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Male steroid hormones and female preference for male body odor

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Abstract

It has been suggested that human scent works as a signal in mate selection, but the empirical evidence is scarce. Here, we examined whether women's olfactory preferences for a man's scent could be correlated with his testosterone, estradiol, or cortisol concentrations, and whether these preferences change along with the menstrual cycle. In line with previous studies, women in their most fertile period gave the highest attractiveness ratings to all men. However, the intensity ratings by women at different menstrual phases did not significantly differ statistically. Interestingly, we found that cortisol concentration in saliva correlated positively with the attractiveness but not with the intensity ratings of male T-shirt odor by all women's groups. However, neither testosterone nor estradiol was significantly associated with the ratings of attractiveness or intensity. Thus, our study suggests that there could be a novel mechanism for odor-based selection in humans.

Keywords: Cortisol; Estradiol; *Homo sapiens*; Mate choice; Menstrual cycle; Olfaction; Phermones, Sexual selection; Testosterone

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1. Introduction

Chemical cues, such as odors and pheromones, have been found to play an important role in sexual selection of many species. Odors and pheromones have been shown to reflect an individual's health (Kavalier, Choleris, Agmo, & Pfaff, 2004; Penn & Potts, 1998) and immunocompetence in choosy females (e.g., Rantala, Jokinen, Kortet, Vainikka, & Suhonen, 2002; Rantala, Kortet, & Vainikka, 2003). In humans, odors can reveal the MHC compatibility with potential mates (Jacob, McClintock, Zelano, & Ober, 2002; Wedekind & Furi, 1997; Wedekind, Seeback, Bettens, & Paepke, 1995), possibly via MHC class I binding ligand proteins (Leinders-Zufall et al., 2004). In addition to MHC composition, odors can convey information about a potential mate's social or reproductive status. For example, it is suggested that 16-androstenes, 5α-androst-16-en-3β-ol and 5α-androst-16-en-3-one, modulate social and sexual behavior as well as the levels of steroid hormones in circulation (see Jacob & McClintock, 2000; Meredith, 2001; Monti-Bloch, Jennnings-White, & Berliner, 1998; Rothardt & Beier, 2001). Thus, circulatory hormones might contribute to the information transmitted by odors.

It has been suggested that whereas men rate visual appearance and odor of a mate as somewhat equally important, women may find olfactory cues of a mate very important in their sexual responsivity and mate choice (Herz & Cahill, 1997; Herz & Inzlicht, 2002). Furthermore, in experiments where women do not see the men, it has been found that women in the fertile phase of their cycle prefer the body odor of dominant men (Havlicek, Roberts, & Flegr, 2005) and men with attractive faces and low fluctuating asymmetry (Gangestad & Thornhill, 1998; Rikowski & Grammer, 1999; Thornhill & Gangestad, 1999). These studies suggest that odors might reflect preferable male qualities to a woman looking for a mate. There is also evidence that olfactory sensitivity changes across the menstrual cycle and that ovulating women evaluate androsterone (a substance that gives a musky smell to sweat; see review by Gower & Ruparelia, 1993) more favorably near ovulation (Grammer, 1993; Hummel, Gollisch, Wildt, & Kobal, 1991). Thus, it has been suggested that symmetric males with attractive faces have higher androstenol levels (e.g., Gangestad & Thornhill, 1998; Rikowski & Grammer, 1999). Androstenol, a chemical precursor of androsterone, is a major contributor to body odor (Gower & Ruparelia, 1993). However, so far it is not known whether females judge males differently in relation to high or low testosterone levels by using their scent.

The immunocompetence handicap hypothesis (ICHH) of sexual selection predicts that the expression of secondary sexual traits should be positively related to the level of testosterone or other immunosuppressive substance (Folstad & Karter, 1992). It has been found that testosterone suppresses some parts of the immune system in mammals (reviewed, for example, by Grossman, 1985; Roberts, Buchanan, & Evans, 2004), but a number of studies suggest that testosterone may actually have a beneficial effect on the immune system (reviewed in Miller & Hunt, 1996; Muehlenbein & Bribiescas, 2005). Thus, it has been suggested that other potentially immunoregulatory hormones, such as the major stress hormone cortisol, might mask or augment the effects of testosterone (Muehlenbein & Bribiescas, 2005). Likewise, 17β-estradiol has been found to enhance some immune

functions (e.g., Ahmed & Talal, 1990; Olsen & Kovacs, 1996). On the other hand, recent studies suggest that the ICHH mechanism could be mediated by stress hormones such as corticosterone or cortisol (see Buchanan, 2000; Muehlenbein & Bribiescas, 2005; Roberts et al., 2004), which, in high chronic exposure, are known to have deleterious effects on immune function (e.g., Hillgarth & Wingfield, 1997; Padgett & Glaser, 2003). According to the ICHH, only genetically immunocompetent (individuals with optimal MHC alleles) individuals can afford to tolerate the costs associated with high concentrations of immunosuppressive hormones and thus are able to invest more on sexual advertisement and primary sexual traits (Skau & Folstad, 2004) than less immunocompetent individuals (Folstad & Karter, 1992; see also Kortet, Vainikka, Rantala, Jokinen, & Taskinen, 2003). Consequently, it has been suggested that male odor associated with circulatory levels of immunosuppressive hormones might contain information on the presence of "good genes" for females (e.g., Gangestad & Thornhill, 1998; Rikowski & Grammer, 1999; Thornhill & Gangestad, 1999).

Thus, in this study, we tested whether attractiveness or intensity of male body odor by female raters is correlated with salivary concentrations of testosterone, estradiol, or cortisol. Concentrations of testosterone and cortisol in saliva are highly correlated with concentrations of the respective free hormones in blood (e.g., Dabbs, 1990, 1991; Kirschbaum & Hellhammer, 1994; Wang, Plymate, Nieschlag, & Paulsen, 1981). If odors work as honest sexual signals about male quality for choosy women, we expect to find that attractiveness of a man's odor correlates with that man's testosterone or cortisol levels in saliva. In addition, we tested whether women's preference for the characteristics of male scent changes during the menstrual cycle approximated by a day of menstrual cycle-based method or by the use of contraceptives. We predicted that females should find male's scent most attractive at the most fertile window of their menstrual cycle.

2. Methods

A total of 19 men aged 20 to 35 (mean=27.2±3.33 years) voluntarily participated in the study. Most of the men were students at the University of Jyväskylä, Finland. As in previous studies, body odors were collected by "T-shirt experiments" (e.g., Gangestad & Thornhill, 1998; Kuukasjärvi et al., 2004; Rikowski & Grammer, 1999; Thornhill & Gangestad, 1999). The white T-shirts were prepared by washing them with nonperfumed soap powder. Participants had been told to avoid perfumes and deodorants on the day of the experiment and to refrain from smoking and eating odorous dishes. Just before the experiments, all participants received one clean T-shirt and they were required to wash their body and hair with provided unscented soap and shampoo before wearing the shirt. These procedures ensured that the personal hygiene of the participants differed minimally. Each participant wore the T-shirt 5 h while watching movies in an auditorium. This was conducted during the evening hours to control for within-day variation on hormone levels. Males were required to wear a light disposable raincoat on top of their T-shirt in order to prevent acquisition of other distracting scents. We collected three saliva samples from

each participant: the first one at the beginning of the experiment, the second after 2.5 h, and the third at the end of the odor collection session. After sampling, all saliva samples were immediately frozen at −20°C until assayed. At the end of this session, each participant folded the T-shirt and placed it in the plastic bag; the T-shirts were then frozen at −20°C for later assessments. This procedure was performed in two parts in consecutive weeks.

The three saliva samples collected from each male participant (beginning, 2.5 h; end of one time, 5 h) were analysed for testosterone, estradiol, and cortisol concentrations in duplicates using the radioimmunoassay technique with commercial kits (DiaSorin, Italy). The average of all six (3×2) determinations per hormone was used in later analyses. Intra-assay variation for testosterone was 10.28%; for estradiol, 8.71%; and for cortisol, 6.06%. Seventy-six nonsmoking Caucasian women [age (mean±S.D.)=23.18±3.85 years] participated in the study by sniffing the T-shirts (in addition to these, two women were excluded from the study since they reported to have extraordinarily short, 20 days, or long, 50 days, cycle length). The participants were mainly students from the Faculties of Science and Arts of the University of Jyväskylä. Before rating, women were given a brief questionnaire to fill out and asked to report their (1) age, (2) whether the woman currently used a contraceptive pill, (3) the first day of the woman's last menstrual period, and (4) the typical length (in days) of their menstrual cycle. The raters were instructed to pick one jar at time, open it and smell it, and rate the odor for intensity (1=*not intense at all* to 10=*very intense*) and sexual attractiveness (−5=*very aversive*, 0=*neutral*, to 5=*very attractive*). It has been found that female perception of male body odor changes with cycle phase and the use of pills (e.g., Gangestad & Thornhill, 1998; Rikowski & Grammer, 1999). Therefore, the included female raters having average phase length 28.41±2.91 days (mean±S.D.; min 21, max 38 days) were divided into four groups: noncontraceptive users: in (1) the follicular phase (days from the first day of the cycle to 20th day from the end of the cycle, n=9), in (2) the fertile phase (Days 20–14 from the end of the cycle, n=11), in (3) the luteal phase (the last 14 days of the cycle, n=16); and (4) contraceptive users (n=40). This method to assign women to groups is based on the information that the luteal phase lasts usually 14 days, and fertile period does not exceed 6 days (Dunson, Baird, Wilcox, & Weinberg, 1999).

Relationships of male hormones with female scores were analysed using Spearman's rank correlation. Pearson's product moment correlation was used to study correlations between hormone concentrations. All variables (testosterone after it was transformed using the equation: the $x = \sqrt{\ln(x+1)}$) were normally distributed according to Kolmogorov–Smirnov test of normality. However, nonparametric tests were used because the ranking scale between women is rather ordinal than true ratio scale, and nonparametric statistics should yield better reliability in such cases. Friedman's test with Tukey's honest significant difference (HSD) tests for several dependent samples was used to analyse differences between women's groups if Friedman's nonparametric ANOVA indicated significant differences among groups. Wilcoxon's signed rank sum test was used to compare the attractiveness and intensity ratings by contraceptive users and noncontraceptive users across menstrual phases.

Table 1
Spearman's correlations (N=19) of cortisol, estradiol, and testosterone with the ratings of attractiveness and intensity by female raters

	Follicular phase (9)				Fertile window (11)				Luteal phase (16)				Contraceptive users (40)			
	Attractiveness		Intensity		Attractiveness		Intensity		Attractiveness		Intensity		Attractiveness		Intensity	
	R	*p*	*R*	*p*	*R*	*p*	*R*	*p*	*R*	*p*	*R*	*p*	*R*	*p*	*R*	*p*
Cortisol	.715	.001	−.084	.732	.490	.033	−.247	.307	.698	.001	−.135	.5981	.644	.003	−.193	.429
Estradiol	−.049	.842	−.334	.162	.060	.808	−.025	.920	−.364	.126	−.117	.634	−.275	.254	.037	.881
Testosterone	−.083	.737	.336	.160	−.245	.313	.341	.153	.033	.892	.244	.315	−.072	.769	.241	.321

The number of women in each group is in parentheses.

3. Results

The mean testosterone, estradiol, and cortisol concentrations measured in saliva were 0.33±0.34 ng ml^{-1}, 8.36±3.42 pg ml^{-1}, and 6.47±2.30 μg l^{-1} (mean±S.D.), respectively, which represent normal saliva values for adult men (e.g., Penton-Voak and Chen, 2004; Wolf, Schommer, Hellhammer, McEwen, & Kirchbaum, 2001; Wynne-Edwards, 2001).

Testosterone and estradiol were not correlated significantly with either the intensity or the attractiveness of the T-shirts (Table 1). Instead, salivary cortisol concentration strongly correlated positively with women's rating of male scent attractiveness in all women's groups (Table 1, Fig. 1), but not with intensity ratings in any women's groups (Table 1). Testosterone concentration did not correlate significantly with estradiol (Pearson's $r=-.308$, $N=19$, $p=.199$), but the correlation with cortisol was nearly significant (Pearson's $r=.439$, $N=19$, $p=.060$). Estradiol did not correlate with cortisol (Pearson's $r=-.328$, $N=19$, $p=.171$).

Average male scent attractiveness ratings of women not using contraceptive pills showed significant variation across the menstrual cycle (Friedman's test, $\chi^2_{(2)}=8.00$, $p=.018$) (Fig. 2), and women at the most fertile phase of the cycle gave the highest ratings of attractiveness for all males (Fig. 2). Tukey's HSD tests performed post hoc indicated that all groups differed from each other at the .05 level (minimum significant difference between rank sums, 14.43; lowest observed difference, 71.00).

Average male scent intensity ratings of women not using contraceptive pills did not change during the cycle (Friedman's test, $\chi^2_{(2)}=4.53$, $p=.104$) (Fig. 2).

Average attractiveness ratings did not differ significantly between women using contraceptive pills and women not using contraceptive pills (Wilcoxon's test $Z=-1.13$, $p=.260$).

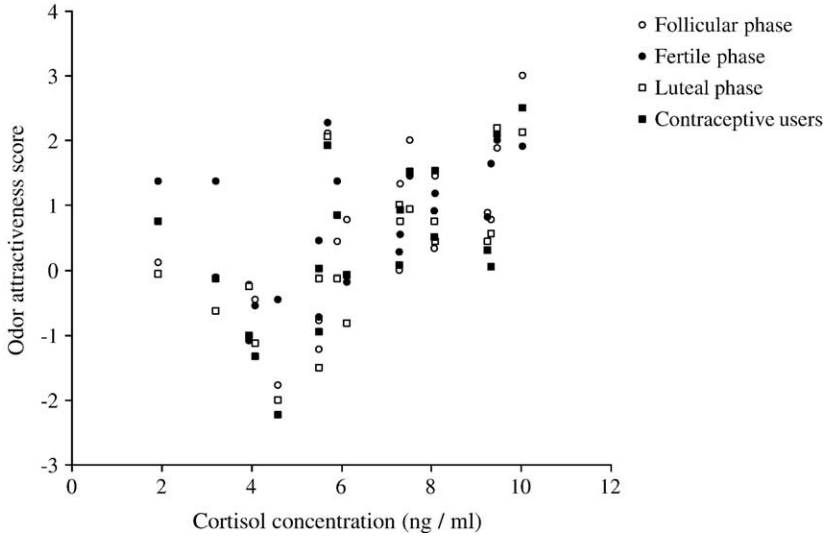

Fig. 1. Relationship between male ($N=19$) saliva cortisol concentration and average attractiveness rating of a man's T-shirt by female raters at different phases of their menstrual cycle (number of females per group: follicular phase, 9; fertile phase, 11; luteal phase, 16; and contraceptive users, 40).

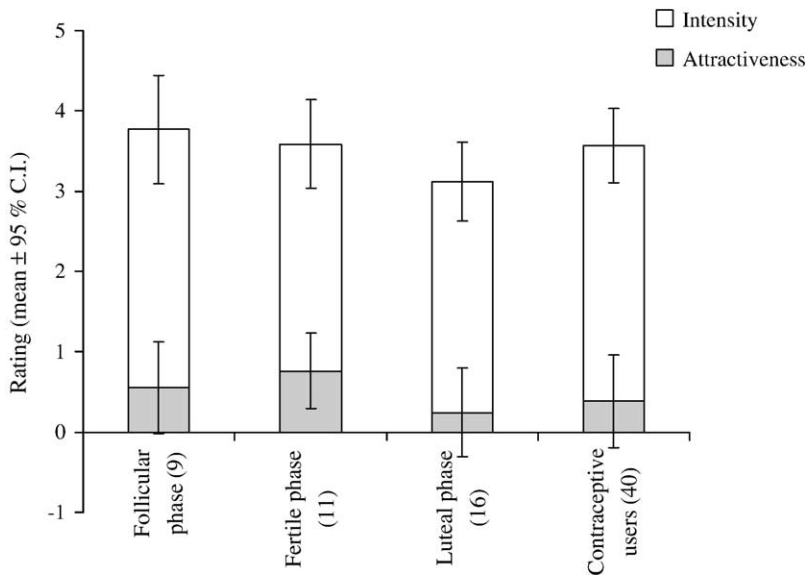

Fig. 2. Average attractiveness ratings of a man's T-shirt by female raters at different phases of their menstrual cycle. Number of women in each group is given in parentheses.

However, women using contraceptive pills gave, on average, higher intensity ratings than normally ovulating women (Wilcoxon's test $Z=-1.97$; $p=.049$; mean±S.D., 3.18±0.98 vs. 2.97±1.18, respectively).

4. Discussion

Interestingly, we found a positive correlation between salivary cortisol level and attractiveness ratings of men's T-shirts by all women's groups, but no significant evidence that the primary androgen, testosterone, could be associated with the odor of a man. Thus, in the light of our study it seems that either cortisol or some other hormone connected to the cortisol metabolism may shape the attractiveness of body odors in humans. For example, several androgens and cortisol are metabolised from the same precursor, pregnenolone (e.g., Nussey & Whitehead, 2001). Further studies are needed to confirm our result.

Recently, it has been found that several women's preferences—males with a masculine face (Johnston, Hagel, Franklin, Fink, & Grammer, 2001; Penton-Voak & Perret, 2000; Penton-Voak et al., 1999), body odor of symmetric men (Gangestad & Thornhill, 1998), body odor of men with immunocompetent genotypes (Thornhill et al., 2003), and masculine behavioral displays (Gangestad, Simpson, Cousins, Garver-Apgar, & Christensen, 2004)—change across the menstrual cycle. However, we did not find evidence that the preference for high saliva cortisol levels changed significantly during the cycle, but all groups of women seemed to prefer males with high cortisol levels.

Why did women prefer the odors of men who had high cortisol level? Physiologically, it is possible that cortisol has either a direct or indirect link via adrenalin to the activity of the apocrine sweat glands which might have effects on the attractiveness of body odor (Ikai & Hasegawa, 1971; Rothardt & Beier, 2001). Further, metabolism of sweat by commensal microbes might make the individual's odor more pleasant depending on sweating rate (see, for example, Austin & Ellis, 2003; Stoddart, 1991). Evolutionarily, immunosuppressive hormones are said to be essential for the production of good-quality sperm since haploid sperm might be susceptible to autoimmune attacks (Skau & Folstad, 2004). Thus, by preferring the scent of cortisol, women might be able to gain both good sperm and good immune genes for their offspring since only genetically immunocompetent males would be able to maintain high cortisol levels (Folstad & Karter, 1992). Unfortunately, we were not able to measure the amount of perspiration in this study. However, it is important to note that cortisol concentration did not correlate with the intensity ratings of T-shirts, suggesting that cortisol affects the scent qualitatively, not quantitatively. Also, it is possible that some of the studied men might have experienced stress, which could affect their cortisol values. Although the experimental conditions were the same for all participants and were planned to be as pleasant as possible.

Women's self-reported sexual desire has been reported to peak at the fertile phase of the menstrual cycle (see, for example, Regan, 1996), when women also exhibit an increased olfactory sensitivity (Doty, 1981; Kohl & Francoeur, 1995). Thus, as indicated in our study, it is likely that the average attractiveness rating of male scent by women not using contraceptive pills changes across the cycle, showing the highest attractiveness at the fertile phase of the cycle. However, the average intensity ratings of women did not change during the cycle among women not using contraceptive pills. The use of contraceptive pills affected the average intensity ratings when analysed as overall difference between contraceptive users and nonusers, suggesting that pills might, in some circumstances, increase the olfactory sensitivity. In this study, we did not collect menstrual cycle diaries or measure salivary estradiol and progesterone. Thus, these results may suffer from some uncontrolled variation in the exact timing of ovulation and fertility groups. To minimise these problems, we excluded all women who had a cycle length either shorter than 21 days or longer than 37 days.

Our study suggests that women's olfactory sensitivity to a man's scent changes during the menstrual cycle, being highest before and during the fertile window of the cycle. Moreover, our results propose that cortisol or its interplay with other causal factors affecting male scent may shape the olfactory cues of mate selection in humans. Further studies are needed to explore the generality of this result in other taxa and the evolutionary significance of this preference to women's fitness.

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