



Original Article

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

Randy Thornhill ^{a,*}, Judith Flynn Chapman ^b, Steven W. Gangestad ^c

^a Department of Biology, MSC 03 2020, 1 University of New Mexico, Albuquerque, NM 87131

^b Department of Human Evolutionary Biology, Harvard University, Boston, MA

^c Department of Psychology, The University of New Mexico, Albuquerque, NM

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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.

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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).

* Corresponding author.

E-mail address: rthorn@unm.edu (R. Thornhill).

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 & Reiersen, 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, Biring, & 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

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