Chemosensory Communication of Gender through Two Human Steroids in a Sexually Dimorphic Manner

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Summary

Recent studies have suggested the existence of human sex pheromones, with particular interest in two human steroids: androstadienone (androsta-4,16-dien-3-one) and estratetraenol (estr-1,3,5(10),16-tetraen-3-ol). The current study takes a critical step to test the qualification of the two steroids as sex pheromones by examining whether they communicate gender information in a sex-specific manner. By using dynamic point-light displays that portray the gaits of walkers whose gender is digitally morphed from male to female [1, 2], we show that smelling androstadienone systemically biases heterosexual females, but not males, toward perceiving the walkers as more masculine. By contrast, smelling estratetraenol systemically biases heterosexual males, but not females, toward perceiving the walkers as more feminine. Homosexual males exhibit a response pattern akin to that of heterosexual females, whereas bisexual or homosexual females fall in between heterosexual males and females. These effects are obtained despite that the olfactory stimuli are not explicitly discriminable. The results provide the first direct evidence that the two human steroids communicate opposite gender information that is differentially effective to the two sex groups based on their sexual orientation. Moreover, they demonstrate that human visual gender perception draws on subconscious chemo sensor y biological cues, an effect that has been hitherto unsuspected.

Results

Pheromones are chemical signals that convey information between members of the same species [3, 4]. Chemical communications of sex and reproductive stage are ubiquitous in the animal kingdom, facilitating sexual selection that arises through competition over mates or for matings [5]. Whereas humans are considered the most highly scented ape of all in terms of numbers and sizes of sebaceous and apocrine glands [6], our lack of a functional vomeronasal organ and an accessory olfactory bulb [7]—structures encoding pheromones in most amphibians, reptiles, and nonprimate mammals [8]—has long been considered to negate the possibility of human pheromone communication. This view is challenged by recent findings of human menstrual synchrony [9], socioemotional communications via natural body odor [10] and tears [11], and, in particular, the gender-specific physiological effects of two human steroids: androstadienone and estratetraenol. Androstadienone is the most prominent androstene present in male semen, in axillary hair, and on axillary skin surface [12]. It heightens sympathetic arousal [13], alters levels of cortisol [14], and promotes positive mood state [15, 16] in female as opposed to male recipients, probably in a context-dependent manner [17, 18]. Estratetraenol, first identified in female urine [19], has been likewise reported to affect men’s autonomic responses [18] and mood [20] under certain contexts, albeit with controversies [13, 17]. These effects are further accompanied by distinct hypothalamic response patterns to the two steroids: androstadienone is found to activate the hypotalamus in heterosexual females and homosexual males, but not in heterosexual males or homosexual females, whereas estratetraenol activates the hypothalamus in heterosexual males and homosexual females, but not in heterosexual females or homosexual males [21–23]. Nonetheless, it remains elusive whether any concrete sexual information is relayed by androstadienone or estratetraenol to the proper recipients, an important criterion for these two steroids to qualify as human sex pheromones. Considering that gender corresponds to the biological makeup of an individual’s reproductive anatomy and that accurate gender perception is the first key step in constraining subsequent sexual interaction between individuals, we ask whether androstadienone and estratetraenol effectively communicate gender information.

We tackled this issue in a gender identification task (see Supplemental Experimental Procedures available online) using visually presented point-light walkers (PLWs), a type of stimuli widely employed to represent the essential properties of human biological motion [24]. Each PLW comprised 15 moving dots depicting the trajectories of major body parts during walking: 12 for the major joints and 3 for the centers of the pelvis, thorax, and head. Their genders were quantified [1, 2] and ranged in seven equal steps, from feminine (−0.45 SD) to masculine (0.45 SD), with 0 marking the approximate gender-neutral point that was individually adjusted for each participant in the absence of olfactory stimulus prior to the actual experiment (Figure 1; Movie S1). Four groups of healthy nonsmokers, including 24 heterosexual males (Kinsey scores = 0), 24 heterosexual females (Kinsey scores = 0), 24 homosexual males (mean Kinsey score ± SEM = 5.25 ± 0.14), and 24 bisexual or homosexual females (Kinsey score = 4.50 ± 0.23) (Figure S1A), performed the task at around the same time of the day on three consecutive days while being continuously exposed to either androstadienone (500 µM, 4 ml), estratetraenol (500 µM, 4 ml), or their carrier solution alone (control condition, 1% v/v clove oil in propylene glycol, 4 ml total), one on each day, in a counterbalanced manner. In each trial, they viewed a PLW for 500 ms (0.5 walking cycle) and made a forced choice judgment on whether it was a male or a female walker. The three olfactory stimuli all smelled like clove and were perceptually indiscriminable, as first tested in an independent group of 32 people (mean accuracy ± SEM = 0.30 ± 0.03 versus chance = 0.333, p = 0.21) and then verified by the participants in the gender identification task (overall accuracy = 0.33 ± 0.03 versus chance = 0.333,
Biological motion has been shown to engage a network of distributed neural areas in the form and motion pathways [25] and to naturally convey gender [26] among other social information. Indeed, all participants could decode gender of the PLWs, exhibiting a sigmoidal response pattern in which a more masculine PLW was more frequently judged as a male (p < 0.0001; Figure 2, left panels).

Considering that the effects of sex pheromones are typically sex specific [5], we first examined in heterosexual participants whether their own gender interacted with the olfactory stimulus they were being exposed to in their gender judgments of the PLWs. Repeated-measures ANOVA with olfactory condition (androstadienone, estratetraenol, or carrier control) and PLW’s gender (seven levels, with Z scores from −0.45 SD to 0.45 SD) as the within-subject factors and odor recipient’s gender (male versus female) as the between-subject factor indeed showed a significant three-way interaction of olfactory condition, recipient’s gender, and PLW’s gender (F[12, 552] = 2.00, p = 0.023). Zooming in on the most ambiguous gender-neutral point of the PLWs (z = 0), we found that smelling estratetraenol relative to the carrier solution alone increased “male” responses in heterosexual males (t23 = −0.66, p = 0.52; Figure 2A, middle panel).

To further characterize the interplays between the human steroids and the recipients’ gender, we fitted the gender judgments of each participant per olfactory condition with a Boltzmann sigmoid function containing two parameters: point of subjective equality (PSE), the point at which the observer perceived a PLW as equally masculine and feminine, and difference limen, an index of discrimination sensitivity (essentially the slope of the fitted psychometric function near the PSE). With the carrier condition serving as the reference, we found that smelling estratetraenol systematically biased heterosexual males toward perceiving the PLWs as more feminine, resulting in a PSE shifted to the feminine PLW side (t23 = 2.84, p = 0.009), whereas androstadienone had no obvious effect (t23 = 0.53, p = 0.60) (Figure 2A, right panel). By contrast, in heterosexual females, smelling androstadienone significantly shifted PSE to the feminine PLW side (t23 = −2.84, p = 0.009), reflecting a bias to perceive the PLWs as more masculine, whereas estratetraenol showed no apparent effect (t23 = −0.33, p = 0.75) (Figure 2B, right panel).

The above results from heterosexual participants revealed clear sex dimorphic effects of androstadienone and estratetraenol in communicating masculine and feminine information, respectively. We next turned to homosexual/bisexual participants to assess whether such effects also depend on recipients’ sexual orientation.

At the most ambiguous gender-neutral point of the PLWs (z = 0), we found that smelling androstadienone relative to the carrier solution alone increased “male” responses in homosexual males (t23 = 2.18, p = 0.04; Figure 2C, middle panel) but did not significantly affect gender judgments in heterosexual males toward perceiving the masculine PLW as more feminine, resulting in a PSE shift to the feminine PLW side (t23 = −0.33, p = 0.75). Conversely, smelling estratetraenol relative to the carrier control increased “male” responses in heterosexual females (t23 = −3.35, p = 0.003; Figure 2A, middle panel) but did not significantly affect gender judgments in heterosexual females toward perceiving the masculine PLW as more masculine, whereas estratetraenol showed no apparent effect (t23 = −0.66, p = 0.52) (Figure 2B, middle panel). Analyses of PSEs yielded parallel results. Homosexual males were not influenced by estratetraenol (t23 = −0.60, p = 0.55) but exhibited a significant PSE shift to the feminine PLW side under the exposure of androstadienone (t23 = −2.86, p = 0.009) (Figure 2C, right panel). This response pattern was similar to that of heterosexual females and opposite to that of heterosexual males. For bisexual/homosexual females, no significant effect of androstadienone significantly affect gender judgments in heterosexual females (t23 = 0.33, p = 0.75; Figure 2B, middle panel).
(t_{23} = -0.32, p = 0.75) or estratetraenol (t_{23} = 0.29, p = 0.77) was evident (Figure 2D, right panel), probably because their sexual orientations were more ambiguous than those of homosexual males (comparison of Kinsey scores, t_{38.12} = -2.84, p = 0.007; Figure S1A).

To facilitate comparison, the central tendencies of the androstadienone- and estratetraenol-induced PSE shifts for the four participant groups are respectively highlighted in Figure 3, which was generated by using a standard bootstrapping procedure [28]. They form three distinct clusters: the bootstrapped sample means of heterosexual males (cyan dots) fall around the vertical axis on the positive side; those of heterosexual females (yellow dots) and homosexual males (lime dots) fall around the horizontal axis on the negative side; in between lie bisexual/homosexual females (orange dots) centered around the origin. The variances in the homosexual/bisexual groups are higher compared to the heterosexual groups [29]. Meanwhile, the difference limens of the four participant groups did not differ from one another (F_{3, 92} = 0.73, p = 0.54) and remained unchanged across the three olfactory conditions (main effect of olfactory condition: F_{2, 184} = 0.13, p = 0.88; interaction: F_{6, 184} = 0.30, p = 0.94). Thus, it was the criterion (reflected in the PSEs) rather than the sensitivity (reflected in the difference limens) of gender judgment that was altered by the chemosensory cues, in manners contingent on the recipient’s gender and sexual orientation.

It could be argued that the above effects are not pheromonal in nature but rather result from learned associations between walking gaits and chemical cues for the gender one is attracted to. To examine this alternative, we conducted a supplemental experiment using isovaleric acid, an odoriferous fatty acid present in axillary apocrine sweat that partly causes body odor [30]. Although men have more apocrine glands than women in all axillary regions [6], isovaleric acid did not significantly bias gender judgments of the PLWs in either heterosexual males or heterosexual females, as compared with the clove oil carrier solution alone (Supplemental Experimental Procedures; Figure S2). This led us to conclude that associative learning is unlikely the basis for the observed gender communication through androstadienone and estratetraenol.

**Discussion**

Our results provide strong behavioral evidence that the human steroids androstadienone and estratetraenol effectively communicate masculine and feminine information, respectively, in a gender- and sexual orientation-dependent manner.
on average, the two substances induced ~8% change in the gender judgments of heterosexuals (Figures 2A and 2B) and homosexual males (Figure 2C) at the most ambiguous gender-neutral point of the PLWs. The size of the effects is actually comparable to that of gender adaptation using visually presented faces or bodies [31], which is quite noteworthy in view of the dominance of vision in daily gender perception.

Pheromones generally exercise their influence in a dose-dependent manner [32]. Androstadienone and estratetraenol are likely no exception [33]. To maximize experimental power, we followed standard practice in the field and used concentrations significantly higher than those naturally occurring in human secretions [12, 19]. It is thus expected that the effects of androstadienone and estratetraenol in daily social encounters would be smaller. The dose-response relationships remain to be tested. Nevertheless, we were able to demonstrate qualitatively that androstadienone signals masculinity to heterosexual males, whereas estratetraenol signals femininity to heterosexual males, without the recipients being aware of the odors. Importantly, the specific sexual information conveyed by androstadienone and estratetraenol strongly supports them as human sex pheromones.

It has been shown in the mouse that the main olfactory bulb recognizes social signals [34] and projects to sexually dimorphic hypothalamic nuclei controlling reproduction and fertility [35]. We suspect a similar pathway underlies the observed gender- and sexual orientation-specific processing of the chemosensory sexual cues in humans, where sex differences in the hypothalamus and adjacent structures have been related to heterosexuality and homosexuality [21–23, 36]. Remarkably, such chemosensory processing operates below awareness yet significantly modulates visual gender perception, indicating itself as part of the human gender code in the brain.
memory and autonomic nervous system function in specific behavioral contexts. Behav. Brain Res. 152, 11–22.
Supplemental Information

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Supplemental Results

An independent group of 48 healthy nonsmokers, including 24 heterosexual males and 24 heterosexual females (Kinsey scores = 0), participated in the supplemental experiment. The experimental procedure was identical to that of the main experiment except that two olfactory stimuli were employed: isovaleric acid (500μM, 4ml) and its carrier solution alone (control condition, 25% v/v clove oil in propylene glycol, 4ml), which the participants could not tell apart (mean accuracy = 0.37 ± 0.03 vs. chance = 0.333, p = 0.20; with no gender difference, t_{46} = 0.11, p = 0.91). Like in the main experiment, their gender judgments of the PLWs exhibited a sigmoidal pattern with more masculine PLWs being more frequently judged as males (p < 0.0001; Fig. S2, left panels). However, no interaction was evident between the participants’ own gender and the olfactory stimulus they were being exposed to (two-way interaction: F_{1,46} = 0.005, p = 0.95; three-way interaction with PLW’s gender: F_{6,276} = 0.29, p = 0.94). At the most ambiguous gender-neutral point of the PLWs (z = 0), smelling isovaleric acid as opposed to the carrier control did not significantly alter the proportion of ‘male’ responses in either heterosexual males (t_{23} = 0.18, p = 0.86; Fig. S2A, middle panel) or heterosexual females (t_{23} = 0.95, p = 0.35; Fig. S2B, middle panel). In parallel, no significant PSE shift was detected in either gender group (t_{23} = -0.45 and -0.86, p = 0.66 and 0.40, for heterosexual males and females, respectively; Fig. S2, right panels). Gender discrimination sensitivity, as indexed by difference limen, also remained unchanged between the olfactory conditions in both heterosexual males (t_{23} = -0.11, p = 0.91) and heterosexual females (t_{23} = 0.64, p = 0.53).
Figure S1: Kinsey scores and odor discriminability. (A) Kinsey scores of the participants in the main experiment. (B) Odor discrimination performances for androstadienone, estratetraenol, and their carrier solution alone. Each open circle represents one participant. Filled circles indicate group means. Error bars, SEM.
Figure S2: Isovaleric acid failed to induce visual gender judgment biases in heterosexual males (A) and heterosexual females (B). Left panels: gender identification performances of the two gender groups under the exposures of isovaleric acid and its carrier control, respectively fitted with sigmoidal curves. Dashed curves, carrier control; error bars, SEM adjusted for individual differences. Middle and right panels: isovaleric acid induced proportional ‘male’ biases at the gender neutral point $z = 0$ (middle panels) and overall PSE shifts (right panels) relative to the carrier control were statistically insignificant in both gender groups. Error bars, SEM.
Supplemental Experimental Procedures

Participants

A total of 96 self-reported heterosexuals and homosexuals participated in the main experiment. Each completed the Kinsey scale (Kinsey Institute), a self-reported rating scale of one’s sexual orientation (0 is exclusively heterosexual, 3 is equally heterosexual and homosexual, and 6 is exclusively homosexual), prior to the actual experiment. They consisted of 24 heterosexual males (mean age ± SEM = 23.50 ± 0.41 yrs, Kinsey scores = 0), 24 heterosexual females (22.67 ± 0.69 yrs, Kinsey scores = 0), 24 homosexual males (22.67 ± 0.59 yrs, mean Kinsey score ± SEM = 5.25 ± 0.14), and 24 bisexual/homosexual females (22.71 ± 0.50 yrs, Kinsey score = 4.50 ± 0.23) (Fig. S1A). Although male sexuality is relatively constant and innate, female sexuality, particularly that of nonheterosexual women, is depicted as fairly malleable and mutable [S1]. In view of the sexual orientation continuum (APA) and the enrollment difficulty of nonheterosexual participants, we did not separate bisexual and homosexual women. An independent panel of 32 people (22.16 ± 0.31 yrs, 16 males) performed the triangle odor discrimination test of the olfactory stimuli used in the main experiment. Another 24 heterosexual males (24.5 ± 0.32 yrs, Kinsey scores = 0) and 24 heterosexual females (22.5 ± 0.39 yrs, Kinsey scores = 0) took part in the supplemental experiment. The female participants in the main and the supplemental experiments were tested around the periovulatory phase of their menstrual cycles (mean ± SEM = 16.5 ± 0.62 days from the onset of their last period of a normalized 28 day cycle). All participants were healthy nonsmokers with normal or corrected-to-normal vision, normal sense of smell, and no respiratory allergy or upper respiratory infection at the time of testing. They gave informed consent to participate in
procedures approved by the Institutional Review Board at Institute of Psychology, Chinese Academy of Sciences, and were unaware of the purposes of the experiments.

**Olfactory Stimuli**

The olfactory stimuli in the main experiment consisted of androstadienone (500μM in 1% v/v clove oil propylene glycol solution, 4ml), estratetraenol (500μM in 1% v/v clove oil propylene glycol solution, 4ml), and their carrier solution alone (1% v/v clove oil in propylene glycol, 4ml). The concentration of 500μM was chosen with an intention to maximize experimental power [S2] while keeping the smells of androstadienone and estratetraenol subliminal [S3-6]. Isovaleric acid (500μM in 25% v/v clove oil propylene glycol solution, 4ml) and its carrier solution (25% v/v clove oil in propylene glycol, 4ml) were employed in the supplemental experiment. They were presented in identical 40 ml polypropylene jars, each connected with two Teflon nosepieces via a Y-structure. Participants were instructed to hold the jar with their non-dominant hand, position the nosepieces inside their nostrils, and continuously inhale through the nose and exhale through their mouth throughout the experiments.

**Visual Stimuli**

Visual stimuli were generated with MATLAB and presented on a 22-inch LCD monitor using the psychophysics toolbox. Parametric, gender-morphable point-light walkers (PLWs) (http://www.biomotionlab.ca/Demos/BMLwalker.html) [S7-8] were adopted. Each walker (visual angle = 2.4°×7.8°) was made up of 15 moving dots (0.2°×0.2°), 12 for the major joints, and 3 for the centers of pelvis, thorax, and head. Their gender was indexed by a normalized z score on an axis reflecting the differences between actual male
and female walkers in terms of a linear classifier. Specifically, the z scores were derived from a 10-dimensional sub-space spanned by the first 10 principal components based on a Fourier-based representation of the walking data from 50 male and 50 female walkers, who walked on a treadmill with retroreflective markers attached to their body [S7-8]. For each participant, seven walkers ranging in equal steps from 0.45 standard deviation (SD) into the female part of the space to 0.45 SD into the male part of the space were employed, with the center individually adjusted to approximately perceived gender neutrality in the absence of olfactory stimulus (Fig. 1A, Supplemental Movie 1).

**Procedures**

Each trial of the gender identification task started with a 500ms fixation cross (0.5°×0.5°), followed by a PLW presented for 500ms (0.5 walking cycle) at a random location 0 - 1° away from fixation. Participants then pressed one of two buttons to indicate whether it was a male or a female walker. The next trial began immediately after they made a response. Each participant viewed seven PLWs ranging in equal steps from -0.45 SD to 0.45 SD along the feminine-masculine axis (Fig. 1A, Supplemental Movie 1), with 0 marking the approximate perceived gender neutral point (50% male responses) individually adjusted and set prior to the actual experiment (baseline and experimental blocks) on the first day of testing. The initial frame of each motion sequence was randomized. There were 70 trials per block (7 PLWs × 10 repetitions in random order). On each day of three successive days, participants in the main experiment first completed 4 blocks of the gender identification task in the absence of olfactory stimulus, which served as the baseline, and then 6 blocks while being continuously exposed to either androstadienone, estratetraenol, or their carrier solution alone, one on each day in a
counterbalanced manner. Those in the supplemental experiment were tested on two consecutive days. On each day they similarly performed 4 baseline blocks in the absence of olfactory stimulus, and then 6 experimental blocks while being continuously exposed to either isovaleric acid or its carrier solution alone, one on each day in a counterbalanced manner. During the baseline blocks, an empty jar was used in place of those containing the olfactory stimuli. The experimenter was blind to the nature of the olfactory stimuli, and was not in the test room while the participants performed the task.

The odor discrimination task adopted a standard triangle procedure. In each trial, blindfolded participants were presented with three smells, two identical (comparison) and the other one different (target), and reported which one was the odd one out. Unknown to them, the same jar containing the comparison stimulus was presented twice in each trial. The probability of arriving at a correct response by chance was 1/3. To assess the discriminability of androstadienone, estratetraenol, and their carrier solution, 32 odor judges each performed 9 trials of the odor discrimination task. Participants in the main experiment also each completed 3 trials on the third day of their testing. The target and comparison stimuli were respectively androstadienone and estratetraenol, estratetraenol and carrier control, and carrier control and androstadienone, each in 1/3 of the trials. For isovaleric acid and its carrier solution, participants in the supplemental experiment each completed 6 trials of the odor discrimination task. The target and comparison stimuli were respectively isovaleric acid and carrier control (3 trials), and carrier control and isovaleric acid (3 trials). The order of the trials was randomized. There was at least a 30s break in between two trials.

Analyses
Participants’ responses from the gender identification task were baseline normalized (mean shifting) per olfactory condition per participant prior to any statistical analysis to account for olfactory irrelevant day-to-day variations in gender judgment criterion. For each of the seven PLWs, the baseline adjusted proportion of ‘male’ responses \( p' \) was calculated as \( p' = p_{\text{exp}} - p_{\text{base}} + \bar{p}_{\text{base}} \), where \( p_{\text{exp}} \) is the averaged proportion of ‘male’ responses in the experimental blocks, \( p_{\text{base}} \) is the averaged proportion of ‘male’ responses in the preceding baseline blocks on the same day, and \( \bar{p}_{\text{base}} \) is the mean proportion of ‘male’ responses in the baseline blocks across the days of testing. For the main experiment, the data were first analyzed with a repeated measures ANOVA for heterosexual participants, using olfactory condition (androstadienone, estratetraenol, carrier control) and PLW’s gender (7 levels, with Z scores from -0.45SD to 0.45SD) as the within-subject factors and odor recipient’s gender (male vs. female) as the between-subject factor. We then zoomed in on the most ambiguous gender-neutral point of the PLWs (\( z = 0 \)) and performed pairwise t tests between androstadienone and the carrier control as well as estratetraenol and the carrier control for each group of participants, using the proportion of ‘male’ responses at \( z = 0 \) (conforming normal distribution under each olfactory condition based on Kolmogorov-Smirnov tests, \( p > 0.05 \)) as the dependent variable.

Next, to better characterize the response criteria and sensitivities, the baseline normalized gender judgments were fitted with a Boltzmann sigmoid function \( f(x) = 1/(1 + \exp((x - x_0)/\omega)) \), where \( x_0 \) corresponds to the point of subjective equality (PSE), at which the observer perceived a PLW as equally masculine and feminine; and half the
interquartile range of the fitted function corresponds to difference limen, an index of
discrimination sensitivity. For each of the four participant groups, paired sample t tests
were then conducted on PSEs (conforming normal distribution under each olfactory
condition based on Kolmogorov-Smirnov tests, ps > 0.05) to compare the gender
judgment criteria under the exposures to androstadienone and estratetraenol, respectively,
with that under the exposure of the carrier solution alone. A repeated measures ANOVA
was performed on difference limens to compare the discrimination sensitivities across the
three olfactory conditions (within-subject factor) in the four participant groups (between-
subject factor).

A standard bootstrapping procedure [S9] was adopted to highlight the central tendencies
of the androstadienone and estratetraenol induced PSE shifts in each group of participants.
Specifically, the original dataset of each group was randomly resampled with
replacement (a participant could be selected multiple times) to form a bootstrap sample of
size 24. The mean androstadienone and estratetraenol induced PSE shifts of this bootstrap
sample was plotted as a dot in a 2D space spanned by androstadienone induced PSE shift
(x axis) and estratetraenol induced PSE shift (y axis) (Fig. 3). This procedure was
repeated 1,000 times, resulting in 1,000 dots per group.

For the supplemental experiment, the baseline-normalized data were first analyzed with a
repeated measures ANOVA, using olfactory condition (isovaleric acid vs. carrier control)
and PLW’s gender as the within-subject factors, and odor recipient’s gender as the
between-subject factor. A series of pairwise t tests were also performed between
isovaleric acid and its carrier control for each gender group, using the proportion of ‘male’
responses at z = 0, PSE, as well as difference limen as the dependent variables. All statistical tests were two-sided.

Supplemental References