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Androstadienone's influence on the perception of facial and vocal attractiveness is not sex specific

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ABSTRACT

The androgen steroid androstadienone, an odorous compound emitted from the human axillary region, has recurrently been considered as a candidate compound involved in human chemical communication and mate choice. Although perception of androstadienone has been shown to influence several affective (mood), attentional, physiological and neural parameters, studies investigating its impact on human attractiveness remain unpersuasive because of incomplete designs (e.g., only female participants) and contradictory results. The aim of this study was to investigate how androstadienone may influence others' attractiveness. Specifically, we used a complete design (male and female raters, male and female faces and voices) to determine whether androstadienone influences the perception of social stimuli in a sex-specific manner, which would favor pheromonal-like properties of the compound, or in a more general manner, which would suggest that the compound has broader influences on human psychological responses. After comparing the ratings of men and women who were exposed to androstadienone masked in clove oil with those of men and women who were exposed to clove oil alone, we found that androstadienone enhanced the perceived attractiveness of emotionally relevant stimuli (opposite-sex stimuli in men and in fertile women). Response times for categorizing the stimuli as attractive or not were also affected by androstadienone, with longer response times in men and in fertile women and shorter response times in non-fertile women, irrespective of the stimulus sex. The results favor the hypothesis of general effects over sex-specific effects of androstadienone, thus questioning the relevance of focusing on that particular compound in the study of human attractiveness through body odor and encouraging the search for other semiochemicals that might be significant for human mate choice.

1. Introduction

Pheromonal communication has been demonstrated in a wide range of species across the animal kingdom (Wyatt 2014) (see the pioneer work on sexual attraction in the moth related to the molecule "bombykol": Butenandt et al., 1959), including several mammals (pups' attraction toward the mother's mammary pheromone in the rabbit: Schaal et al., 2003; the Darcin effect on sexual attraction in mice: Roberts et al., 2010). Research in humans, however has led to much more ambiguous and controversial results. Among the wide variety of substances excreted in human body fluids (urine, saliva, genital secretions and sweat; Stoddart, 1990), several androgen derivatives present in apocrine sweat have received much attention from scientists in the quest to identify human pheromones: androstenone (5α-androst-16-en-3-one; e.g., Kirk-Smith and Booth, 1980; Pause, 2004), androstenol (5α-androst-16-en-3α-ol; e.g., Kirk-Smith et al., 1978; Maiworm and Langthaler, 1992) and, in the most recent studies, androstadienone (androsta-4,16-dien-3-one; e.g., Bensafi et al., 2004a; Hummer and McClintock, 2009; Saxton et al., 2008). At least two main historical reasons can be cited for studying these volatile steroids as possible human pheromones. First, they have been directly linked with the reproductive behavior of another mammal (lordosis in the female pig: Dorries et al., 1995). Second, some studies have shown that these steroids are emitted in a sexually dimorphic manner, with higher concentrations, on average, in men (androstenone: Bird and Gower, 1981; Gower et al., 1985; androstadienone: Brooksbank et al., 1972). Despite the fact that these justifications are highly debatable (e.g., see Gower et al., 1994; for a counterexample of a woman secreting more of these compounds than most men who were tested), numerous studies have

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focused on these compounds as potential candidates for a human pheromone.

Precise definitions have been proposed for the concept of pheromone (Beauchamp et al., 1976; Karlson and Lüscher, 1959; Wyatt, 2010),[1] but so far studies in humans have not managed to identify molecules fitting these criteria (Wyatt, 2015) and some authors are skeptical about the existence of pheromones in humans (Doty, 2010). Studies investigating putative pheromonal properties of some compounds (mostly those cited earlier, chosen on the basis of questionable arguments) have tested, using varied methodologies, their influence on human behavior and physiological and emotional states. Rather than thoroughly testing the classic definitions of pheromones, studies in humans have instead hypothesized that if these compounds had a biological function in sexual behavior, then (1) perception of candidate compounds could be sex specific, in that they could elicit responses differing in intensity or in quality between the sexes; (2) variations should occur during the menstrual cycle of women, with an enhanced effect of the compounds around ovulation, when the risk of conception is higher; (3) sexual orientation should be influential; and (4) age, a correlate of reproductive ability (young adults versus children for example), should also be linked with variations in the perception and effects of these compounds.

Mitigated evidence has been obtained so far on these four criteria for the androgen compound that has recently been receiving the greatest attention: androstadienone. Psychophysical and neuroscientific evidence suggests that this odorous compound is processed in a sex-dimorphic manner. First, it has been shown that women detect androstadienone at lower concentrations than men do (Koelega and Köster, 1974; Lundström et al., 2003b). These differences may appear from puberty onwards (Hummel et al., 2005), but the role of sexual maturation remains uncertain because other studies also found sex differences in pre-pubertal children's neural response to this molecule (Burke et al., 2014). Whether such a phenomenon is specific to androstadienone also remains uncertain, because similar puberty-related changes have been found for other malodors (Chopra et al., 2008). Second, Savic et al. (2001) found that androstadienone induces hypothalamic activation in a sex-specific manner (higher activation of this area in women compared with men) and in a sexual orientation-specific manner (like heterosexual women, homosexual men have higher hypothalamic activation than do heterosexual men: Savic et al., 2005). The sex specificity of these brain activations was, however, questioned in a study that used different concentrations and found hypothalamic activations in both men and women (Burke et al., 2012). Regarding the variations during the menstrual cycle, women were found to be more sensitive to androstadienone around ovulation than were women in the non-fertile phase or women who were using oral contraceptives, which was not the case for another non-body odor, phenyl-ethanol (Lundström et al., 2006).

Further, the effect of androstadienone on human behavior and on physiological and emotional states has received much attention. Several studies have highlighted positive effects of androstadienone on participants' mood and alertness: some in women only (Bensafi et al., 2004a,b; Jacob and McClintock, 2000), some in both sexes (Hummer and McClintock, 2009; Jacob et al., 2002) and some in female participants without comparison to males (Grosser et al., 2000; Lundström et al., 2003a; Lundström and Olsson, 2005). Discordant evidence has, however, been reported regarding physiological responses of the autonomous nervous system (sympathetic-like effects in Bensafi et al., 2004a; versus parasympathetic-like effects in Grosser et al., 2000), and these were context dependent (varying according to the sex of the experimenter: Lundström and Olsson, 2005). Although these studies did not specifically investigate sexual behavior or mate choice (but it has been claimed that "a positive mood is known to facilitate women's sexual response, and increased focus improves sexual satisfaction," Verhaeghe et al., 2013), other studies have more specifically tested the effect of androstadienone on the perception of social stimuli. First, androstadienone was found to enhance attention toward sexless drawings of emotional faces in both men and women (Frey et al., 2012; Hummer and McClintock, 2009). The specificity of this effect toward social stimuli versus non-social objects is under debate (nonspecific: Hummer and McClintock, 2009; specific: Parma et al., 2012). Studies that have explicitly investigated the effect of androstadienone on perceived attractiveness are scarce, having involved only female participants and having evaluated only male stimuli (Lundström and Olsson, 2005; Saxton et al., 2008) or male and female stimuli (Parma et al., 2012). Whereas earlier studies suggested that other similar compounds such as androstenol or androsterone could modulate face attractiveness (Kirk-Smith et al., 1978; Maiworm and Langthaler, 1992), androstadienone was found to have no impact on the perception of face attractiveness (Lundström and Olsson, 2005), to have an effect that is not replicable (significant in one of three speed-dating studies: Saxton et al., 2008), or to have an effect on the perception of same-sex faces only (Parma et al., 2012).

Given the inconsistencies in these results and the methodological shortcomings of these studies (no comparison between male and female responses in the presence of androstadienone; menstrual cycle taken into account in only one study), we devised a new study with a more complete design to investigate how androstadienone may influence others' attractiveness. More generally, this study aimed to present new elements to determine whether it is relevant – for a better understanding of human chemosignaling in mate choice – to keep focusing on this particular compound rather than on others (Wyatt, 2015). With this aim, we collected attractiveness evaluations of male and female participants, the latter being allocated to a "fertile" group or a "non-fertile" group according to the phase of their menstrual cycle at the time they participated in the study. We used a highly standardized set of social stimuli that were varied in attractiveness, including male and female faces and – for the first time in androstadienone studies – voices, taken from the GEneva Faces and Voices database (GEFAV: Ferdenzi et al., 2015). We used both faces and voices because we wanted to test whether the effects that have mostly been tested in the visual domain would replicate in another relevant modality. A between-subject design allowed us to compare the responses of participants exposed to androstadienone with the responses of participants exposed to a control odor. We examined (i) the speed of processing of faces/voices, measured by response time to categorize the stimulus as attractive or unattractive, and (ii) the valence of faces/voices, measured by attractiveness ratings.

With this design, we tested whether androstadienone influences the perception of others' faces and voices and whether this effect is sex specific (regarding the perceiver and the person

[1] According to Karlson and Lüscher (1959), pheromones are "substances which are secreted to the outside by an individual and received by a second individual of the same species, in which they release a specific reaction, for example, a specific behavior or a developmental process." The concept of pheromone was then redefined by Beauchamp et al. (1976) to better fit the mammalian model: to them, a pheromone is a single molecule (or at most a mix of only a few compounds) having a well-defined behavioral or endocrinological function that is species specific and expressed through stereotyped responses that do not result from learning or exposure effects. More recently, emphasizing the difference between pheromones and signature mixtures (highly variable odors learned for individual/family recognition), Wyatt (2010) proposed a modified version of Karlson and Lüscher (1959) definition of pheromones: "molecules that are evolved signals, in defined ratios in the case of multiple component pheromones, which are emitted by an individual and received by a second individual of the same species, in which they cause a specific reaction, for example, a stereotyped behavior or a developmental process."

evaluated) or more general. In the first hypothesis (sex-specific effects), androstadienone would act as a signal of mate quality (see Thornhill and Gangestad, 1999; for a link between body odor and mate quality). Being a by-product of testosterone (Rennie et al., 1989), androstadienone could constitute a testosterone-dependent sexual trait: these traits, such as deep voices or masculine facial features, signal biological quality to a prospective mate (Folstad and Karter, 1992) and increase attractiveness (Collins, 2000; Perrett et al., 1998). Consequently, men should be more attractive to women in the presence of androstadienone, and this effect should be enhanced during the fertile phase of the perceiver's menstrual cycle (in accordance with the increased preference for masculine faces, voices and bodies around ovulation: Gangestad and Thornhill, 2008). Note that masculinity/femininity ratings were collected to test how this dimension could mediate potential effects on attractiveness. Although androstadienone should have no effect, or a negative effect, on women's attractiveness, because femininity – not masculinity – tends to drive preferences in this case (Collins and Missing, 2003; Fraccaro et al., 2010), male raters may be able to infer other men's quality from the odor of androstadienone associated with them (Huoviala and Rantala, 2013) and therefore rate them as more attractive. Because of the cost of attractiveness evaluations in terms of attentional resources (Jung et al., 2012) and the decrease in processing speed of faces with increasing attractiveness (Kranz and Ishai, 2006), the time needed to categorize the stimuli as attractive or not would be expected to follow attractiveness changes, i.e., to increase if attractiveness increases in the presence of androstadienone and to decrease if attractiveness decreases. In the second hypothesis (more general), androstadienone would have an influence that is not sex specific, but instead specifically directed to emotionally relevant information (Hummer and McClintock, 2009). Here, the most emotionally relevant stimuli are, given the nature of the tasks (attractiveness judgments) and the sexual orientation of the participants (heterosexual), opposite-sex stimuli. Androstadienone may thus specifically modulate attention to the emotional content of opposite-sex stimuli: if, as suggested by Hummer and McClintock (2009, p.556), "emotional content [is] more difficult to ignore when androstadienone [is] present," then opposite-sex stimuli should capture attention more and subsequently increase the time taken to process them in the categorization task. As suggested by Villemure and Bushnell (2007), it could be that only attention to the emotional content of these stimuli, not the emotional content itself (attractiveness), may be affected by androstadienone.

2. Method

2.1. Participants

Forty men and 40 women with a mean age of 23.1 years (SD = 4.4) were recruited from the students of the University of Geneva. Inclusion criteria, based on self-declaration, were as follows: 18–35 years of age; of European origin; heterosexual; a native French speaker; not a regular smoker; having normal olfaction, vision and audition; and, for women, not being pregnant or taking any form of hormonal contraception. One female participant who failed the test for normal olfaction (see Section 2.3.2) was excluded from the data analysis. Participants were randomly allocated to one of two experimental groups: one group (CA) was exposed to androstadienone masked in clove oil, and the other (control) group (C) was exposed to clove oil alone. The CA group comprised 20 men and 20 women, including 8 who were in the fertile phase of their menstrual cycle. The C group comprised 20 men and 19 women, including 11 fertile women. Fertility status was estimated from the participants' reports of the onset of their current cycle (first day of last menstruation) and of their usual cycle length. We first computed the probable date of the end of the cycle before using a backward counting method (Ferdenzi et al., 2009; Thornhill and Gangestad, 1999), estimating the fertile period between 14 and 20 days from the expected end of the cycle. Appointments were scheduled so as to include approximately as many fertile as non-fertile women. The C and CA groups did not differ in age ($t_{77} = 1.69$; $p = .094$) or in the number of fertile/non-fertile women ($\chi^2 = 1.25$, $p = .26$). Participants were informed that we aimed to test the effect of common odors on the perception of faces and voices, but no information was provided regarding the nature of the odorous stimuli. Participants received financial compensation for their participation. They gave written informed consent prior to participation, and the Committee on Research Ethics of the Faculty of Psychology and Education Sciences at the University of Geneva approved the study.

2.2. Stimuli and questionnaires

2.2.1. Odorants

Participants took part in two sessions: the main evaluation session and the olfactory screening session (see Section 2.3). In the main evaluation session, to enable comparison with other studies, we used the same concentration, nature and administration of the odorants as those proposed by Jacob and McClintock (2000) and later used by other researchers (e.g., Lundström et al., 2003a; Saxton et al., 2008). The experimental solution (CA) was a 250 μM concentration of androstadienone in propylene glycol with 1% clove oil as a mask odor, and the control solution (C) was 1% clove oil in propylene glycol. The odorous solutions were placed in two identical flasks, A and B, by one experimenter (CF), while another experimenter (RA), who was blind to the content of the odor flasks, ran the experimental sessions. For the olfactory screening session, three triplets of odor pens (Sniffin' Sticks; Burghart Gmbh, Germany) were used to test 1) the efficiency of the clove mask, 2) anosmia to androstadienone and 3) general olfaction, respectively. Triplet 1 comprised two pens filled with C and one with CA, triplet 2 consisted of two blanks versus androstadienone at a high concentration (5000 μM), and triplet 3 consisted of two blanks versus a complex strawberry aroma. All substances were provided by Firmenich SA, Geneva.

2.2.2. Faces and voices

All participants were presented with the same 120 stimuli, consisting of pictures of neutral faces and voice excerpts (saying the French word "bonjour") of 30 men and 30 women from the GEneva Faces and Voices Database (GEFAV; Ferdenzi et al., 2015). All 60 GEFAV donors were native French speakers, of European origin and 18–35 years old. Raters were not informed that the faces and the voices came from the same donors.

2.2.3. Mood questionnaire

Participants had to rate their current mood twice, before and after the evaluation session. We selected 12 items taken from the validated French versions of the Profile of Mood States (POMS-f; Cayrou et al., 2003) and of the Positive and Negative Affect Schedule (PANAS; Gaudreau et al., 2006): attentive, confused, energetic, sluggish, relaxed, nervous, cheerful, sad, enthusiastic, irritated, considerate and sensual. Ratings were given by placing a cursor on a continuous visual analog scale from "not at all" to "extremely." Participants were also asked to rate their general mood from "very negative" to "very positive." The position of the cursor was then transformed into a score ranging from 0 to 100.

2.3. Procedure

Participants took part in two experimental sessions on different days. During the first session (evaluation session), they rated voices and faces in either the C or CA odor condition, depending on the group they were assigned to. During the second session (olfactory screening session), their olfactory abilities were tested. Fertility status of the female participants (fertile or not fertile) had to be the same during the evaluation and the olfactory screening sessions. For both sessions, the participants were instructed not to wear any perfume, not to smoke on the day of the experiment, and not to eat or drink anything but water in the hour preceding the test. In case raters had a cold or a blocked nose on the day of the experiment, they had to reschedule the session.

2.3.1. Evaluation session

C and CA groups performed the same task on different days to avoid odor contamination of the testing room. The room was well ventilated at the end of each testing day. At the beginning of the rating session, the odorous solution was applied on the skin just beneath the participant's nostrils by using a cotton swab. Male participants were thus allowed to take part only if they had shaved, so as not to interfere with odor application. Participants were then seated in front of a computer equipped with headphones and presented with the rating interface designed with E-Prime 2.0 (Psychology Software Tools, Pittsburgh, PA, USA). A maximum of four participants underwent the study simultaneously. First, they had to rate their current mood on the 13 items of the mood questionnaire presented randomly. Second, they were presented with two blocks of stimuli: voices followed by faces. Each block was divided into two tasks: a "first-impression" task followed by a "rating" task, each being performed with opposite-sex stimuli before same-sex stimuli (Fig. 1). Within each sub-block (e.g., first impression of opposite-sex voices), stimuli were presented randomly.

In the first-impression task, participants had to categorize the stimuli as either attractive or unattractive as fast as they could and based on their gut feeling, using the digits 1 and 3 of the numeric keypad (label positions were counterbalanced across participants). Stimulus presentation was preceded by a 1000 ms fixation cross to ensure that the participants were prepared for the upcoming stimulus. Each stimulus was presented once for 100 ms for the faces and for 430–870 ms for the voice excerpts (depending on the speaker; duration was not modified to prevent alteration of attractiveness: Ferdenzi et al., 2013). Response time from the beginning of the stimulus was recorded, with a 3000 ms maximum response time allowed after the end of the stimulus presentation. A 3000 ms blank screen separated the response from the fixation cross that announced the next stimulus. Four practice trials with two male and two female voices and faces not present in the main experiment were conducted before the real task started.

In the rating task, participants rated the same stimuli that they saw/heard in the first-impression task on continuous scales for attractiveness, from "not attractive at all" to "very attractive," as well as for masculinity/femininity, from "very feminine" to "very masculine" for male stimuli and from "very masculine" to "very feminine" for female stimuli. The position of the cursor was then transformed into a score ranging from 0 to 100. Responses were not limited in time: the vocal stimuli could be replayed ad libitum and the facial stimuli remained visible until the participant validated his/her response.

After having rated the faces, participants rated their current mood again on the 13 items of the mood questionnaire. At the end of the evaluation session, participants were asked to rate how pleasant and intense they found the odor applied on their upper lip (on a 0–8 scale) and to briefly describe it.

2.3.2. Olfactory screening

The 10-min olfactory screening was conducted individually and took place after the rating session, with at least one day between them. For each of the three triplets of odor pens described earlier (see Section 2.2.1), participants were asked to indicate which pen smelled different from the other two. This was repeated five more times per triplet with the pens presented in random order, allowing us to calculate the number of correct answers between zero and six. Triplet 1 (testing efficiency of the clove mask) was used first because of the odorants' lower concentration, whereas the other two triplets were used afterwards in random order. No feedback was given. At the end of the screening session, participants were paid and debriefed.

2.4. Data analysis

First, we examined how the experimental odors were perceived, namely whether some participants were anosmic to androstadienone and whether androstadienone was efficiently masked. Discrimination performances of CA participants between both experimental odors, and between a high concentration of androstadienone and blanks (olfactory screening session), were analyzed with a single sample t-test to compare the scores with chance level (i.e., 2) and with a one-way analysis of variance (ANOVA) to compare rater sex groups. Two-way ANOVAs were conducted to test the effect of odor condition (C, CA) and rater sex (men, non-fertile women, fertile women) on the perceived intensity and pleasantness of the experimental odor (evaluations collected at the end of the rating session). Post hoc analyses were Tukey HSD tests at $\alpha = .05$.

Second, we tested the effect of odor condition and rater sex on mood ratings and on responses to the faces and voices. For mood data, we conducted two ANOVAs: (1) a two-way ANOVA with odor condition (C, CA) and rater sex (men, non-fertile women, fertile women) as between-subjects factors on general mood rating, and (2) a repeated-measure ANOVA with mood item (12 mood adjectives) as a within-subjects factor, and odor condition and rater sex as between-subjects factors. For face and voice data, scores were averaged by stimulus, and analyses were conducted for same-sex and opposite-sex stimuli separately: stimulus sex was not included as a factor because opposite-sex stimuli were always presented first, thus making the comparison irrelevant. Analyses were thus performed on matrices composed of 90 cases (30 stimuli $\times$ 3 rater sexes: men, fertile women, and non-fertile women) by 2 average scores (in each of the C and CA groups), separate matrices being used for same- and opposite-sex stimuli. Therefore, we used repeated-measures ANOVAs with odor condition as a within-subjects factor ("subject" being "stimulus" here) and rater sex as a between-subjects factor to test the effects of these factors on (i) log-transformed response times in the first-impression task, (ii) the percentage of raters in each sex group who categorized the stimulus as attractive in the first-impression task, (iii) average attractiveness ratings and (iv) average masculinity ratings in the rating task. For the latter, because the rating scale was inverted for female stimuli, ratings were transformed into 100 minus the femininity rating. Note that, because response times in the first-impression task did not follow a normal distribution, we log-transformed them after removing outliers defined on an individual rater basis by a duration equal to the mean $\pm$ 3 standard deviations (i.e., 1.4% of the face trials and .7% of the voice trials). Post hoc planned comparisons were performed when significant ($p < .05$) or near significant ($p < .10$) effects were found. All statistical tests were conducted with Statistica v.12 (Statsoft Inc., Tulsa, OK, USA).

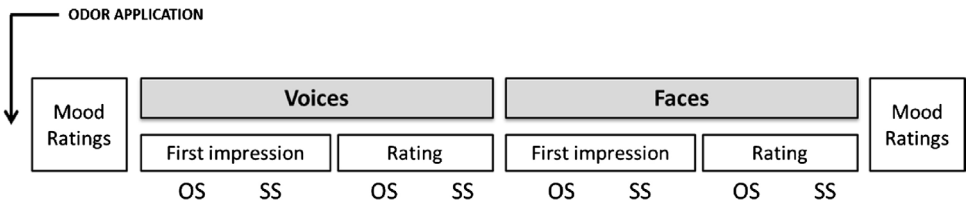

Fig. 1. Diagram of the experimental design. OS: opposite-sex stimuli, SS: same-sex stimuli.

3. Results

3.1. Detection and perception of androstadienone

3.1.1. Anosmia to androstadienone

Results of the discrimination test for the blanks and high-concentration androstadienone triplet (olfactory screening session) revealed that CA participants were able to detect androstadienone at a better than chance level (3.6 correct detections of six trials, $t_{39} = 5.29$, $p < .001$). Taken separately, women clearly had this ability (fertile women: $t_7 = 3.79$, non-fertile women: $t_{11} = 4.84$, $ps < .01$), whereas men only tended to have it ($t_{19} = 1.96$, $p = .065$). There was a significant effect of rater sex ($F_{(2,37)} = 5.02$, $p < .05$) because women (fertile and non-fertile, not different) performed better than men (post hoc tests). Consequently, before performing the analyses presented after, we removed the data from anosmic participants, that is, 11 participants from the CA group (9 men and 2 non-fertile women) and 9 participants from the C group (3 men, 2 non-fertile women and 4 fertile women) based on the fact that they had only zero, one or two correct detections of six in the screening tests involving androstadienone (masked, and high-concentration androstadienone). For the remaining participants of the CA group ($N = 29$), the detection of pure androstadienone was unaffected by rater sex ($F_{(2,26)} = 1.45$, $p = .252$) and occurred at a better than chance level in fertile women ($t_7 = 3.79$, $p < .01$), non-fertile women ($t_9 = 6.33$, $p < .001$), and men ($t_{10} = 3.01$, $p < .05$) (see Fig. 2)

3.1.2. Efficiency of androstadienone masking

Perceptual ratings of the experimental odor collected at the end of the rating session were similar in C and CA groups. Indeed, there was no main effect of experimental condition on the odor's perceived pleasantness (C: 4.7 ± 1.8; CA: 4.3 ± 1.9; $F_{(1,52)} = .99$, $p = .324$) or intensity (C: 3.9 ± 1.9; CA: 3.8 ± 1.9; $F_{(1,53)} = .00$, $p = .976$). For these two variables, we found no main effect of rater sex (men, non-fertile women, fertile women: $ps > .298$) and no interaction between odor condition and rater sex ($ps > .352$). Descriptions of the experimental odors were similar in both groups. They were mostly related to clove and other spices or plants, to the dentist and medication, or to sweets and fruits. Perfume and deodorant were evoked twice in each group, and the only references to natural human body odor ("masculine odor" and "earwax") came from two non-fertile women belonging to the CA group.

To further test whether the masking of androstadienone was efficient, we analyzed the results of the C versus CA discrimination task (triplet 1 of the olfactory screening session) of participants from the CA group. Average correct detection of CA was 2.7 ± 1.4 trials of 6, which was significantly higher than chance ($t_{28} = 2.44$, $p < .05$). Taken separately, men, non-fertile women and fertile women did not answer at a better than chance level ($ps > .094$) and did not differ ($F_{(2,26)} = .36$, $p = .697$; Fig. 2). These results thus provide mixed evidence regarding the efficiency of androstadienone masking in the CA group.

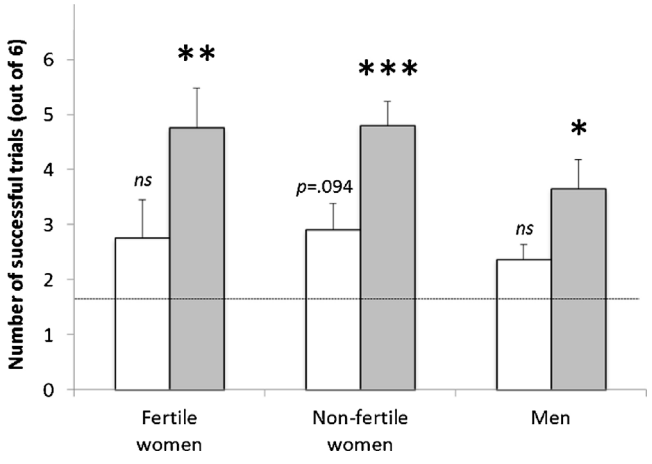

Fig. 2. Androstadienone detection in fertile women ($N = 8$), non-fertile women ($N = 10$) and men ($N = 11$) for the non-anosmic participants exposed to androstadienone (CA group). The average number of successful detections of six trials is in white bars for masked androstadienone (i.e., successful discrimination of a sample with 250 μM androstadienone in clove oil from two samples with clove only) and in grey bars for pure androstadienone (i.e., successful discrimination of a sample with 5000 μM of androstadienone from two samples with solvent only). Comparison with chance level (chance level = 2): $^{***}p < .001$, $^{**}p < .01$, $^{*}p < .05$, *ns* non-significant.

3.2. Effects of androstadienone

3.2.1. Effects on mood

As expected, an overall degradation of mood occurred during the experiment (increase of negative mood items and decrease of positive and general mood items). Analysis of the 12 mood ratings at the beginning of the experiment, of the 12 mood ratings at the end of the experiment, and of the difference between the end and the beginning revealed no effect of odor condition ($ps > .804$ for the three variables), no effect of rater sex (i.e., no difference between men, non-fertile women and fertile women: $ps > .218$), no significant interaction between odor condition and rater sex ($ps > .253$), and no significant interactions between odor condition or rater sex and mood items ($ps > .134$). Analysis of general mood rating also did not show any significant main effects or interactions of these factors (all $ps > .055$).

3.2.2. Effects on first impressions

In the first-impression task, analyses of response time (the time taken to categorize the stimuli as either attractive or unattractive) revealed significant interactions between odor condition and rater sex for all stimulus types (Table 1). These interactions are illustrated in the first column of Fig. 3 with results of the post hoc tests. They are characterized by a slowing effect of androstadienone for opposite-sex faces categorized by fertile women and for all stimuli except same-sex faces categorized by men. Inversely for non-fertile women, all stimulus types were categorized more quickly in the presence of androstadienone than in the control condition. With respect to the percentage of raters categorizing the stimuli as attractive, there was no significant interaction between odor condition and rater sex (Table 1).

Table 1
Results of the repeated-measures ANOVAs with odor condition (C, CA) and rater sex (men, non-fertile women, fertile women) as between-subjects factors, on the variables recorded in the first-impression task (Response time: average log-transformed response time per stimulus, and Attractiveness (categ.): number of raters categorizing each stimulus as attractive) and in the rating task ($N = 59$ raters). Interactions are illustrated in Fig. 3.

	First Impression task				Rating task			
	Response time		Attractiveness (categ.)		Attractiveness		Masculinity	
Faces	F	p	F	p	F	p	F	p
Opposite-sex								
(1) Odor	$F_{(1,87)} = 2.8$	.100	$F_{(1,87)} = 1.6$	.205	$F_{(1,87)} = 50.9$	<.0001	$F_{(1,87)} = 18.2$	<.0001
(2) Rater sex	$F_{(2,87)} = 1.1$	.350	$F_{(2,87)} = 2.8$	.068	$F_{(2,87)} = 0.0$	.984	$F_{(2,87)} = 9.2$	<.001
(3) Odor × rater sex	$F_{(2,87)} = 22.8$	<.0001	$F_{(2,87)} = 2.8$	.067	$F_{(2,87)} = 22.8$	<.0001	$F_{(2,87)} = 6.1$	<.01
Same-sex								
(4) Odor	$F_{(1,87)} = 5.3$	<.05	$F_{(1,87)} = 2.6$	.111	$F_{(1,87)} = 14.5$	<.001	$F_{(1,87)} = 9.8$	<.01
(5) Rater sex	$F_{(2,87)} = 1.4$	.262	$F_{(2,87)} = 1.1$	.330	$F_{(2,87)} = 1.9$	.158	$F_{(2,87)} = 17.0$	<.0001
(6) Odor × rater sex	$F_{(2,87)} = 6.1$	<.01	$F_{(2,87)} = 1.4$	.241	$F_{(2,87)} = 12.3$	<.0001	$F_{(2,87)} = 15.3$	<.0001

	First Impression task				Rating task			
	Response time		Attractiveness (categ.)		Attractiveness		Masculinity	
Voices	F	p	F	p	F	p	F	p
Opposite-sex								
(7) Odor	$F_{(1,87)} = 0.2$	.619	$F_{(1,87)} = 2.6$	.148	$F_{(1,87)} = 8.3$	<.01	$F_{(1,87)} = 1.0$	.311
(8) Rater sex	$F_{(2,87)} = 2.1$	.130	$F_{(2,87)} = 2.0$	.110	$F_{(2,87)} = 3.2$	<.05	$F_{(2,87)} = 33.7$	<.0001
(9) Odor × rater sex	$F_{(2,87)} = 15.8$	<.0001	$F_{(2,87)} = 0.8$	.473	$F_{(2,87)} = 3.9$	<.05	$F_{(2,87)} = 1.7$	.195
Same-sex								
(10) Odor	$F_{(1,87)} = 0.1$	.736	$F_{(1,87)} = 0.8$	.387	$F_{(1,87)} = 1.4$	.245	$F_{(1,87)} = 25.3$	<.0001
(11) Rater sex	$F_{(2,87)} = 1.1$	.324	$F_{(2,87)} = 2.2$	.122	$F_{(2,87)} = 1.8$	.178	$F_{(2,87)} = 39.3$	<.0001
(12) Odor × rater sex	$F_{(2,87)} = 6.2$	<.01	$F_{(2,87)} = 0.7$	.490	$F_{(2,87)} = 2.5$	.085	$F_{(2,87)} = 21.6$	<.0001

3.2.3. *Effects on stimulus ratings*

In the attractiveness rating task, there were significant interactions between odor condition and rater sex for all stimulus types except same-sex voices (Table 1). These effects occurred because, in the presence of androstadienone, higher attractiveness judgments were made by fertile women (for opposite-sex stimuli), by non-fertile women (for faces only) and by men (opposite-sex voices only), compared with the control condition (Fig. 3).

Contrary to our expectations, the typically masculine compound androstadienone did not reliably increase perceived masculinity of the stimuli (Table 1 and Fig. 3). It did so only for faces evaluated by non-fertile women, which might have accounted for the higher perceived attractiveness of male faces when these women were exposed to androstadienone. However, in all other instances, no reliable link could be established between the effect of androstadienone on masculinity and its effect on attractiveness.

4. Discussion

The aim of this study was to investigate how androstadienone influences others' attractiveness. More specifically, we used a complete design (male and female raters, male and female faces and voices) to determine whether androstadienone influences the perception of social stimuli in a sex-specific manner, which would favor pheromonal-like properties of the compound, or in a more general manner, which would suggest that the compound has broader influences on human psychological responses. Using a protocol of androstadienone masking (Jacob and McClintock, 2000) used by several research groups, we found that, compared with a control condition, androstadienone: (1) slowed the categorization of attractiveness in fertile women and in men but accelerated it in non-fertile women, and (2) had a positive effect on attractiveness ratings made by women, but also on attractiveness ratings made by men in one instance (opposite-sex voices) (see summary, Fig. 4). Results on facial and vocal stimuli were relatively concordant, and the effects of androstadienone on attractiveness ratings did not seem to be mediated by modulation of perceived masculinity or mood.

The positive effect of androstadienone on perceived attractiveness (see Fig. 4) is consistent with results of previous studies in women evaluating male (with androstadienone: Saxton et al., 2008) or female stimuli (with androstenol: Kirk-Smith et al., 1978). Our study thus presents additional evidence for an effect that has proved difficult to replicate (Saxton et al., 2008; Lundström and Olsson, 2005). Could this effect be the result of a general positivity of affective dispositions triggered by androstadienone? This question makes sense regarding previous research that shows both mood improvement after exposure to this compound (Jacob et al., 2002; Jacob and McClintock, 2000; Lundström et al., 2003a) and a favorable impact of good mood on the evaluation of others' attractiveness (Verhaeghe et al., 2013). However, the answer is "no" because androstadienone did not have any significant influence on mood in our study. This was probably due to the absence of contextual influences: the female experimenter stayed behind a one-way mirror during the experiment, and stimuli had balanced emotional valence: same versus opposite sex (see Hummer and McClintock, 2009; Lundström and Olsson, 2005; Bensafi et al., 2004a, for the importance of the context on androstadienone's effects). How then can the positive effect of androstadienone on perceived attractiveness that we found in our study be interpreted? In accordance with Kirk-Smith et al. (1978), we found that this effect was not sex specific, which helps rule out the hypothesis of possible pheromone-like properties of this compound: not only women, but also men gave higher attractiveness ratings when they were exposed to androstadienone. Moreover, in fertile female and male raters, this applied only to stimuli of the opposite sex. This finding is in accordance with the hypothesis that androstadienone influences responses to emotionally salient stimuli (Hummer and McClintock, 2009), i.e., in this case, faces and/or voices of individuals of the opposite sex. Consistent with this, the boosting effect of androstadienone in non-fertile female raters applied to stimuli of both sexes, probably because the discrepancy between the relevance of male and female stimuli is attenuated during that phase of the menstrual cycle (a phase in which perceiving the attractiveness of males may lose its adaptive value).

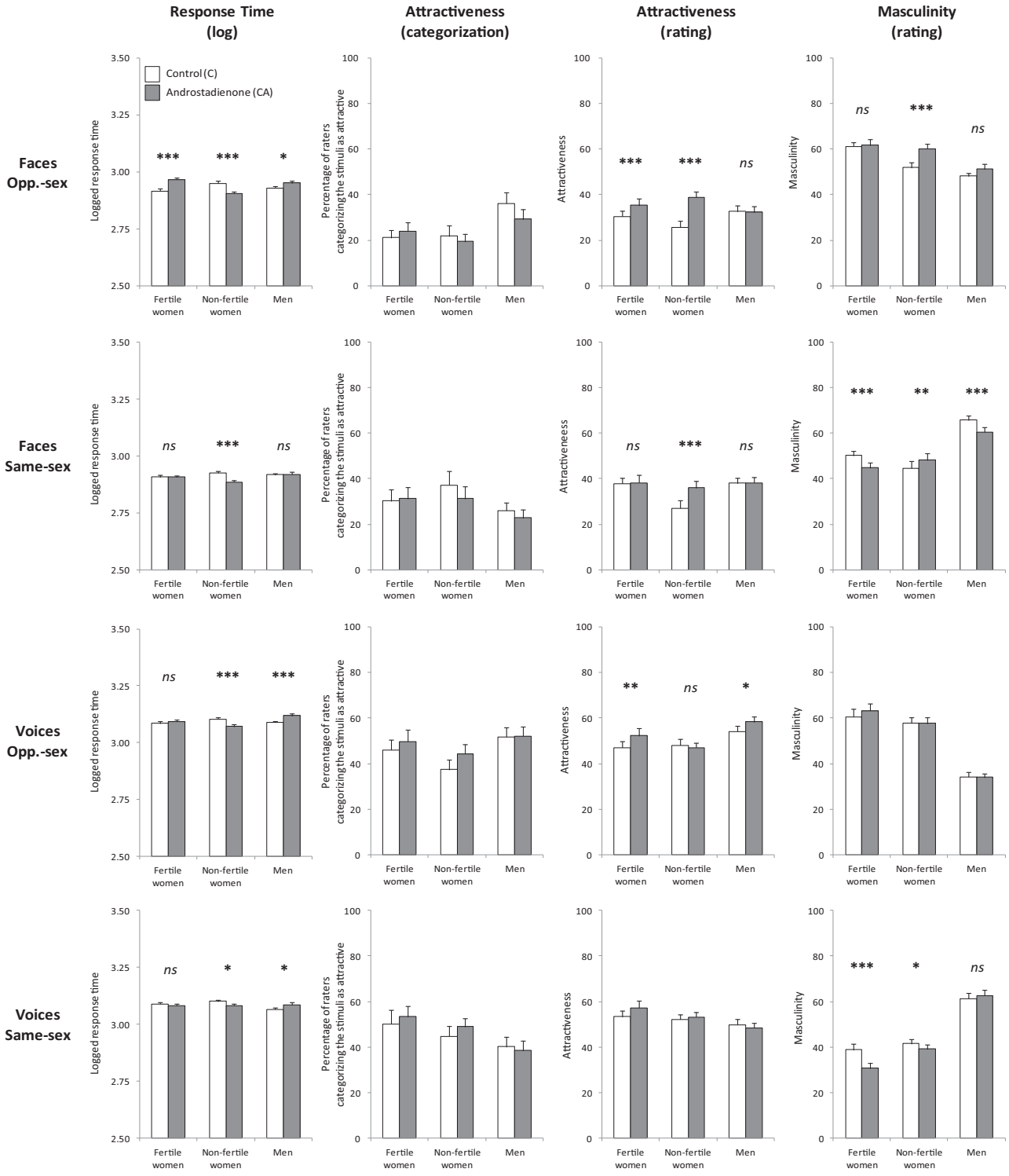

Fig. 3. Average response time (in seconds, log-transformed) to categorize the stimuli as attractive or not, proportion of raters categorizing the stimuli as attractive (%), attractiveness ratings (0–100) and masculinity ratings (0–100) (in columns) for opposite-sex faces, same-sex faces, opposite-sex voices and same-sex voices (in lines) by fertile women, non-fertile women and men ($N = 59$ raters). $^{***}p < .001$, $^{**}p < .01$, $^{*}p < .05$, *ns* not significant: results of the post hoc planned comparisons conducted on odor condition × rater sex interactions (only when these interactions were significant).

Using another task, we showed that, in fertile women and men, androstadienone slowed the process of categorizing a face or a voice as attractive or not. This can be related to previous studies on the role of androstadienone in attention to emotional visual stimuli. Indeed, in addition to increasing women's and men's feelings of being focused (Hummer and McClintock, 2009; Lundström and Olsson, 2005), exposure to androstadienone was found to effectively increase attentional capture by human faces (but not by neutral non-social stimuli: Lundström and Olsson, 2005; Parma et al., 2012). More specifically, androstadienone enhances attention to emotional faces versus expressionless faces (Hummer and McClintock, 2009), facilitates emotion recognition in faces (Frey et al., 2012) and increases face viewing time (Parma et al., 2012). In our study, response time depended on the amount of

A. CATEGORIZATION TIME

RATERS	STIMULI: Opposite-sex	STIMULI: Same-sex
Fertile females	↗[f]	-
Non-fertile females	↘	↘
Males	↗	↗[v]

B. ATTRACTIVENESS RATING

RATERS	STIMULI: Opposite-sex	STIMULI: Same-sex
Fertile females	↗	-
Non-fertile females	↗[f]	↗[f]
Males	↗[v]	-

Fig. 4. Summary of the effects of androstadienone on (A) categorization time in the first impression task, and (B) attractiveness judgments in the rating task. ↗: increase in the presence of androstadienone compared with the control condition; ↘ decrease in the presence of androstadienone compared with the control condition; v: for voices only; f: for faces only.

attentional resources put into the processing of the emotional stimulus or attending to it and into outputting a response to this stimulus (Yiend, 2010). Moreover, determining whether a face is attractive or not requires attentional resources (Jung et al., 2012). According to the literature cited earlier, it is likely that androstadienone delayed decision making because of greater attention capture by – and thus longer examination time of – the perceptual characteristics of the faces/voices when they were processed in the working memory. This result may also relate to the fact that, in the rating task, stimuli were perceived as being more attractive in the presence of androstadienone: response times are known to be longer for more attractive faces (e.g., Bensafi et al., 2002; Kranz and Ishai, 2006). The fact that, again, men displayed the same behavioral response to exposure to androstadienone as fertile women did reinforces the hypothesis of the general effect of this molecule on attention to relevant emotional information, namely stimuli of the opposite sex, serving decisional processes in mate choice. The same effect was found for male voices categorized by male raters (see Fig. 4): if androstadienone is an indicator of male quality, as suggested elsewhere (Huoviala and Rantala, 2013), then it is likely to increase the level of intrasexual competition and therefore the level of vigilance – and thus examination – of the competitors. Despite the fact that similar effects related to female-female competition have been suggested previously (Parma et al., 2012), they were not replicated here. Finally, the reverse effect of androstadienone occurred in non-fertile women (acceleration of attractiveness categorization): the presented stimuli had lower emotional relevance than they did for fertile women and for men because – unlike these groups – non-fertile women are at low risk of conception. Of the two components of the response cited earlier (attending to the stimulus versus providing a response to that stimulus), the first one may have remained intact because it is less relevant for non-fertile than for fertile women, whereas the second one may have been facilitated in accordance with previous observations that androstadienone increases a participant's focus (Lundström et al., 2003a).

The present study adds evidence to the existing literature that androstadienone influences human behavior and presents new evidence of a general but not sex-specific influence on psychological responses. However, some limitations must be mentioned. First, we did not elucidate the mechanisms governing the activity of androstadienone. To enable comparisons between studies, we used a skin-application protocol that is widely used in androstadienone studies. This procedure does not enlighten us about which olfactory (through stimulation of the nasal mucosa) or pharmacological (through its passage into the bloodstream) mode of action is in play. The ecological validity of such a protocol is questionable as well, since transdermal diffusion may not be the preferential way that androstadienone acts in day-to-day interpersonal relationships (rather, it may be engaged during close physical contact). Second, it is still unclear how changes in attractiveness or in attention to social stimuli, as measured in a psychological experiment such as ours, influence actual sexual behavior or social behavior between odor releaser and receiver. Finally, our study has methodological limitations. It can be argued that the presentation order of opposite-sex and same-sex stimuli, and of voices and faces, should be counterbalanced rather that fixed. However, it is possible that the conditions influence each other (for example, seeing faces or not before evaluating voices could modulate the attractiveness ratings of the voices; likewise for opposite- versus same-sex stimuli). We thus believe that a randomized block design might have introduced some noise into the data that could have masked the effect of the androstadienone. Additionally, the use of a between-subjects design, chosen because of logistical constraints, is not the most powerful design, since we cannot exclude the possibility that the two groups (with and without androstadienone) differed on variables influencing their responses to the task. These potential differences were limited, though, because (i) both groups were homogeneous in terms of age, sex, occupation (mostly students) and sexual orientation; (ii) allocation to a group was performed randomly; (iii) the protocol was double-blind; and (iv) both groups equally respected the instructions given to prevent alterations of the sense of smell (such as not using perfumed cosmetic products, not smoking, etc.).

Apart from these reservations, we can conclude that together, our results on response time and attractiveness ratings raise doubts about the proposition that androstadienone has sex-specific, pheromone-like effects. Rather, they better fit the model of a more general effect of androstadienone on emotional stimuli, as advocated by Hummer and McClintock (2009), even though we did not test the effects on non-social stimuli. Indeed, it was only when the faces/voices were relevant to the mate-choice context that the attention paid to them and their valences were modulated by androstadienone: attention capture by, and attractiveness of, opposite-sex faces/voices increased in perceivers who theoretically were able to reproduce (i.e., men and fertile women). Non-fertile women reacted very differently to androstadienone: in particular, androstadienone influenced responses to both opposite- and same-sex stimuli, which likely reflects that both categories are emotionally equivalent during this phase of the menstrual cycle. Our conclusions were always consistent between modalities, even though they did not always apply to both faces and voices. Moreover, the fact that in our study male raters were non-anosmic to androstadienone is important. As men tend to be less sensitive to this compound (Hummel et al., 2005; Lundström et al., 2003b; our study), it is likely that a design that includes men regardless of their ability to smell androstadienone would conclude that androstadienone has no behavioral effect on them. This may generate erroneous inferences about the function of this compound, in particular about its sex specificity. Our design discredited sex specificity in accordance with the results of other studies (Hummer and McClintock, 2009), but the fact that, in real-life conditions, a substantial part of the population is anosmic to androstadienone (25% of the participants in our study) must also be taken into consideration when discussing the role of androstadienone. Indeed, this is another reason to doubt that androstadienone acts as a pheromone (Wyatt 2015).

Androstadienone, which has been investigated in numerous studies, might thus not be the best candidate as a pheromone involved in human mate choice. Indeed, if it were, why would this compound also be found in human secretions that are most likely not involved in male-female attractiveness, such as amniotic fluid (Loos et al., 2014), a finding that further challenges the presumptions about the sex specificity of androstadienone production? Why would anosmia to androstadienone have such a high prevalence in the population, whereas deleterious mutations of the genes responsible for the detection of a human pheromone should be counter-selected (Wyatt, 2015)? Studies focusing on androstadienone and related compounds are increasingly being criticized (Doty, 2014, 2010; Wyatt, 2015). These criticisms point to the fact that many researchers use the term "human pheromone" when they study this family of compounds, although no evidence of pheromonal effects has been rigorously demonstrated thus far. They also point to the lack of grounded scientific justification for focusing on this family of compounds, as recently detailed by Wyatt (2015): involvement in sexual behavior in animals (pigs), commercial availability of the molecule and heavy communication by company-funded researchers were initially the only motivations to shed light on androgen steroids. We share Wyatt's belief that, to better understand human chemical communication, it is necessary to enlarge the scope of investigated molecules by trying to identify new compounds, not necessarily in the axillary area, through multidisciplinary research involving expertise in both chemistry and human physiology and behavior.

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Contributors

CF, SD and DS designed the research; RA collected the data; CF, SD, RA and DS analyzed and interpreted the data; CF wrote the paper and SD, RA and DS provided significant contributions to the content of the manuscript and language help. All authors have approved the final article.

Conflict of interest

None.

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