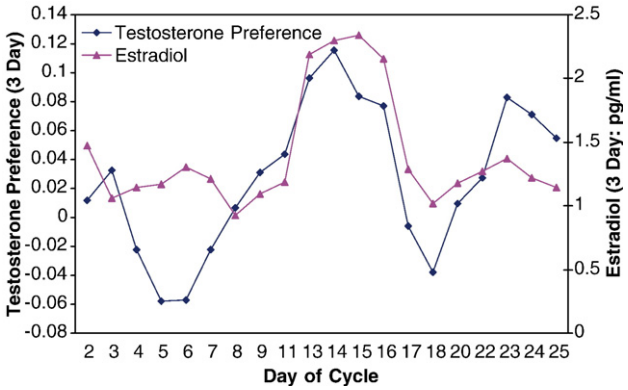

Fig. 1. Women's testosterone preferences and estradiol concentrations as a function of day of the cycle. Values are 3-day moving averages. Testosterone preferences are expressed as standardized regression coefficients (primary y-axis) and estradiol concentrations are expressed as pg/ml (secondary y-axis). Day of cycle ends at day 25 due to consecutive missing days later in the cycle.

poor predictor of fertility early in the cycle. Estradiol needs to be low early in the follicular phase in order to avoid negative feedback suppression of follicle-stimulating hormone (e.g., Fauser and Van Heusden, 1997; Zeleznik, 2004), for instance, and dominant follicle maturation – from which cycle fertility is ultimately derived – does not typically produce peripheral increases in estradiol until about 5 days before the mid-cycle gonadotropin surge (Zeleznik, 2004). When we excluded the first 8 days of the cycle (before estradiol concentrations began rising; see Fig. 1), the overall correlation between estradiol and testosterone preference rose to r (47)=0.55, $p<0.001$. As such, the testosterone preference and estradiol curves were closely aligned over precisely those regions of the cycle in which estradiol best indexes current cycle fertility.

Our secondary hypothesis predicted that women's estradiol concentrations would predict their testosterone preferences when analyses were restricted to women tested during the luteal phase. Fig. 2 demonstrates confirmation of this prediction. This result suggests that the overall correlation between estradiol and testosterone preference does not arise entirely from mid-cycle peaks in both variables since the correlation persists when comparing women who were tested at roughly the same stage of the cycle. Because conception is not possible during the luteal phase, this relationship cannot be explained as the functional output of a mechanism designed to increase attraction to good genes markers during fertile days of the cycle, although the correlation might arise as a non-functional by-product of a mechanism that uses estradiol concentrations to estimate the timing of ovulation. Alternatively, the pattern in Fig. 2 does represent the expected functional output of a between-cycle mechanism that up-regulates attraction to androgen-dependent cues in more fertile cycles characterized by higher concentrations of estradiol. As such, this finding provides at least preliminary evidence for the existence of a between-cycle mechanism.

The overall pattern of results in this study supports the proposition that estradiol – or some signal associated with estradiol – promotes women's attraction to androgen-dependent cues in men. Because estradiol is elevated across most cycle days in higher vs. lower fertility cycles (Lipson and Ellison, 1996; Venners et al., 2006), and because it reaches a maximum near ovulation within individual ovulatory cycles, it provides an efficient signal for calibrating women's attractiveness judgments to two related circumstances: (1) whether a woman is currently experiencing a fertile cycle, and (2) whether a woman is currently within the fertile portion of a fertile cycle. The first circumstance has been completely neglected in the extant mating psychology literature, despite the fact that both types of calibrations may have offered adaptive advantages. Ancestral women may have routinely gone years without experiencing fertile menstrual cycles (see Strassmann, 1997), and reduced attraction to androgen-dependent cues at such times may have functioned in part to preferentially allocate effort into the solution of adaptive problems other than mate choice. Upon experiencing higher fertility cycles, though, assessment of men's heritable fitness would clearly take on relatively greater importance. Since human mate choice and courtship occur throughout the cycle and not only during a circumscribed estrous, furthermore, greater attraction to good genes markers was likely functional across cycle days in higher vs. lower fertility cycles (for example, attention to men's sexual attractiveness would be important even during the luteal phase of more fertile cycles since partners chosen at such times could sire offspring in subsequent cycles). This was likely true even among women with romantic partners, as there would presumably be advantages to updating a partner's perceived mate quality relative to possible alternatives, and the weighting placed on genetic quality in any such calculus should be relatively higher during stretches of the life span when a woman is more likely to conceive. Within-cycle adjustments in mating psychology follow as a direct extension of this same logic, as the importance of careful mate choice (especially with respect to markers of genetic quality in sexual partners) would have reached a maximum on days of high fertility cycles when conception was actually possible. In summary, regulation of attraction to androgen-dependent cues by estradiol makes functional sense as a mechanism for calibrating mating psychology to continuous gradations in women's likely fertility.

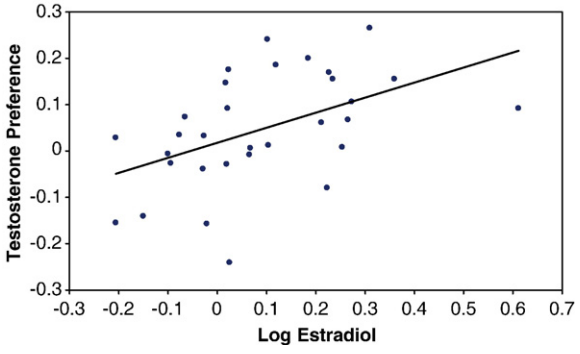

Fig. 2. Women's testosterone preferences (expressed as standardized regression coefficients) plotted against their estradiol concentrations for women tested after day 16 of the cycle. Estradiol is log transformed for graphical purposes; the rank-order correlation between raw estradiol and testosterone preference is r (31)= 0.524, p=0.002.

A limitation of the present study is that each woman was measured only once and thus the analyses were entirely between-subjects. A more ideal design would measure the same women both multiple times within the same cycles and on equivalent cycle days across different cycles, thus allowing for a more precise quantification of possible within-cycle and between-cycle co-variance between hormone concentrations and preferences for specific traits. Although the present design does not allow us to precisely parcel how much of the correlation between estradiol and testosterone preference is due to within-cycle vs. between-cycle (including between women) sources of variance, the results strongly support roles for both. The estradiol and testosterone preference curves would not track one another across cycle days (see Fig. 1), for instance, unless the two variables were changing in concert within-cycles, and the results in Fig. 2 show that higher estradiol concentrations predicted stronger testosterone preferences when women were tested at roughly the same stage of the cycle. The between-subjects nature of the design notwithstanding, then, the overall

findings unambiguously demonstrate an association between estradiol and testosterone preference, and thereby provide empirical motivation for further studies that could more precisely parcel the within- and between-cycle sources of that association.

Another potential limitation of the study concerns the extent to which a single testosterone measurement may accurately index aspects of men's mate quality. A man's testosterone concentration is in many respects a state-like variable that has been shown to vary with circumstances such as relationship status (e.g., Gray et al., 2002) and transient exposure to potential mates (e.g., Roney et al., 2007). Nonetheless, studies that have measured testosterone in the same individuals up to a year apart (e.g., Granger et al., 2004) have reported high correlations between samples ($r > 0.70$), suggesting that the relative rank ordering of men may be fairly stable despite fluctuations in concentrations within individuals. State-like variables, furthermore, can be used to index underlying traits related to heritable fitness as long as those underlying traits probabilistically explain variance in the states—as long as men with greater immunocompetence on average produce higher testosterone concentrations within specific states, for instance, cues of current androgen concentrations could function as probabilistic indicators of heritable fitness. The present design does not allow us to determine the specific cues that women in this study were using, however, and possibilities include fairly stable physiognomic cues (assuming that current androgen production is correlated with testosterone exposure during pubertal development) or subtle facial expressions that might vary with current testosterone concentrations. Identification of these cues presents an important avenue for future research.

Our findings are at odds with results from a previous study that reported a significant association between women's salivary testosterone concentrations and their preferences for artificially masculinized faces (Welling et al., 2007). Although the reasons for this discrepancy are unclear, it is possible that there are important differences between natural and computer-generated stimuli. Studies that measure the same women's responses to both types of stimuli would be ideal for testing this possibility.

In conclusion, our findings are the first to directly demonstrate in humans that sex hormone concentrations in one sex are associated with preferences for cues to sex hormone concentrations in the opposite sex. The results complement previous studies (Penton-Voak and Chen, 2004; Roney et al., 2006) in showing that men's faces contain information regarding their androgen concentrations; greater attractiveness ratings of higher testosterone faces by more fertile women also support the application to humans of handicap models (e.g., Folstad and Karter, 1992) that propose the fitness-signaling value of elevated androgens. On the perceiver side of the equation, the data provide evidence that estradiol may be an important physiological regulator of cycle phase shifts in mate preferences, though conflicting findings from other studies highlight the importance of further research on this topic. Finally, the close association between women's estradiol and testosterone preference during the luteal phase is suggestive evidence that attractiveness judgments may adjust not only to proximity to ovulation but also to signals that a woman is currently experiencing fertile menstrual cycles.

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