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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."