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Sex-hormone dependent perception of androstenone suggests its involvement in communicating competition and aggression

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HIGHLIGHTS

- We measure sex hormonal influences on androstenone perception.
- A high testosterone level relates to heightened androstenone sensitivity in men.
- A high testosterone level relates to unhappiness in response to androstenone in men.
- A high estradiol level relates to disliking of androstenone in women.
- Androstenone is likely involved in communicating aggression or competition.

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ABSTRACT

Androstenone, a compound of human male body odor, might act as a chemosensory signal communicating dominance or aggressiveness. In order to clarify its communicative significance, the relationship between androstenone perception and the level of circulating steroid hormones was investigated in both men and women. Androstenone perception was assessed within n = 26 men and n = 25 women. Female participants were not currently using hormonal contraception and were in their follicular menstrual cycle phase. Androstenone perception was assessed in terms of olfactory sensitivity, quality judgments, and emotional self-ratings. The perception of isovaleric acid served as a control. Over the course of 2 h five saliva samples were collected, aliquots were mixed and levels of estradiol and testosterone were analyzed via enzyme-linked immunosorbent assays.

In men, higher testosterone levels were associated with lower olfactory sensitivity to androstenone ($p = 0.014$) and negative feelings when exposed to it ($p = 0.047$). In women, higher estradiol levels were related to judging androstenone as less pleasant ($p = 0.009$) and more unpleasant ($p = .0036$). The perception of isovaleric acid was unrelated to sex-hormone levels.

The current results support the notion of androstenone communicating dominance, aggression or competition. Men with higher testosterone levels are more sensitive to androstenone and dislike its odor, possibly indicating that androstenone signals the readiness for competition in men. Similarly, the fact that women with higher estradiol levels dislike androstenone may be due to androstenone being a signal of reduced willingness for social cooperation and an increased likelihood to engage in extramarital sex.

1. Introduction

Evidence is increasing that humans effectively communicate a wide variety of information on the basis of chemosensory signals (for reviews see [1,2]). For example, human axillary secretions have been demonstrated to transmit information as diverse as gender [3–6] or transiently experienced affect [7–9]. Of the single molecules contained in human axillary secretions [10,11], androstenone and related 16-androstenes are the most investigated for communicative features (for an overview see [12]). In animals, the production and secretion of androstenone are tightly linked to the level of circulating testosterone [13–16]. Similarly, in humans, axillary androstenone is detected in larger quantities in men than in women [17], and its source seems to be mainly located in the testis [18]. Thus, a link between androstenone and testosterone in humans seems as likely as it is in animals.

The level of circulating testosterone has been shown to correlate with aggressive, dominant, and competitive behavior [19]. In detail, it has been proposed that testosterone is primarily linked to social status seeking, dominance and competitiveness [20,21], traits that may promote aggression, for example in case the individual is challenged. Results linking human aggression to the testosterone level (e.g. [22], for meta-analyses see [23–25]) involve behavioral measures of aggressiveness

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as well as self reports via questionnaires or peer ratings. Most of these findings relate the level of circulating testosterone to direct, physical forms of aggression as opposed to indirect forms (e.g. verbal aggression). Recently reviewed results show that even in laboratory settings, baseline testosterone levels and reactive, direct aggression feature a positive relationship (reviewed in [26]). Moreover, in men, testosterone is linked to instability in intersexual partnerships and reduced paternal investment [27].

Taking into account both the link between circulating testosterone and aggression on one hand, and circulating testosterone and androstenone on the other hand, the communicative function of androstenone is likely signaling dominance and aggression, especially in males. Nonetheless, possibly due to the fact that androstenone serves a sex attracting role in animals, androstenone and related 16-androstenes have been studied extensively for similar effects in humans (for overviews see [12,28]). However, yielding largely inconsistent results these studies offer little basis for inferring that sex attractant like effects occur in humans [28–30]. Moreover, as already stated by Pause [12], the fact that androstenone is a sex attractant in pigs does not preclude a different function, such as communicating dominance or aggression, in humans.

To summarize, androstenone production is tightly linked to the level of endogenous testosterone. Similarly, androstenone perception is, besides being affected by genetic [31,32] and experiential influences [33], linked to circulating sex hormones. Men and women differ in their sensitivity, rates of specific anosmia, and hedonic judgments of androstenone, but only after puberty, with women typically being more sensitive than men [34,35]. Moreover, women tend to vary in their judgment of androstenone's pleasantness during the course of the menstrual cycle [36]. Similar effects have been shown in regard to the perception of the closely related compound androstadienone [37,38].

Within the current study, we sought to determine whether the perception of androstenone directly relates to the level of circulating sex hormones in women and men. The perception of androstenone was assessed at the level of sensitivity, subjective ratings of intensity, pleasantness, unpleasantness, and familiarity, as well as emotional self reports. Isovaleric acid was introduced as a control odor, because similar to androstenone it constitutes an axillary odor compound that humans possess specific receptors for, but data do not suggest hormonal effects on its perception (e.g. sex differences [39]). Individual levels of unbound testosterone and 17-beta-estradiol (estradiol) were assessed via multiple saliva samples. Men with higher circulating testosterone levels themselves should be more sensitive to individuals that could challenge their social status and pose a significant social threat. Therefore, it was hypothesized that in men, higher levels of circulating testosterone should be associated with an increased sensitivity to androstenone and disliking of its odor. In women, on the other hand, androstenone sensitivity and liking should rather be related to estradiol levels, as within an individual woman, the estradiol level is correlated to fertility. It would be of importance to women with increasing fertility to avoid men displaying a tendency for physical aggression and reduced paternal investment.

2. Materials and methods

2.1. Participants

Via advertisement at the university and at local bars, n = 54 (n = 27 male) participants were recruited.[1] However, due to contamination saliva samples of one man and two women had to be excluded from the analysis, resulting in a total of n = 26 men and n = 25 women. Participants had a mean age of 26.0 years (SD = 5.6, range 19–42), and the mean age did not differ with respect to gender [$F(1,47) = 1.741$, $p = 0.193$]. Participating women were not taking any hormonal contraceptives, reported having a regular menstrual cycle and were in the follicular phase of their menstrual cycle (days 5–10, after menses). The participants in general were in good health, non-smokers, were not under acute or long-term medication, had not had any surgery known to influence olfactory perception, did not suffer from any somatic or mental disease and reported no drug abuse. Participants gave written informed consent and were paid for their participation. The study was carried out in accordance with the Declaration of Helsinki and was approved by the ethical committee of the German Society of Psychology (DGPs).

2.2. Odor detection thresholds

Sixteen concentration steps of each androstenone (5-α-androst-16-en-3-one, 98%, Sigma-Aldrich, Germany, No. W50900) and isovaleric acid (99%, Sigma-Aldrich, Germany, No. 129542) were prepared for the threshold tests. Androstenone was dissolved in 1,2-propanediol (99%, Sigma-Aldrich, Germany, No. 134368). A concentration of 1.25 mg/ml was used as the highest concentration that was diluted 1:2 (v/v) for each consecutive step. In the lowest concentration 0.04 μg androstenone was diluted in 1 ml [40,41]. For isovaleric acid, diethyl phthalate (≥96%, Sigma-Aldrich, Germany, No. 80080) was used as the solvent. A 1:2 (v/v) dilution was the highest concentration which was diluted in half decimal log steps for each consecutive concentration [40,42]. In the lowest concentration isovaleric acid was diluted 1:63,000,000 (v/v).

Thresholds were measured according to a two-alternative forced-choice single-staircase detection procedure [43]. With this method, the odor concentrations are presented near the perception threshold in ascending and descending series. When seven staircase reversal points are obtained the procedure is finished and the geometric mean of the last four reversals is used as the threshold estimate. Participants who were unable to detect androstenone at the highest concentration and thus displaying specific hyposmia to androstenone were assigned a threshold of 0.

2.3. Odor ratings

Participants rated both odors with regard to perceived intensity (0 = not detectable, to 10 = extremely intensive), pleasantness (0 = not at all pleasant, to 10 = extremely pleasant), unpleasantness (0 = not at all unpleasant, to 10 = extremely unpleasant) and familiarity (0 = not at all familiar, to 10 = extremely familiar) on four different visual analog scales. For the ratings, participants were presented with the fifth dilution step of each androstenone (78.13 μg/ml) and isovaleric acid (1:200 v/v).

2.4. Emotional ratings

Participants indicated their experienced pleasure (−4 to +4), arousal (1 to 9), and dominance (1 to 9) while smelling androstenone and isovaleric acid by means of the language-free Self-Assessment Manikin (SAM, [44]). Again, androstenone was presented in a concentration of 78.13 μg/ml and isovaleric acid in a dilution of 1:200 v/v (see odor ratings).

2.5. Saliva sampling and biochemical analysis of testosterone and 17-beta-estradiol

Participants refrained from meals, alcoholic beverages and stimulating drinks (e.g. coffee or tea) at least 30 min prior to the beginning of the session. In order to avoid arbitrary results due to the periodic secretion patterns of steroid hormones, five saliva samples were collected over the course of approximately 2 h. Passive drooling devices (Salicaps, IBL International GmbH, Hamburg, Germany) were used for sampling, and samples were frozen at −20 °C. To remove mucins, samples were

[1] In order to increase variance (see [40] Lübke K, Schablitzky S, Pause BM. Male sexual orientation affects sensitivity to androstenone. Chemosens Percept 2009;2:154–60.), both homosexual (n = 13 gay men, n = 12 lesbian women) and heterosexual individuals were included as participants.

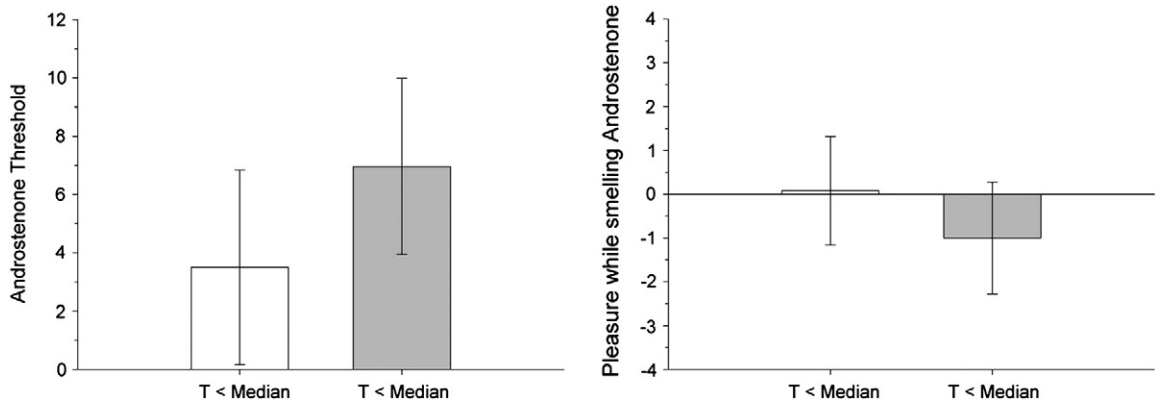

Fig. 1. Mean androstenone thresholds (left) and mean self ratings of pleasure (Self Assessment Manikin, right) of men (n = 24) featuring testosterone levels lower than median (white bars, T < median) and men featuring testosterone levels higher than median (gray bars, T > median). The error bars represent the standard deviation. Note that higher thresholds also indicate higher sensitivity, and that pleasure may range from −4 (indicating least pleasurable feelings) to 4 (indicating most pleasurable feelings).

subjected to two freeze–thaw-centrifuge (10 min at 3000*g*) cycles before mixed aliquots of each participant's samples were analyzed for levels of free testosterone and estradiol. Analysis was conducted by means of commercially available enzyme-linked immunosorbent assays with chemiluminescence detection (IBL International GmbH, Hamburg, Germany). Intra-assay coefficients of variation were below 20.0% for both testosterone and estradiol assays, while inter-assay coefficients of variation were stated as below 6.1% for testosterone and below 9.4% for estradiol within the assay manuals. Analytical sensitivity was 2.0 pg/ml and 0.4 mg/ml for testosterone and estradiol assays, respectively.

2.6. Procedure

In individual sessions, participants first rated androstenone with regard to intensity, pleasantness, unpleasantness, and familiarity. Then the threshold test was carried out, followed by the emotional ratings. This procedure was repeated for isovaleric acid. Sessions lasted about 2 h (M = 113 min, SD = 26 min) and were paused every 20 to 30 min for collection of the saliva samples. Room temperature was kept constant (M = 22 °C, SD = 1 °C).

2.7. Data analysis

Within both male and female subsamples, individuals with estradiol as well as testosterone levels above median were compared to those with hormone levels below median (median split technique, see for example [45]) in regard to the perception of androstenone and isovaleric acid using a 2 (factor "group") × 2 (factor "odor") ANOVA. In case of significant interactions, correlational analyses were performed in order to test for linear relationships between odor perception and the level of circulating hormones.

Exploratorily, student's T-tests were used in order to directly test for hormonal effects on the perception of each odor. One male participant had to be excluded from testosterone related analyses due to his extremely high level of testosterone (exceeding two SDs from mean; M = 81.44 pg/ml, SD = 23.22 pg/ml, participant's testosterone level: 193.75 pg/ml). An alpha level of $p < 0.05$ was used for all statistical tests.

3. Results

3.1. Hormonal effects on the perception of body odor compounds in men

Men with a testosterone level higher than median (HT, testosterone > 79.38 pg/ml) differed from men with a testosterone level lower than median (LT, testosterone < 79.38 pg/ml) in their olfactory sensitivity [main effect "group": $F(1, 22) = 6.08$, $p = 0.022$, $\eta_p^2 = 0.217$]. This effect, however, was solely attributable to differences in the sensitivity to androstenone ["group" by "odor" interaction: $F(1, 22) = 6.02$, $p = 0.023$, $\eta_p^2 = 0.215$]. HT men were more sensitive (M = 6.96, SD = 3.02) to androstenone than LT men [M = 3.50, SD = 3.34; $T(22) = 2.662$, $p = 0.014$, Cohen's $d = 1.087$; see Fig. 1].[2] This effect was further qualified by a medium sized positive correlation, showing that, by trend, the higher the level of circulating testosterone, the higher the sensitivity to androstenone ($r = 0.357$, $p = 0.080$).

Further, the exploratory analysis showed that HT men (M = −1.00, SD = 1.28) reported less pleasure when smelling androstenone than LT men [Fig. 1; M = 0.08, SD = 1.24; $T(22) = 2.106$, $p = 0.047$, Cohen's $d = 0.857$]. The level of estradiol was found unrelated to the perception of androstenone in men, and both levels of estradiol and testosterone were unrelated to the perception of isovaleric acid.

3.2. Hormonal effects on the perception of body odor compounds in women

Women featuring an estradiol level lower than median (LE, E < 4.25 pg/ml) judged androstenone as more pleasant (M = 4.63, SD = 2.08) than women featuring an estradiol level higher (HE, E > 4.25 pg/ml) than median [M = 2.33, SD = 1.86; "group" by "odor" interaction: $F(1, 22) = 6.97$, $p = 0.015$, $\eta_p^2 = 0.241$; LE vs. HE in "androstenone": $T(22) = 2.859$, $p = 0.009$, Cohen's $d = 1.166$; Fig. 2]. Moreover, the level of estradiol was negatively correlated to individual pleasantness ratings of androstenone ($r = -0.415$, $p = 0.039$).

Results of the exploratory analysis showed that unpleasantness ratings mirrored those of pleasantness, as HE women (M = 6.73, SD = 2.96) found androstenone more unpleasant than LE women [M = 4.44, SD = 1.94; $T(22) = 2.239$, $p = 0.036$, Cohen's $d = 0.915$]. The sensitivity to androstenone, however, did not vary with estradiol levels in the perceiving women ($p > 0.250$).[3] Further, the perception of androstenone was unrelated to testosterone levels, while the perception of isovaleric acid again was unrelated to both estradiol and testosterone levels.

3.3. "Odor" main effects

Both men and women displayed higher sensitivity to androstenone than to isovaleric acid (all $p_s < 0.001$). Moreover, isovaleric acid was

[2] Additionally, an ANCOVA was performed including sexual orientation (as measured by self-report using a visual analog scale ranging from 0 = homosexual to 10 = heterosexual) as a covariate. The analysis yielded a comparable result to the main ANOVA, with HT men being more sensitive to androstenone than LT men [$F(1,21) = 7.300$, $p = 0.013$, $\eta_p^2 = 0.258$].

[3] For comparison with the male sample, additionally an ANCOVA was performed including sexual orientation as a covariate. The analysis yielded a comparable result to the main ANOVA showing no difference between the HE and LE group regarding the sensitivity to androstenone ($p > 0.250$).

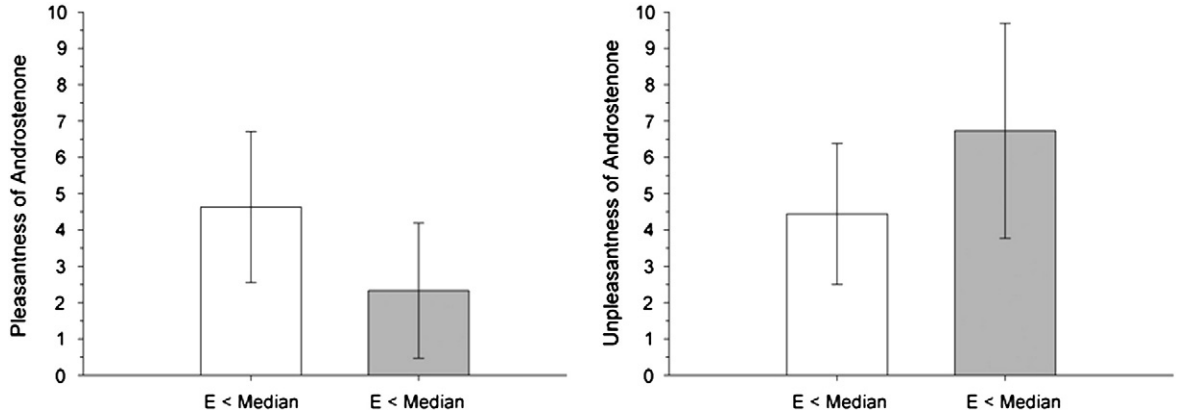

Fig. 2. Mean pleasantness (left) and unpleasantness ratings (right) for androstenone of women featuring estradiol levels lower than median (white bars, E < median) and women (n = 24) featuring estradiol levels higher than median (gray bars, E > median). Note that "0" refers to "not at all pleasant/unpleasant" and "10" refers to "extremely pleasant/unpleasant". The error bars represent the standard deviation.

rated as more intense (all $p_s < 0.001$), less pleasant (all $p_s < 0.05$), and more unpleasant (all $p_s < 0.05$) compared to androstenone by men and women. Regarding emotional self reports, men reported higher arousal while smelling isovaleric acid compared to androstenone ($p < 0.05$), while women reported less pleasurable feelings when smelling isovaleric acid compared to androstenone (all $p_s < 0.05$). See Tables 1 and 2 for detailed descriptive values.

4. Discussion

The current study is the first to show that in both men and women, the perception of androstenone, a significant compound of human body odor, is directly associated to levels of circulating sex hormones. These results are in line with studies demonstrating gender depending changes in androstenone perception during puberty [34,35] and effects of the female menstrual cycle on androstenone perception [36].

In detail, as predicted, men with higher compared to men with lower levels of circulating testosterone are more sensitive to androstenone and report more negative feelings when presented with its odor. As stated within the Introduction section, several lines of evidence support the notion that the chemosensory signal of androstenone, due to its correlation to testosterone [14,17,18], might convey the readiness for aggression of the signal sender [27]. As androstenone has already been shown to be a significant compound to especially human male body odor [41], it probably indicates the presence of an aggressive or dominant male and thus may constitute a signal of social threat. In fact, only recently, the closely related substance androstadienone has been shown to enhance behavioral responses to social threat signals [46]. Similar to the testosterone dependent perception of androstenone reported here, several studies have demonstrated testosterone dependent sensitivity for visual signals of social threat. For example, using a pictorial emotional Stroop task, van Honk and colleagues [47] showed that salivary testosterone in men was positively correlated with selective attention to angry faces. Also, neuroimaging studies repeatedly demonstrated that amygdala activation (generally known to be involved in emotion perception and associated with aggression regulation) in response to pictures of angry faces is positively correlated to the endogenous level of testosterone in the perceiver [48,49]. The current results point into a similar direction in terms of a testosterone modulated perception of androstenone as a chemosensory signal of social threat.

Women, on the other hand, dislike the odor of androstenone more with rising levels of estradiol. Considering androstenone to be a male signal of social threat suggests that disliking its odor with rising estradiol levels (and thus rising fertility) could be an adaptive strategy in women within a mating context. Testosterone has not only been shown to be related to aggression itself, but also to counteract positive and socially skillful behaviors. Several studies report an administration of testosterone leading to decreases in facial mimicry [50], to interfere with the ability of inferring the emotional states of others by their facial expressions [51], and to disrupt social cooperation [52]. In the context of mating and reproductive behavior, results support the notion that long-term committed relationships and parenting behavior are associated with relatively lower levels of circulating testosterone in men, whereas engaging in short-term mating opportunities is related to relatively higher levels of testosterone [53]. Even desiring uncommitted sexual activity while being in a long-term relationship is associated with relatively higher testosterone levels in men [54,55]. Male testosterone levels have further been found to be negatively associated with marital

Table 1
Sensitivity, odor ratings and emotional ratings in response to androstenone and isovaleric acid in men.

	Androstenone		Isovaleric acid	
	LT	HT	LT	HT
Sensitivity	5.08 ± 1.38	6.96 ± 3.02	12.42 ± 0.91	12.63 ± 1.65
Intensity	5.53 ± 2.73	6.10 ± 2.32	9.02 ± 1.17	8.48 ± 1.96
Pleasantness	3.58 ± 1.86	2.55 ± 1.72	1.75 ± 1.85	1.58 ± 2.08
Unpleasantness	5.52 ± 2.83	5.83 ± 2.78	8.25 ± 1.95	7.71 ± 2.14
Familiarity	3.48 ± 3.33	4.50 ± 3.31	3.20 ± 2.43	5.19 ± 2.80
Pleasure	0.10 ± 1.24	−1.00 ± 1.28	−1.08 ± 1.56	−1.42 ± 1.78
Arousal	4.92 ± 1.73	5.50 ± 1.88	6.08 ± 1.62	6.17 ± 1.03
Dominance	5.08 ± 1.38	4.58 ± 1.56	5.42 ± 1.08	5.00 ± 2.09

Notes: Values are presented as mean ± standard deviation; LT = individuals with testosterone levels below medium, HT = individuals with testosterone levels above medium.

Table 2
Sensitivity, odor ratings and emotional ratings in response to androstenone and isovaleric acid in women.

	Androstenone		Isovaleric acid	
	LE	HE	LE	HE
Sensitivity	6.15 ± 5.02	6.96 ± 3.02	12.85 ± 1.40	13.46 ± 2.86
Intensity	5.21 ± 2.63	6.12 ± 2.86	9.16 ± 0.80	9.37 ± 0.81
Pleasantness	4.63 ± 2.08	2.33 ± 1.86	0.83 ± 0.81	1.15 ± 1.24
Unpleasantness	4.44 ± 1.94	6.73 ± 2.96	8.77 ± 0.84	8.72 ± 1.64
Familiarity	3.58 ± 3.30	3.16 ± 3.46	4.19 ± 3.13	4.28 ± 3.40
Pleasure	0.25 ± 0.87	−0.17 ± 1.59	−0.67 ± 1.37	−1.08 ± 1.98
Arousal	4.17 ± 1.64	5.67 ± 1.97	5.92 ± 1.68	5.50 ± 1.93
Dominance	5.58 ± 1.68	5.75 ± 1.29	5.00 ± 2.00	5.33 ± 1.07

Notes: Values are presented as mean ± standard deviation; LE = individuals with estradiol levels below medium, HE = individuals with estradiol levels above medium.

satisfaction and parental relationships [56] and investment in the respective spouse [57]. Moreover, men with higher testosterone levels report higher numbers of sexual partners [58–60] and are less likely to marry, more likely to have experienced a divorce, and are more likely to report extramarital sex [61]. While the issue of causation is not settled yet, authors suggest a bidirectional link between the level of testosterone and "mating behavior" in men. For example, men with high levels of endogenous testosterone are less likely to engage in stable relationships, but stable relationships also decrease testosterone levels [53]. In any case, based on the theory of differential parental investment women should search for partners willing to invest into offspring [62]. Consequently women should, with increasing fertility, more dislike the odor of androstenone in order to avoid engaging in a relationship with a man featuring a high level of endogenous testosterone who would not make a reliable partner or father to potential offspring.

Isovaleric acid was selected as a control odor for functional similarities to androstenone, e.g. being a monomolecular compound of human body odor, and binding to specific receptors within the human mucosa [39]. It was not intended to match androstenone in terms of perceptual quality, e.g. intensity. (As androstenone sensitivity is distributed trimodally within the population [63,64], matching any odor to androstenone for its perceived intensity is hardly feasible.) However, the observed linear relationships between androstenone perception and both hormone levels, and the fact that in the respective instances about 68% of the participants ($M \pm 1$ SD) scored within the scale ranges for androstenone as well as for isovaleric acid, strongly contradict any confounding effects of perceptual differences between the odors.

Taken together, the results of the current study suggest that the perception of androstenone, as a significant component of male body odor, is in fact affected by sex hormonal levels, not only in women but also in men. The hormonal effects on its perception in both genders point to a role for androstenone in communicating traits like dominance or even aggression. As androstenone has – in the past – mostly been investigated for possible sex-attractant like effects, paradigms examining its effect in the realms of dominance or aggression are lacking. Future research might show whether androstenone is able to prime respective behaviors, and how such effects might differ between men and women.

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References

[1] Lundström JN, Olsson MJ. Functional neuronal processing of human body odors. Vitam Horm 2010;83:1–23.
[2] Pause BM. Processing of body odor signals by the human brain. Chemosens Percept 2012;5:55–63.
[3] Doty RL, Orndorf MM, Leyden JJ, Kligman A. Communication of gender from human axillary odors: relationship to perceived intensity and hedonicity. Behav Biol 1978;23:373–80.
[4] Lübke KT, Hoenen M, Pause BM. Differential processing of social chemosignals obtained from potential partners in regards to gender and sexual orientation. Behav Brain Res 2012;228:375–87.
[5] Martins Y, Preti G, Crabtree CR, Runyan T, Vainius AA, Wysocki CJ. Preference for human body odor is influenced by gender and sexual orientation. Psychol Sci 2005;16:694–701.
[6] Schleidt M, Hold B. Human axillary odour: biological and cultural variables. In: Steiner JZ, editor. Determination of behavior by chemical stimuli. London: IRL; 1982. p. 91–104.
[7] Mujica-Parodi LR, Strey HH, Frederick B, Savoy R, Cox D, Botanov Y, et al. Chemosensory cues to conspecific emotional stress activate amygdala in humans. PLoS One 2009;4:e6415. doi:10.1371/journal.pone.0006415.
[8] Prehn-Kristensen A, Wiesner C, Bergmann TO, Wolff S, Jansen O, Mehdorn HM, et al. Induction of empathy by the smell of anxiety. PLoS One 2009;4:e5987. doi:10.1371/journal.pone.0005987.
[9] Zhou W, Chen D. Fear-related chemosignals modulate recognition of fear in ambiguous facial expressions. Psychol Sci 2009;20:177–83.
[10] Gower DB, Ruparelia BA. Olfaction in humans with special reference to odorous 16-androstenes: their occurrence, perception and possible social, psychological and sexual impact. J Endocrinol 1993;137:167–87.
[11] Nixon A, Mallet AI, Gower DB. Simultaneous quantification of five odorous steroids (16-androstenes) in the axillary hair of men. J Steroid Biochem 1988;29:505–10.
[12] Pause BM. Are androgen steroids acting as pheromones in humans? Physiol Behav 2004;83:21–9.
[13] Andresen O. Concentrations of fat and plasma 5-alpha-androstenone and plasma testosterone in boars selected for rate of body-weight gain and thickness of back fat during growth, sexual-maturation and after mating. J Reprod Fertil 1976;48:51–9.
[14] Bonneau M. Compounds responsible for boar taint, with special emphasis on androstenone — a review. Livest Prod Sci 1982;9:687–705.
[15] Zamaratskaia G, Babol J, Andersson H, Lundstrom K. Plasma skatole and androstenone levels in entire male pigs and relationship between boar taint compounds, sex steroids and thyroxine at various ages. Livest Prod Sci 2004;87:91–8.
[16] Zamaratskaia G, Babol J, Andersson HK, Andersson K, Lundstrom K. Effect of live weight and dietary supplement of raw potato starch on the levels of skatole, androstenone, testosterone and oestrone sulphate in entire male pigs. Livest Prod Sci 2005;93:235–43.
[17] Gower DB, Bird S, Sharma P, House FR. Axillary 4-alpha-androst-16-en-3-one in men and women: relationships with olfactory acuity to odorous 16-androstenes. Experientia 1985;41:1134–6.
[18] Kwan TK, Kraevskaya MA, Makin HLJ, Trafford DJH, Gower DB. Use of gas chromatographic mass spectrometric techniques in studies of androst-16-ene and androgen biosynthesis in human testis; cytosolic specific binding of 5 alpha-androst-16-en-3-one. J Steroid Biochem Mol Biol 1997;60:137–46.
[19] Mazur A, Booth A. Testosterone and dominance in men. Behav Brain Sci 1998;21:353–63.
[20] Eisenegger C, Naef M, Snozzi R, Heinrichs M, Fehr E. Prejudice and truth about the effect of testosterone on human bargaining behaviour. Nature 2010;463:356–9.
[21] Eisenegger C, Haushofer J, Fehr E. The role of testosterone in social interaction. Trends Cogn Sci 2011;15:263–71.
[22] van Bokhoven I, van Goozen SH, van Engeland H, Schaal B, Arseneault L, Seguin JR, et al. Salivary testosterone and aggression, delinquency, and social dominance in a population-based longitudinal study of adolescent males. Horm Behav 2006;50:118–25.
[23] Archer J. The influence of testosterone on human aggression. Br J Psychol 1991;82(Pt 1):1–28.
[24] Archer J, Graham-Kevan N, Davies M. Testosterone and aggression: a reanalysis of Book, Starzyk, and Quinsey's (2001) study. Aggress Violent Behav 2005;10:241–61.
[25] Book AS, Starzyk KB, Quinsey VL. The relationship between testosterone and aggression: a meta-analysis. Aggress Violent Behav 2001;6:579–99.
[26] Carre JM, McCormick CM, Hariri AR. The social neuroendocrinology of human aggression. Psychoneuroendocrinology 2011;36:935–44.
[27] Archer J. Testosterone and human aggression: an evaluation of the challenge hypothesis. Neurosci Biobehav Rev 2006;30:319–45.
[28] Kirk-Smith MD. Culture and olfactory communication. In: Gardner A, editor. Ethological roots of culture. Dordrecht: Kluwer Academics Pubs; 1995. p. 385–406.
[29] Wyatt TD. Fifty years of pheromones. Nature 2009;457:262–3.
[30] Wysocki CJ, Preti G. Facts, fallacies, fears, and frustrations with human pheromones. Anat Rec A Discov Mol Cell Evol Biol 2004;281A:1201–11.
[31] Knaapila A, Zhu G, Medland SE, Wysocki CJ, Montgomery GW, Martin NG, et al. A genome-wide study on the perception of the odorants androstenone and galaxolide. Chem Senses 2012;37:541–52.
[32] Wysocki CJ, Beauchamp GK. Ability to smell androstenone is genetically determined. Proc Natl Acad Sci U S A 1984;81:4899–902.
[33] Wysocki CJ, Dorries KM, Beauchamp GK. Ability to perceive androstenone can be acquired by ostensibly anosmic people. Proc Natl Acad Sci U S A 1989;86:7976–8.
[34] Dorries KM, Schmidt HJ, Beauchamp GK, Wysocki CJ. Changes in sensitivity to the odor of androstenone during adolescence. Dev Psychobiol 1989;22:423–35.
[35] Schmidt HJ, Beauchamp GK. Adult-like odor preferences and aversions in three-year-old children. Child Dev 1988;59:1136–43.
[36] Hummel T, Gollisch R, Wildt G, Kobal G. Changes in olfactory perception during the menstrual cycle. Experientia 1991;47:712–5.
[37] Lundström JN, Hummel T, Olsson MJ. Individual differences in sensitivity to the odor of 4,16-androstadien-3-one. Chem Senses 2003;28:643–50.
[38] Hummel T, Krone F, Lundström JN, Bartsch O. Androstadienone odor thresholds in adolescents. Horm Behav 2005;47:306–10.
[39] Menashe I, Abaffy T, Hasin Y, Goshen S, Yahalom V, Luetje CW, et al. Genetic elucidation of human hyperosmia to isovaleric acid. PLoS Biol 2007;5:2462–8.
[40] Lübke K, Schablitzky S, Pause BM. Male sexual orientation affects sensitivity to androstenone. Chemosens Percept 2009;2:154–60.
[41] Pause BM, Rogalski KP, Sojka B, Ferstl R. Sensitivity to androstenone in female subjects is associated with an altered brain response to male body odor. Physiol Behav 1999;68:129–37.
[42] Pause BM, Ferstl R, Fehm-Wolfsdorf G. Personality and olfactory sensitivity. J Res Pers 1998;32:510–8.
[43] Doty RL, Laing DG. Psychophysical measurement of human olfactory function, including odorant mixture assessment. In: Doty RL, editor. Handbook of olfaction and gustation. New York: Marcel Dekker; 2003. p. 203–28.
[44] Bradley MM, Lang PJ. Measuring emotion: the self-assessment manikin and the semantic differential. J Behav Ther Exp Psychiatry 1994;25:49–59.
[45] Mehta PH, Josephs RA. Testosterone and cortisol jointly regulate dominance: evidence for a dual-hormone hypothesis. Horm Behav 2010;58:898–906.

[46] Frey MCM, Weyers P, Pauli P, Muhlberger A. Androstadienone in motor reactions of men and women toward angry faces. Percept Mot Skills 2012;114:807–25.
[47] van Honk J, Tuiten A, Verbaten R, van den Hout M, Koppeschaar H, Thijssen J, et al. Correlations among salivary testosterone, mood, and selective attention to threat in humans. Horm Behav 1999;36:17–24.
[48] Derntl B, Windischberger C, Robinson SJ, Kryspin-Exner I, Gur RC, Moser E, et al. Amygdala activity to fear and anger in healthy young males is associated with testosterone. Psychoneuroendocrinology 2009;34:687–93.
[49] Hermans EJ, Ramsey NF, van Honk J. Exogenous testosterone enhances responsiveness to social threat in the neural circuitry of social aggression in humans. Biol Psychiatry 2008;63:263–70.
[50] Hermans EJ, Putman P, van Honk J. Testosterone administration reduces empathetic behavior: a facial mimicry study. Psychoneuroendocrinology 2006;31:859–66.
[51] van Honk J, Schutter DJ, Bos PA, Kruijt A-W, Lentjes EG, Baron-Cohen S. Testosterone administration impairs cognitive empathy in women depending on second-to-forth digit ratio. Proc Natl Acad Sci U S A 2011;108:3448–52.
[52] Wright ND, Bahrami B, Johnson E, Di Malta G, Rees G, Frith CD, et al. Testosterone disrupts human collaboration by increasing egocentric choices. Proc Biol Sci 2012;279:2275–80.
[53] Burnham TC, Chapman JF, Gray PB, McIntyre MH, Lipson SF, Ellison PT. Men in committed, romantic relationships have lower testosterone. Horm Behav 2003;44:119–22.
[54] Edelstein RS, Chopik WJ, Kean EL. Sociosexuality moderates the association between testosterone and relationship status in men and women. Horm Behav 2011;60:248–55.
[55] McIntyre M, Gangestad SW, Gray PB, Chapman JF, Burnham TC, O'Rourke MT, et al. Romantic involvement often reduces men's testosterone levels — but not always: the moderating role of extrapair sexual interest. J Pers Soc Psychol 2006;91:642–51.
[56] Julian T, McKenry PC. Relationship of testosterone to men's family functioning at mid-life: a research note. Aggress Behav 1989;15:281–9.
[57] Gray PB, Kahlenberg SM, Barrett ES, Lipson SF, Ellison PT. Marriage and fatherhood are associated with lower testosterone in males. Evol Hum Behav 2002;23:193–201.
[58] Bogaert AF, Fisher WA. Predictors of university mens number of sexual partners. J Sex Res 1995;32:119–30.
[59] Daitzman R, Zuckerman M. Disinhibitory sensation seeking, personality and gonadal hormones. Pers Individ Differ 1980;1:103–10.
[60] van Anders SM, Hamilton LD, Watson NV. Multiple partners are associated with higher testosterone in North American men and women. Horm Behav 2007;51:454–9.
[61] Booth A, Dabbs JM. Testosterone and men's marriages. Soc Forces 1993;72:463–77.
[62] Trivers RL. Parental investment and sexual selection. In: Campbell B, editor. Sexual selection and the descent of man. Chicago: Aldine Publishing Company; 1972. p. 136–79.
[63] Labows JN, Wysocki CJ. Individual differences in odor perception. Perfumer Flavorist 1984;9:21–6.
[64] Bremner EA, Mainland JD, Khan RM, Sobel N. The prevalence of androstenone anosmia. Chem Senses 2003;28:423–32.