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Original Article

Women's preferences for men's scents associated with testosterone and cortisol levels: Patterns across the ovulatory cycle

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ABSTRACT

Women in the fertile phase of their menstrual cycle show an enhanced sexual preference for masculine expressions in behavioral, morphological and scent traits. These masculinity preferences may be associated with testosterone (T) levels in males and hence connote male quality as a sire. Thus, a scent preference of fertile-phase women for T is predicted. A recent study, however, found no evidence for this, but reported that women prefer the scent of men with high cortisol (C). That study had low power to detect the predicted effect, as well as other methodological limitations. We tested women's preferences across their ovulatory cycle for the body scent of men who varied in T and C, using a larger sample of men and methods used in research on cycle preferences for symmetry-related male body scent. Conception risk in the cycle positively predicted women's scent ratings of men's T; scent ratings of C or T × C interaction were not robustly related to conception risk. Conception risk is related positively to a preference for scent of men's symmetry. This preference is distinct from that arising from a preference for the scent of T. The male-emitted chemical(s) responsible for these preferences shifts across women's cycle remain unknown.

1. Introduction

1.1. Fertility-related cyclic variations in preferences for scents and other male features

Women's scent preferences vary across the ovulatory menstrual cycle. Androstenol, a steroid chemical precursor of androstenone, importantly contributes to body odor (giving it a musky smell), and men produce much more of the chemical than women (see the review by Gower & Ruperelia, 1993; see also Pause, Sojka, Krauel, Fehm-wolfsdorf, & Ferstl, 1996). Hummel, Gollisch, Wildt, and Kobal (1991) and Grammer (1993) found that normally ovulating women evaluate androstenone more favorably near ovulation, despite not evaluating a number of other odors more favorably when fertile in their cycle (e.g., Hummel et al., 1991). These findings led researchers to conjecture that women's scent preferences near ovulation have been shaped by natural selection to favor men who possess features that, ancestrally, would have made preferred sires for offspring, as revealed by their scents. And, indeed, studies show that women near ovulation particularly prefer the scents of men who exhibit developmental stability (as reflected by low fluctuating asymmetry; Gangestad & Thornhill, 1998; Gangestad & Thornhill, 1999; Gangestad & Thornhill, 2008; Gangestad, Thornhill, & Garver-Apgar, 2005; Rikowski & Grammer, 1999; Thornhill & Gangestad, 1999; Thornhill, Gangestad, Miller, Scheyd, Knight, & Franklin, 2003) and social dominance (as assessed by self-report; Havlicek, Roberts, & Flegr, 2005).

Subsequent research indicates that women's preferences of other male features, as assessed through a number of different modalities, change across the cycle as well. During the late follicular or fertile phase of the cycle, compared to the luteal phase, normally ovulating women appear to be more attracted to men who possess several masculinized sexually dimorphic traits, including facial masculinity (Johnston, Hagel, Franklin, Fink, & Grammer, 2001; Little, Jones, & DeBruine, 2008; Penton-Voak & Perrett, 2000; Penton-Voak, Perrett, Castles, Burt, Koyabashi, & Murray, 1999; cf. Peters, Simmons, & Rhodes, 2009; Scarbrough & Johnston, 2005; see also Welling et al., 2007), body masculinity (e.g., muscularity; Gangestad, Garver-Apgar, Simpson, & Cousins, 2007; Little, Jones, & Burriss, 2007; cf. Peters et al., 2009), vocal masculinity (Feinberg et al., 2006; Puts, 2005; see also Puts, 2006), and tallness (Pawlowski & Jasienska, 2005), as well as men who display behavioral traits of social presence and intrasexual competitiveness (Gangestad, Simpson, Cousins, Garver-Apgar, & Christensen, 2004, Gangestad et al., 2007).

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1.2. A possible link between testosterone and some preferred traits

Testosterone (T) may be a common link to some of these traits preferred by women in the fertile phase of their cycle. T leads to the masculinization of the human face, perhaps in a dose-dependent fashion during development (e.g., Swaddle & Reierson, 2002). In both men and women, T promotes the maintenance and growth of skeletal muscle, particularly the sexually dimorphic mass in the chest, upper arms and shoulders (Basaria et al., 2002; Bhasin, 2003; Schroeder et al., 2003). Male upper body musculature is thought to have facilitated success in competition between men among human ancestors and, hence, the sexual dimorphism in muscle mass is thought to be partly the result of sexual selection on men's abilities to compete for mates (through direct competition with each other and display of intrasexual competitive abilities to women; Ellison, 2001, pp. 273–274; Gaulin & Sailer, 1984; Martin, 1980). Furthermore, T supports psychological and behavioral outcomes that appear to encourage success in male–male competition and sexual behavior. T appears to be associated with aspects of social assertiveness (Ellison, 2001, p. 265) or dominance-seeking (Mazur & Booth, 1998). In chimpanzees, males become more aggressive when parous, but not nulliparous, females exhibit sexual swellings, which parallels changes in the males' T (Muller & Wrangham, 2004). Associations between T and overt intrasexual aggressiveness in humans are weak, though meta-analysis reveals that they are reliable (Archer, Birring, & Wu, 1998; Book, Starzyk, & Quinsey, 2001). T-mediated dominance-seeking, among other behaviors, may be expressed in greater selective attention to angry faces (van Honk et al., 1999, 2000), in less pronounced smiling (Dabbs, 1997), or in more visual attention toward interaction partners (Dabbs, Bernieri, Strong, Campo, & Milun, 2001).

Theoretical perspectives on why T levels might be associated with underlying male quality or condition have been proposed. Folstad and Karter (1992) (influenced by Hamilton & Zuk, 1982) proposed the immunocompetence handicap theory of T's association with quality. They argued that testosterone (T) is immunosuppressive, a "handicap" that only immunocompetent males can afford; thereby, T-facilitated traits are favored by female preference as signals of immunocompetence. Current theory, reviewed by Kokko, Brooks, Jennions, and Morley (2003), casts doubt on this theory, at least as explicitly formulated – specifically, its claims that specific components of fitness are signaled. Male breeding values for fitness vary. Males of higher fitness are better able to translate energetic resources into fitness-enhancement. Precisely what features (components of viability, attractiveness, etc.) covary with male heritable fitness depends on the allocation strategies that benefit highly fit and less fit males; female preference for these features, whatever they might be, will be favored by selection. In certain systems, immunocompetence will be among the traits preferred by females; in others, it won't (see Getty, 2006; Kokko, Brooks, McNamara, & Houston, 2002).

An alternative conceptualization of the association between T and heritable fitness, however, is possible. At a broad conceptual level, T might be thought of as a messenger that facilitates male mating effort (Bribiescas, 2001), often associated with willingness to enter intrasexual competition and attempts at mate attraction. Males must trade off allocation of effort to mating vs. somatic maintenance and (in species with male parental care) parenting. Arguably, T has a conserved function: to promote features that facilitate successful mating effort, and diminish allocation toward other efforts. Certain quality-independent factors (e.g., paternal status) affect strategic allocation of mating effort (e.g., Gray, Kahlenberg, Barrett, Lipson, & Ellison, 2002). Theory, however, provides compelling reasons why males of higher quality often *strategically* allocate more energetic resources toward mating effort than low quality individuals (e.g., Kokko et al., 2002): not only should males of higher quality more efficiently convert resources into fitness-enhancing features in general, but individuals of higher quality also should benefit often from dedicating proportionately more resources to reproductive efforts (on men's masculinity, see Thornhill & Gangestad, 2008, Chapter 7).

Whatever the reason T might be associated with quality, the purported association leads to the expectation that, when fertile in their cycle, women might prefer particularly features of men who possess high T itself. Two studies suggest that, in fact, fertile women prefer the faces of men with high T. Roney and Simmons (2008) found that women's estrogen levels (which peak near ovulation) covary with preferences (assessed via attractiveness ratings) for the faces of men with high T, an effect conceptually replicated by Roney, Simmons, and Gray (2011). Moore, Cornwell, Smith, Al Dujaili, Sharp, and Perrett (2011a,b); Moore et al. (2011a), however, did not find robust associations between women's fertility status in the cycle and preference for the facial cues of T.

1.3. Fertility-related cyclic variation in preferences for scents associated with testosterone

Based on Hummel et al. (1991) and Grammer's (1993) findings that women in the fertile phase of their cycle prefer the scent of androgen metabolites more than infertile women do, as well as the purported positive association between T and male condition, one might expect similarly that fertile women particularly prefer the scent of men of high T (either mediated by androgen metabolites or other chemical cues of T). One study assessed this prediction. Rantala, Eriksson, Vainikka, and Kortet (2006) found evidence that women in general prefer the body scent of men with high cortisol levels. They detected no association, however, between women's fertility status in the cycle and women's preferences for the scent of men of high T. Rantala et al. (2006) studied cortisol-related scent because, as they discuss, cortisol (C), a stress hormone, apparently has an immunoregulatory function and thus may be involved in female preference of males of high genetic quality.

Rantala et al.'s (2006) study had limitations. Most notably, sample size was small. Only 19 men provided the worn t-shirts rated by women. The width of the confidence interval of r (transformed to Fisher's z, nearly identical to r through the range of −0.5 to 0.5) with a sample size of 19 is close to 1. Hence, their study had low power to detect any association between T and scent preferences at any phase of women's cycle. In addition, they had men wear the shirts for five hours. Although the optimal length of scent collection in t-shirt studies is unknown (Havlicek et al., 2011), studies demonstrating preferences for the scent of symmetrical men have collected scents in shirts worn for two consecutive nights (Gangestad & Thornhill, 1998; Rikowski & Grammer, 1999; Thornhill & Gangestad, 1999; Thornhill et al., 2003). Moreover, an additional difference between the symmetry-scent studies and the study by Rantala et al. (2006) was that the latter had male participants wear a raincoat while wearing their t-shirt. This may have increased perspiration and altered the scent of the shirts.

In the current study, we examined changes in women's preferences for the scent of high-T men across the ovulatory cycle using a larger sample of men (46) and the procedures used in studies examining women's preferences for the scent associated with men's symmetry. Our study also investigated men's scent related to cortisol (C) because C is immunoregulatory and hence may be involved in female mate preference for heritable fitness.

1.4. A potential interaction between testosterone and cortisol

Furthermore, T and C may interact to affect outcomes. C may inhibit the effects of T through downregulation of expression of T receptors (see Liening & Josephs, 2010, for a review). Similarly, T may

inhibit the expression of C (see Rantala et al., 2012). The stress-linked immunocompetence handicap hypothesis is based on the notion that T and C are covarying, and their effects interactive. Moore et al. (2011a,b) found that women prefer composite faces created from men of low C, but only when T was also low; high T suppressed these effects, especially for infertile women. Rantala et al. (2012) reported that men's T positively covaried with their facial attractiveness and a particular immune response (antibody production in response to hepatitis B vaccine), but especially when men's C also was relatively elevated. In contrast, other research shows that men's T positively covaries with aggressiveness and other behavioral responses, especially when C is low (see Liening & Josephs, 2010). In any case, we explored whether men's T and C interact to predict scent attractiveness, and whether the interactive effect depends on normally ovulating women's fertility status in the menstrual cycle.

2. Methods

2.1. Participants

This sample is one previously reported on in Thornhill and Gangestad (1999); a fuller description of all methods is available there. Participants enrolled were 80 men and 82 women, of whom 46 men and 48 women could be used for analyses examining preferences for scents associated with male hormones. Ages ranged from 17 to 33 for men (mean ± SD = 20.4 ± 2.9) and 17 to 53 for women (mean ± SD = 22.3 ± 6.8). Self-reported ethnicities of men were 55% Caucasian, 30% Hispanic, 8% African American, 4% Asian, 4% Native American; of women, 52% Caucasian, 32% Hispanic, 6% African American, 2% Asian, and 7% Native American. Participants received experimental course credit in an introductory psychology course in return for their participation in the study. Recruitment postings specifically asked for women who did not use hormone-based contraception (i.e., a pill or DepoProvera). Some nonetheless did, and we analyzed only ratings of those who did not (see below). The study was approved by the internal review board at our university.

In the full study reported in Thornhill and Gangestad (1999) both men and women wore, as well as smelled and rated, t-shirts; this report concerns only men's scents (no hormone assays were obtained on women) and, hence, in the present study we refer to shirt donors as exclusively men and scent raters as women.

2.2. Procedures

Men reported in groups of up to four for an initial session. After reading and signing an informed consent form, each participant was given a brief questionnaire on demographic and other information (e.g., age, height, weight, sexual orientation, socioeconomic status of family of origin, lifetime number of sex partners). One at a time, they were taken into an adjoining room, where the right and left sides of 10 characters were measured using a digital caliper, sensitive to 0.01 mm: ear length, ear width, elbow width, wrist width, ankle width, foot breadth, and lengths of all fingers excluding the thumb. These procedures were used to assess body fluctuating asymmetry (FA), a measure of developmental stability. Full description of this procedure and statistical analyses of FA (not the primary focus of this paper) are provided in Thornhill and Gangestad (1999).

After measurements were taken and the questionnaire completed, each participant was given a clean, white t-shirt and provided with explicit wearing instructions. Each was told that he should wear the shirt a particular two consecutive nights (identical for each sex) while sleeping. Each was also instructed to wash his/her bed sheets with unscented laundry detergent (provided by us) prior to those two nights and, during the two-day period, refrain from: (1) using scented soaps, deodorant, or fragrance such as perfume, cologne or aftershave, and instead use only unscented soap (which we provided); (2) eating garlic, onion, green chile, pepperoni, pungent spices, herbs, strong cheeses, cabbage, celery, asparagus, yogurt, and lamb; (3) drinking alcohol or using recreational drugs; (4) smoking tobacco; (5) engaging in sex with another person; or (6) sleeping with another person. Each participant was further instructed to place the t-shirt in a plastic bag (provided and identified with an arbitrary code number) during the day, when not worn, and return the shirt to our lab in the bag, the morning following the second night at 9 a.m.

Men were also provided with a test tube, a stick of sugarless gum, and instructions for how to collect saliva. Each tube had a small amount of a preservative, sodium azide. Each individual brought a tube with approximately 1 ml of saliva when the shirts were returned. They were asked to collect the saliva upon waking the morning of returning their shirts to control for diurnal variation in T.

Of all participants, 74 (92%) returned their shirts on time. When dropping off their shirts, each filled out a brief questionnaire about any guidelines they had violated during the two-day period when shirts were worn during sleep. They were told that there was no loss of research course credit for violating any instructions, but nonetheless we desired to know of any violations. Despite clear instructions, the smell of fragrance (from perfume, soap or lotion) or smoke was evident on some shirts. Assistants (see below) were asked to indicate if they smelled a non-human odor on any shirt. Guided by these comments, three assistants systematically smelled shirts and confirmed ones that had such odors; two smelled of fragrance and four smelled of smoke, and were eliminated from all analyses. In addition, we removed shirts of men who reported violating rules by applying a fragrance or scented deodorant during the two-day period. This procedure left 49 men in the sample, 46 of whom provided a sample of saliva.

The questionnaire also obtained information about bathing frequency during the two-day period during which shirts were worn.

At 10 a.m. of the morning when the shirts were returned, female participants began reporting in groups of up to five. Following informed consent, women were placed in separate rooms. Shirts had been separated into groups of approximately 10 and each group placed in a box. In addition to the shirts worn by men, one clean shirt that had not been worn was included in the sample. Boxes were circulated through the sample of raters present during a session. Though no attempt was made to randomize fully the order in which raters smelled shirts, it is likely that no two raters smelled them in precisely the same order. For each shirt, raters were asked to open the top of the plastic bag, smell the shirt, and rate it on three dimensions: (1) pleasantness, on a scale of 1 = very unpleasant to 10 = very pleasant; (2) sexiness, on a scale of 1 = very unsexy to 10 = very sexy; and (3) intensity, where 1 = not at all intense to 10 = very intense. They were instructed to roll the top of the bag shut before putting it back in its box and moving onto the next shirt.

Women raters also were given a brief questionnaire to fill out, which assessed: (1) whether the woman currently used a contraceptive pill or other hormone-based contraceptive; (2) the first day of the woman's last menstrual period (women were provided a calendar to assist with this task); and (3) the typical length (in days) of the woman's menstrual cycle.

In total, the rating sessions lasted about one hour and were conducted through 1400 hours the day following the collection of the T-shirts.

2.3. Data treatment: scent attractiveness

Two women reported a homosexual or bisexual orientation. Because this study examined attractiveness of opposite-sex scents, analyses focused on the olfactory responses of the exclusively heterosexual participants.

Of the 72 heterosexual women who reported to rate scents, 16 currently used a pill or related contraceptive (e.g., DepoProvera), one had recently taken a morning-after pill, two did not have menses for medical reasons, two were post-menopausal, one was pregnant, and two did not complete the rating sheet. For the remaining 48 women, we estimated conception risk (probability of conception following sexual intercourse) on the basis of their day of the cycle and values reported by Wilcox, Duncan, Weinberg, Trussell, and Baird (2001). Wilcox et al. report two tables of conception risk: one for normally cycling women in general, without regard to typical cycle length, and one for women with regular cycles of 28–29 days. We used the latter table, but first converted each woman's day of the cycle to a day of the cycle she would be estimated to be on if she had a typical 29-day cycle length, taking into account her own cycle length (mean ± SD = 28.5 ± 3.5; women reported cycle length at two different sessions, and the two reports correlated 0.80, $p<0.0001$; we used the average). We assumed that the typical day of ovulation was 15 days prior to the end of their typical cycle (e.g., day 14 in a 29-day cycle). Women's probability of conception was then based on how far they had come toward or after their assumed day of ovulation. This "backward" method of calculating conception risk is considered superior to methods that ignore typical cycle length (Wilcox et al., 2001). Results we report, however, are generally similar to those based on an average of a forward and backward method. (We note that Thornhill and Gangestad (1999) used a different table to estimate conception risk, one reported by Jöchle (1973). Wilcox et al.'s (2001) estimates are considered superior: They are based on more accurate, sonographic determinations of true day of ovulation, apply more sophisticated statistical analysis yielding a well-formed conception risk function, and yield more reasonable probabilities of conception. Naturally, Wilcox et al.'s values were not available at the time of Thornhill and Gangestad's (1999) initial analysis. Thornhill & Gangestad's results, however, replicate when these new values are used; see below.)

The mean correlation between individual participants' "pleasantness" and "sexiness" ratings was 0.85. Hence, these ratings were averaged for each sex into a total attractiveness index.

In assessing predicted associations between preference for the scent of T and FA, we applied directed tests, which allocate .04 of a total alpha of .05 to the predicted tail, and .01 to the unpredicted tail (Rice & Gaines, 1994).

2.4. Hormone assays

Saliva samples were assayed for hormone concentrations of testosterone and cortisol using methods provided by Ellison (1988). Concentrations were estimated using a modification of a commercially available fluroimmunoassay DELFIA testosterone kit (Wallac, Turku, Finland [now part of Perkin-Elmer, Boston MA]). C concentrations were estimated using a modified protocol of the I^{125} kit produced by Diagnostic Systems Laboratories, Inc (Webster, TX). All assays were performed in the Reproductive Ecology Laboratory at Harvard University.

3. Results

3.1. Mean scent attractiveness predicted by T, C, and T x C

To examine associations between overall scent attractiveness of t-shirts and hormone levels, we treated men as units of analysis (as these questions concern generalizability of associations to a population of men). First, we regressed scent attractiveness on T and C. Neither T ($t_{44}=-0.38$, $p=0.705$, partial $r=-0.06$) nor C ($t_{44}=0.31$, $p=0.753$, partial $r=0.04$) significantly predicted scent attractiveness. Then we added the interaction term. It, too, had a small, non-significant effect, $t_{43}=0.80$, $p=0.430$, partial $r=0.13$. Statistically controlling for male age did not affect these outcomes.

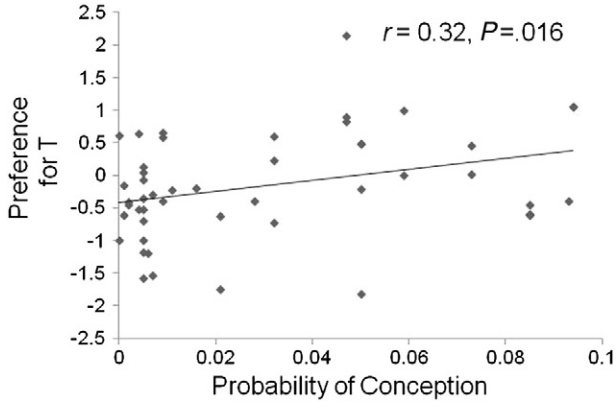

Fig. 1. Association between women's estimated conception risk and their preference for scents associated with male T.

3.2. The effect of conception risk on preferences for scents associated with T

Next, we examined whether women's preferences for scent associated with men's T levels change as a function of women's fertility, as it changes across the cycle. As this question concerns generalizability of an association across a population of women, women were treated as units of analysis. Conception risk did covary significantly and positively with preferences for male scents associated with T levels, $r_{46}=0.32$, $p=0.016$. Fig. 1 depicts this association. Controlling for female age did not change it.

When male scents were adjusted for the number of showers men took or whether they had used scented shampoo, women's conception risk similarly predicted their preference for scents associated with high T, $r_{46}=0.32$, $p=0.016$.

3.3. The effect of conception risk on preferences for scents associated with C or T x C

Women's conception risk did not robustly predict their preferences for scents associated with C, though this association approached significance, $r_{46}=0.27$, $p=0.060$. As men's T and C covaried in this sample (see above), it is no surprise that women's preferences for scents associated with T covaried with their preferences for scents associated with C, $r_{46}=0.41$, $p=0.003$. With preferences for the scent of C statistically controlled, conception risk predicted women's preference for scents associated with T at a marginal level of significance, partial $r_{45}=0.24$, $p=0.067$. By contrast, with preferences for scents associated with T controlled, conception risk was not at all related to preferences for scents associated with C, partial $r_{45}=0.16$, $p=0.274$.

Conception risk did not predict preferences for scents associated with the interaction between T and C, either in a simple zero-order correlational analysis, $r_{46}=0.03$, $p=0.822$, or with preferences for scents associated with T and C controlled, partial $r_{44}=-0.12$, $p=0.408$.

In sum, evidence indicates that women's conception risk across the cycle significantly and positively predicts their preferences for men's T-related scent. This association remains at a marginally significant level when men's C-related scent is controlled. But women's conception risk does not robustly predict their preferences for men's scent corresponding to C, C with T controlled, the interaction between T and C, or the interaction of T and C with the effects of each of the two hormones controlled.

3.4. Preferences for the scent of T and preferences for the scent of symmetry

As noted earlier, women in this sample already were reported to prefer the scent associated with developmental stability. That association also was observed using the current, improved method of assessing conception risk, $r_{46} = 0.38$, $p = 0.005$. Men's FA did not predict their T levels in this sample, $r_{63} = 0.09$, $p = 0.490$. In addition, women's preferences for scents associated with symmetry did not covary with their preferences for scents associated with high levels of T, $r_{46} = 0.06$, $p = 0.673$. Similarly, women's preferences for scents associated with symmetry did not predict their preferences for scents associated with C, $r_{46} = 0.20$, $p = 0.165$. Unexpectedly, preferences for scents of symmetry did predict scents associated with a T × C interaction in this sample, $r_{46} = -0.30$, $p = 0.036$. Controlling for the latter, however, did not affect the association between women's conception risk and their preference for the scent of symmetry, $r_{46} = 0.41$, $p = 0.003$.

4. Discussion

Women's conception risk predicted their preferences for male scents associated with T. Women in the fertile phase of their cycle, on average, demonstrated a preference for scents of men with higher T levels, relative to women outside of the fertile phase of their cycle.

One previous study failed to find this association (Rantala et al., 2006). Why the discrepancy in findings? As noted earlier, one possibility is Type I error. Rantala et al.'s sample size of men was just 19 men. The current sample size was approximately 2.5 times that – 46 men. In small samples, T may possess sample-specific, chance associations with particular scents not attractive to ovulating women, or happen to not be associated with scents T typically is associated with. In addition, there were certain procedural differences across the studies: We had men wear t-shirts for two nights, whereas Rantala et al. had them wear the shirts for only five hours, during which time shirts were covered by a raincoat; and we explicitly checked (prior to any analysis) for shirts with non-human fragrances (perfumes, smoke) as well as eliminated men who reported certain violations of rules regarding application of scents. Rantala et al.'s association, however, was actually (through non-significantly) in the opposite direction to ours. Ultimately, replication in a separate sizable sample is needed to confirm that, in fact, women's preferences for scents associated with high T do robustly vary across the cycle.

If this preference shift is robust, one possible explanation is the shifts in preferences for the scents of androgen metabolites, documented by Hummel et al. (1991) and Grammer (1993). That is, testosterone levels may be associated with concentrations of these metabolites detectable in male body odors. While this conjecture is reasonable, it remains speculative at this time. Preferences for T may be a function of other odors in male scents (e.g., those associated with the nature of bacterial flora). The chemical(s) responsible for these preference shifts remains unknown.

In this sample, preferences for scents associated with T cannot explain preferences for scents associated with developmental stability. T and FA did not significantly covary in this sample. And preferences for scents associated with T did not predict preferences for scents associated with symmetry.

Rantala et al. (2006) reported that women are attracted particularly to the scents of men with high C. By contrast, Moore et al. (2011a,b) reported that women find the faces of men with low C attractive (though Rantala et al., 2012 did not replicate this finding). In this sample, we detected no systematic scent preference in women for high or low C, though a positive association neared significance. Moreover, when preferences for scents associated with T were controlled, preferences for scents associated with C did not robustly covary with conception risk.

Previous work has found that T and C interact to predict men's facial attractiveness (Moore et al., 2011a,b; Rantala et al., 2012), an effect particularly pronounced when women rate men during non-fertile cycle phases (Moore et al., 2011a,b). The positive association between T and men's attractiveness may be most pronounced when men also experienced high levels of C (Rantala et al., 2012). We, however, found no interactive effect of T and C in predicting men's scent attractiveness, and we did not detect any association between women's conception risk and male T and C interactive effects on women's scent attractiveness ratings.

In addition to replicating the association between women's conception risk and their preference for male scents associated with testosterone, future work should aim to identify chemicals males emit responsible for shifts in preferences for scents associated with both T (if robust) and developmental stability. From an evolutionary perspective, one major outstanding question is whether these chemicals constitute specialized signals of male qualities or byproducts of male qualities (see Thornhill & Gangestad, 2008).

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References

Archer, J., Birring, S. S., & Wu, F. C. W. (1998). The association between testosterone and aggression among young men: Empirical findings and a meta-analysis. *Aggressive Behavior*, *24*, 411–420.
Basaria, S., Leib, J., Tang, A. M., DeWeese, T., Carducci, M., Eisenberger, M., & Dobs, A. S. (2002). Long-term effects of androgen deprivation therapy in prostate cancer patients. *Clinical Endocrinology*, *56*, 779–786.
Bhasin, S. (2003). Regulation of body composition by androgens. *Journal of Endocrinological Investigation*, *26*, 814–822.
Book, A. S., Starzyk, K. B., & Quinsey, V. L. (2001). The relationship between testosterone and aggression: A meta-analysis. *Aggression and Violent Behavior*, *6*, 579–599.
Bribiescas, R. G. (2001). Reproductive ecology and life history of the human male. *Yearbook of Physical Anthropology*, *44*, 148–176.
Dabbs, J. M. (1997). Testosterone, smiling, and facial appearance. *Journal of Nonverbal Behavior*, *21*, 45–55.
Dabbs, J. M., Bernieri, F. J., Strong, R. K., Campo, R., & Milun, R. (2001). Going on stage: Testosterone in greetings and meetings. *Journal of Research in Personality*, *35*, 27–40.
Ellison, P. T. (1988). Human salivary steroids: Methodological considerations and applications in physical anthropology. *Yearbook of Physical Anthropology*, *31*, 115–142.
Ellison, P. T. (2001). *On fertile ground: A natural history of reproduction.* Cambridge, MA: Harvard University Press.
Feinberg, D. R., Jones, B. C., Law Smith, M. J., Moore, F. R., DeBruine, L. M., Cornwell, R. E., Hillier, S. G., & Perrett, D. I. (2006). Effects of menstrual cycle and trait estrogen level on masculinity preferences in the human voice. *Hormones and Behavior*, *46*, 215–222.
Folstad, I., & Karter, A. J. (1992). Parasites, bright males and the immunocompetence handicap. *American Naturalist*, *139*, 603–622.
Gangestad, S. W., Garver-Apgar, C. E., Simpson, J. A., & Cousins, A. J. (2007). Changes in women's mate preferences across the ovulatory cycle. *Journal of Personality and Social Psychology*, *92*, 151–163.
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., & Thornhill, R. (1998). Menstrual cycle variation in women's preference for the scent of symmetrical men. *Proceedings of the Royal Society of London B*, *265*, 927–933.
Gangestad, S. W., & Thornhill, R. (1999). Individual differences in developmental precision and fluctuating asymmetry: A model and its implications. *Journal of Evolutionary Biology*, *12*, 402–416.
Gangestad, S. W., & Thornhill, R. (2008). Human oestrus. *Proceedings of the Royal Society of London B*, *275*, 991–1000.
Gangestad, S. W., Thornhill, R., & Garver-Apgar, C. E. (2005). Women's sexual interests across the ovulatory cycle depend on primary partner developmental instability. *Proceedings of the Royal Society of London B*, *272*, 2023–2027.
Gaulin, S. J., & Sailer, L. D. (1984). Sexual dimorphism in weight among the primates: The relative impact of allometry and sexual selection. *International Journal of Primatology*, *5*, 515–535.
Getty, T. (2006). Sexually selected signals are not similar to sports handicaps. *Trends in Ecology and Evolution*, *21*, 83–88.
Gower, D. B., & Ruperelia, B. A. (1993). Olfaction in humans with special reference to odorous 16-androstenes: Their occurrence, perception and possible social, psychological and sexual impact. *Journal of Endocrinology*, *137*, 167–187.
Grammer, K. (1993). 5-α-androst-16-en-3α-on: A male pheromone? A brief report. *Ethology and Sociobiology*, *14*, 201–214.

Gray, P. B., Kahlenberg, S. M., Barrett, E. S., Lipson, S. F., & Ellison, P. T. (2002). Marriage and fatherhood are associated with lower testosterone in males. *Evolution and Human Behavior*, *23*, 193–201.

Hamilton, W. D., & Zuk, M. (1982). Heritable true fitness and bright birds: A role for parasites. *Science*, *218*, 384–387.

Havlicek, J., Lenochova, P., Oberzaucher, E., Grammer, K., & Roberts, S. C. (2011). Does length of sampling affect quality of body odor samples? *Chemosensory Perception*, *4*, 186–194.

Havlicek, J., Roberts, S. C., & Flegr, J. (2005). Women's preference for dominant male odour: Effects of menstrual cycle and relationship status. *Biology Letters*, *1*, 256–259.

Hummel, T., Gollisch, R., Wildt, G., & Kobal, G. (1991). Changes in olfactory perception during the menstrual cycle. *Experientia*, *47*, 712–715.

Jöchle, W. (1973). Coitus induced ovulation. *Contraception*, *7*, 523–564.

Johnston, V. S., Hagel, R., Franklin, M. L., Fink, B., & Grammer, K. (2001). Male facial attractiveness: Evidence for hormone mediated adaptive design. *Evolution and Human Behavior*, *23*, 251–267.

Kokko, H., Brooks, R., Jennions, M. D., & Morley, J. (2003). The evolution of mate choice and mating biases. *Proceedings of the Royal Society of London Series B*, *270*, 653–664.

Kokko, H., Brooks, R., McNamara, J. M., & Houston, A. I. (2002). The sexual selection continuum. *Proceedings of the Royal Society of London B*, *269*, 1331–1340.

Liening, S. H., & Josephs, R. A. (2010). It's not just about testosterone: Physiological mediators and moderators of testosterone's behavioral effects. *Social and Personality Psychology Compass*, *4*, 982–994.

Little, A. C., Jones, B. C., & Burriss, R. P. (2007). Preferences for masculinity in male bodies change across the menstrual cycle. *Hormones and Behavior*, *31*, 633–639.

Little, A. C., Jones, B. C., & DeBruine, L. M. (2008). Preferences for variation in masculinity in real male faces change across the menstrual cycle: Women prefer more masculine faces when they are fertile. *Personality and Individual Differences*, *45*, 478–482.

Martin, R. D. (1980). Sexual dimorphism and the evolution of higher primates. *Nature*, *287*, 273–275.

Mazur, A., & Booth, A. (1998). Testosterone and dominance in men. *Behavioral and Brain Sciences*, *21*, 353–397.

Moore, F. R., Al Dujaili, E. A. S., Cornwell, R. E., Smith, M. J. L., Lawson, J. F., Sharp, M., & Perrett, D. I. (2011a). Cues to sex- and stress-hormones in the human male face: Functions of glucocorticoids in the immunocompetence handicap hypothesis. *Hormones and Behavior*, *60*, 269–274.

Moore, F. R., Cornwell, R. E., Smith, M. J. L., Al Dujaili, E. A. S., Sharp, M., & Perrett, D. I. (2011b). Evidence for the stress-linked immunocompetence handicap hypothesis in human male faces. *Proceedings of the Royal Society B*, *278*, 774–780.

Muller, M. N., & Wrangham, R. W. (2004). Dominance, aggression and testosterone in wild chimpanzees: A test of the "challenge hypothesis". *Animal Behaviour*, *67*, 113–123.

Pause, B. M., Sojka, B., Krauel, K., Fehmwolfsdorf, G., & Ferstl, R. (1996). Olfactory information-processing during the course of the menstrual cycle. *Biological Psychology*, *44*, 31–54.

Pawlowski, B., & Jasienska, G. (2005). Women's preferences for sexual dimorphism in height depend on menstrual cycle phase and expected duration of relationship. *Biological Psychology*, *70*, 38–43.

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., Perrett, D. I., Castles, D., Burt, M., Koyabashi, T., & Murray, L. K. (1999). Female preference for male faces changes cyclically. *Nature*, *399*, 741–742.

Peters, M., Simmons, L. W., & Rhodes, G. (2009). Preferences across the menstrual cycle for masculinity and symmetry in photographs of male faces and bodies. *PLoS ONE*, *4*, e4138.

Puts, D. A. (2005). Mating context and menstrual phase affect women's preferences for male voice pitch. *Evolution and Human Behavior*, *26*, 388–397.

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

Rantala, M. J., Eriksson, C. J. P., Vainikka, A., & Kortet, R. (2006). Male steroid hormones and female preference for male body odor. *Evolution and Human Behavior*, *27*, 259–260.

Rantala, M. J., Moore, F. R., Skirinda, I., Karma, T., Kivleniece, I., Kecko, S., & Krams, I. (2012). Evidence for the stress-linked immunocompetence handicap hypothesis in humans. *Nature Communications*, *3*, 694.

Rice, W. R., & Gaines, S. D. (1994). 'Heads I win, tails you lose': Testing directional alternative hypotheses in ecological and evolutionary research. *Trends in Ecology and Evolution*, *9*, 235–237.

Rikowski, A., & Grammer, K. (1999). Human body odour, symmetry and attractiveness. *Proceedings of the Royal Society of London B*, *266*, 869–874.

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.

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.

Scarbrough, P. S., & Johnston, V. S. (2005). Individual differences in women's facial preferences as a function of digit ratio and mental rotation ability. *Evolution and Human Behavior*, *26*, 509–526.

Schroeder, E. T., Singh, A., Bhasin, S., Storer, T. W., Azen, C., Davidson, T., Martinez, C., Sinha-Hikim, I., Jaque, S. V., Terk, M., & Sattler, F. R. (2003). Effects of an oral androgen on muscle and metabolism in older, community-dwelling men. *American Journal of Physiology-Endocrinology and Metabolism*, *284*, E120–E128.

Swaddle, J. P., & Reierson, G. W. (2002). Testosterone increases perceived dominance but not attractiveness of human males. *Proceedings of the Royal Society of London B*, *269*, 2285–2289.

Thornhill, R., & Gangestad, S. W. (1999). The scent of symmetry: A human sex pheromone that signals fitness? *Evolution and Human Behavior*, *20*, 175–201.

Thornhill, R., & Gangestad, S. W. (2008). *The evolutionary biology of human female sexuality*. New York: Oxford University Press.

Thornhill, R., Gangestad, S. W., Miller, R., Scheyd, G., Knight, J., & Franklin, M. (2003). MHC, symmetry, and body scent attractiveness in men and women. *Behavorial Ecology*, *14*, 668–678.

van Honk, J., Tuiten, A., van den Hout, M., Koppeschaar, H., Thijssen, J., de Haan, E., & Verbaten, R. (2000). Conscious and preconscious selective attention to social threat: Different neuroendocrine response patterns. *Psychoneuroendocrinology*, *25*, 577–591.

van Honk, J., Tuiten, A., Verbaten, R., van den Hout, M., Koppeschaar, H., Thijssen, J., & de Haan, E. (1999). Correlations among salivary testosterone, mood, and selective attention to threat in humans. *Hormones and Behavior*, *36*, 17–24.

Welling, L. L. M., Jones, B. C., DeBruine, L. M., Conway, C. A., Law Smith, M. J., Little, A. C., Feinberg, D. R., Sharp, M. A., & Al-Dujaili, E. A. S. (2007). Raised salivary testosterone in women is associated with increased attraction to masculine faces. *Hormones and Behavior*, *52*, 156–161.

Wilcox, A. J., Duncan, D. B., Weinberg, C. R., Trussell, J., & Baird, D. D. (2001). Likelihood of conception with a single act of intercourse: providing benchmark rates for assessment of post-coital contraceptives. *Contraception*, *63*, 211–215.