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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.