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Women's fertility cues affect cooperative behavior: Evidence for the role of the human putative chemosignal estratetraenol

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ABSTRACT

Previous studies demonstrating that women’s body odor during ovulation is perceived as more attractive suggest that exposure to women’s chemosignals of high fertility increases mating motivation. Building on previous evidence showing that cooperative behaviors are perceived as attractive, in the current study we investigated whether chemosignals of women's fertility affect men's tendency to behave cooperatively. In the first experiment we found that in the presence of women's body odor during ovulation, men increase their tendency to apply a cooperative strategy, while their tendency to apply an individualistic strategy decreases. To examine the mechanism underlying this effect, we tested a different sample of men exposed to the putative human pheromone estratetraenol (estra-1,3,5(10),16-tetraen-3-ol) or to a control solution. Exposure toestratetraenol compared with control yielded strikingly similar effects of increased cooperation. The results indicate that women's chemosignals of high fertility increase mating motivation among man, encouraging them to act in a cooperative manner toward others, a response that may highlight their attractive qualities and thus attract mates. We further conclude that estratetraenol may serve as one of the biological agents that mediate the behavioral effects of women's chemosignals of fertility on social behavior.

1. Introduction

Human body odors have been shown to convey social signals of many kinds. In the animal kingdom, many mammalian species use odorous cues to communicate periods of reproduction readiness among females. Specifically, female body odor and other body secretions take on an attractive character around the ovulation period (Doty, 1986). In rodents for example, females' body odors are known to stimulate males' reproductive systems, causing an increase in males' testosterone levels (Brown & Macdonald, 1985). In humans as well, women's body odor detectably changes throughout the menstrual cycle (Havlíček et al., 2006; Kuukasjärvi et al., 2004; Singh and Bronstad, 2001; Thornhill et al., 2003; Thornhill & Gangestad, 1999). Moreover, several studies show that olfactory cues of women's fertility lead to an elevation in testosterone levels among men (Cerda-Molina, Hernández-López, de la O, Chavira-Ramírez, & Mondragón-Ceballos, 2013; Miller & Maner, 2010), a reaction previously linked to sexual arousal (Stoléru et al., 1993). Furthermore, Cerda-Molina et al. (2013) reported that exposure to women's auxiliary and vulvar scents during ovulation increased men's cortisol levels. It is important to note that although an abundance of studies show hormonal changes in men following exposure to women’s olfactory cues signaling fertility, other studies failed to replicate this finding (Roney & Simmons, 2012; Strom et al., 2012). Nonetheless, another line of studies demonstrates that men exposed to women's body odor during high fertility periods display higher implicit accessibility to mating-related concepts (Miller & Maner, 2011). Taken together, the evidence appears to indicate that chemosignals of ovulating women play a role in shaping mating behaviors by increasing men's mating motivation (Miller & Maner, 2011).

One behavior that may be altered by increased mating motivation is cooperation. Cooperation is an act that benefits the recipient individual (West et al., 2007) or a joint action that provides mutual benefit to all parties (Mesterton-Gibbons & Dugatkin, 1992; Tuomela, 2011). The development of cooperation between individuals has intrigued researchers and intellectuals for many years, and numerous theories have been proposed to explain this phenomenon. In the animal kingdom, models of "group selection" (Maynard-Smith, 1964) and "kin selection" (Hamilton, 1964) were suggested. These models justify cooperative behavior by its contribution to the group or to family relatives. Others have suggested that cooperative behaviors are compensated by the reciprocity of other individuals in the group (Trivers, 1971). In addition to kin and group selection theories, theorists have also suggested that the unique cognitive, linguistic and physical abilities of humans promote the formation of social behavioral norms and regulations (Bowles

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& Gintis, 2003), which together with the formation of large-group cultures (Boyd and Richerson, 2009) support and promote cooperative behavior.

According to the "handicap principle" put forth by Zahavi (1995), altruistic collaboration between individuals in the animal kingdom can be explained in terms of an advertisement for qualities aimed to attract mates. In humans, cooperation has also been suggested to play a role in a sexual selection context. Early studies indicated that the tendency to cooperate in a context of the prisoner's dilemma varies according to the level of attraction to the partner (Fisher & Smith, 1969). Further studies demonstrated that men are inclined to donate money to female, rather than male, panhandlers when they are alone (Goldberg, 1995) and that attractive people have been found to receive higher offers in ultimatum games (Solnick & Schweitzer, 1999). Another series of experiments revealed that participants demonstrate more cooperative behavior toward more attractive individuals of the opposite sex, an effect that was not found toward individuals of the same sex. Cooperative individuals were, in turn, rated as more attractive by their partners in a game (Farrelly et al., 2007). It has also been found that compared to women, men are more inclined to use cooperative behaviors as a sexual display to attract opposite-sex individuals (Bhogal et al., 2016; Raihani & Smith, 2015; Van Vugt and Iredale, 2013). According to Maestripieri et al. (2017), the mere presence of attractive individuals biases men into a more pro-social behavior. For example, in the study of Iredale et al. (2008), participants played a social dilemma game in which they made charity donations. It was found that men were inclined to make higher donations when observed by attractive women compared to when they were observed by another man. Similar findings were also found in a public-goods game (Van Vugt and Iredale, 2013) and in dictator games (Jensen, 2013). By doing so, men in particular (Raihani & Smith, 2015) signal that they possess resources which they are willing to share (as suggested by Farrelly, 2011; Van Vugt and Iredale, 2013). Similarly, studies demonstrate that exposure to a chemosignal of male dominance, which may suggest the presence of a male competitor, cause an increase in men’s cooperative behavior, a reaction that positively correlated with testosterone levels (Huoviala & Rantala, 2013). Overall, it seems that individuals increase their sexual appeal and improve their reputation by cooperating with others, a behavior that functions as a costly signaling of one's quality as a mate (Arnocky et al., 2017; Gintis et al., 2001; Lotem et al., 2003). Thus, cooperative behavior, which is perceived as representing attractive traits, is used more frequently when mating motivation is on the rise. It is important to note that findings from primate studies may possibly indicate that increased mating motivation drives men to express more aggressive behavior (e.g. Cavigelli and Pereira, 2000; Manson, 1994). Nevertheless, as humans rarely express competition using such aggressive behavior (Marlowe and Berbesque, 2012), it is possible that such a mating motivation may increase men's willingness to cooperate with each other instead.

One candidate compound suggested as communicating female mating cues is the human putative pheromone estratetraenol (estra-1,3,5(10),16-tetraen-3-ol) (Verhaeghe et al., 2013). Estratetraenol (EST) was first detected in women's late-pregnancy urine in the late 1960s (Thysen et al., 1968). It is secreted mainly by women through several body secretions and it is possible that it is present also in axillary sweat (Verhaeghe et al., 2013). Although it is important to note that there is no direct evidence demonstrating EST’s presence in apocrine sweat or its natural biological role (Wyatt, 2015), early studies demonstrate that EST influences selectively men's electrical potential vomeronasal cells, a finding that was not found for women's vomeronasal cells or for other olfactory epithelium cells (Monti-Bloch and Grosser, 1991). Importantly, more recent studies claim that a functional vomeronasal system had been lost or became vestigial during human evolution (Smith et al., 2014). Likewise, more recent studies show that exposure to EST is linked with increased sexual arousal within a sexually arousing context (Bensafi et al., 2004) and was found to contribute to gender communication (Zhou et al., 2014). In addition, a correlation was found between men's preferences for feminine face shapes and ratings of EST pleasantness (Cornwell et al., 2004). Moreover, imaging studies demonstrated a differential reaction to EST among men and women (Savic et al., 2001), indicating that this compound may play a role in sexual and gender-specific reactions. Based on these findings, we suggest that EST may serve as one of the compounds that mediate the influences of women's body odor on men's mating behavior and thus may regulate their cooperative behavior.

Here we propose that chemosignals associated with women's fertility affect men's behavior in a competitive environment, so that men who are exposed to women's chemosignals of high fertility adopt a cooperative strategy toward others. To examine this hypothesis we collected women's body odor at two phases of the menstrual cycle: during ovulation and during the luteal phase. Due to large variations in menstrual cycle across women, we used hormonal ovulation examinations in order to confirm the occurrence of ovulation. Men were exposed to women's body odor samples while performing the Social Orientation Paradigm (SOP), a monetary game that assesses cooperative behavior along with individualistic and aggressive behavior in the context of provocations. In a second experiment, we tested the potential role played by the chemosignal EST in cooperation. We exposed a different sample of men to a pharmacological concentration of EST and to a control solution while they performed the SOP task. We hypothesized that exposure to EST would increase the frequency of men's cooperative behavior toward other unfamiliar players, similar to the influence of chemosignals of high fertility.

2. Materials and Methods

2.1. Experiment I

2.1.1. Participants

Sixty-five men were recruited via advertisements posted at the University of Haifa and on social media. The participants completed an online screening questionnaire designed to determine their suitability for the experiment. Male participants were 20-35 years old (M = 26.56, SD = 3.23). They were included after being confirmed to be native Hebrew speakers with normal vision and sense of smell. Male participants further reported being heterosexual, non-smokers and healthy, and stated they had not been sick during the last three weeks. The study was approved by the University of Haifa Ethics Committee. All participants signed an informed consent form and were given payment or course credit for their time. Two participants were omitted from the statistical analysis because they had difficulties understanding the task instructions. Both had an extremely low number of responses compared with other participants (> 4 SD below the mean number of overall responses). Since the experiment was part of a project examining the effects of exposure to chemosignals on social behavior, we also collected data concerning participants' emotion recognition which will be reported elsewhere.

2.1.2. Materials

2.1.2.1. Odor collection. Forty-three female participants ranging in age from 19 to 31 years (M = 24.73, SD = 2.33) were recruited to collect pools of samples containing body odor. Women completed a screening questionnaire and were included after having confirmed that they have regular menstrual cycles and do not use hormonal contraceptives. They also reported being heterosexual, not currently living with a spouse, non-smokers and not using medications or suffering from any physical or mental disease. Women monitored their menstrual cycles using a commercial ovulation test (ZER Hitech LTD) and collected body odor samples during two phases of the menstrual cycle: during ovulation and during the luteal phase. As in previous studies, we used cotton T-shirts to collect the body odor samples (Kuukasjärvi et al., 2004; Miller & Maner, 2010, 2011; Oren & Shamay-Tsoory, 2017). Women were requested to begin using the ovulation test on the 11th day of their menstrual cycle (from the beginning of menses). On the evening that the test was positive (indicating that ovulation is taking place), the women were asked to shower thoroughly with no soap or shampoo and to refrain from using deodorant, perfumes or lotions after their shower. Furthermore, they were asked to refrain from smoking, drinking alcohol, eating odorous food (e.g., garlic, onion, strong spices, asparagus) and engaging in odor-inducing activities (such as cooking or sexual intercourse). The instructions were similar to those given in previous studies (Chen and Haviland-Jones, 1999; Havlíček et al., 2006; Kuukasjärvi et al., 2004; Miller and Maner, 2010, 2011; Oren and Shamay-Tsoory, 2017; Singh and Bronstad, 2001; Thornhill et al., 2003). During the following night, the women slept wearing a new, odorless, white cotton T-shirt that had been previously stored in a sealed plastic bag. In the morning, the women were asked to put the T-shirt back in the bag and seal it tightly. The armpit areas were cut from each T-shirt and then cut into 12 pieces. T-shirt pieces taken from the first 23 women during ovulation served together as a pooled stimulus with a large number of duplications. T-shirt pieces from the next 20 women were mixed into a separate pooled stimulus. These T-shirts pools served as stimuli for the high fertility body odor condition. One week after the positive test (presumably at the luteal phase of the menstrual cycle), all the women repeated the procedure once more. Pools of these T-shirts served as stimuli for the low fertility body odor condition. We pooled body odor stimuli for each condition in order to maintain procedure uniformity for all participants (Mujica-Parodi et al., 2009; Prehn-Kristensen et al., 2009). When not in use, all stimuli were stored in a freezer (approximately −20 °C).

2.1.2.2. Odor presentation. As described previously (Oren & Shamay-Tsoory, 2017), stimuli were placed in a glass jar covered with non-transparent paper. The jar was sealed by a cover containing two holes, one connected to an air pump (AS-1061, Chuang Xing Manufacturing) and the other to a nasal cannula (Over-the-Ear nasal cannula with 7 ft star lumen, Hudson RCI®). The pump continually compressed air through the jar to the participants' nostrils during the entire session.

2.1.3. Experimental task

The Social Orientation Paradigm (SOP) was developed by Perach-Barzilay et al. (2013) based on the Point Subtraction Aggression Paradigm (PSAP), initially designed in order to assess aggressive behavior (Cherek, 1981). The SOP task evaluates different social orientations using a monetary game over three different behavioral categories—individualistic, aggressive and cooperative—by assessing patterns of reaction toward a fictitious player.

Participants were told that they were about to play a game involving decision-making together with another male participant currently sitting in another room. They were further told that in order to maintain anonymity they would not meet the other player, who was receiving instructions from a different experimenter. In fact, all trials were pre-programmed since the other player was fictitious. The participants were told they would undergo the task twice, each time playing with a different player.

The game lasted for ten minutes. It began with 20 credit points that were displayed at the bottom of the screen under three numbers displayed at the top of the screen (Fig. 1.A.). In each trial, participants were given three possible choices: (i) pressing the '1' key 30 times would add one point to their score. This choice is considered to be an individualistic response. (ii) Pressing the '2' key 10 times would subtract one point from the other participant, a response that is considered aggressive. (iii) Pressing the '3' key 15 times would add half a point to the player and half a point to the other participant, a choice that is considered cooperative (Fig. 1.B). The participants were told that the other player's game was similar except for one change. By pressing the '2' key ten times, the other player would not only subtract one point from the participant, but would also increase his own score by one point. The task is programmed to include two pre-programed provocations every minute—representing use of the aggressive reaction by the fictitious participant—and one fictitious cooperative response. All changes in the credit point total were shown in the credit counter and were accompanied by a sound. To encourage engagement in the task, extra payment was offered as an incentive for participants whose gains were high. The task was programmed using E-prime 2.0 software package.

2.1.4. Experimental procedure

We used a double-blind, within-subject design. Each participant underwent two experimental sessions within a one-week interval. The participants were greeted by a female experimenter who was using hormonal contraceptives at the time in order to eliminate changes resulting from her own periodicity (Kuukasjärvi et al., 2004; Miller et al., 2007). The experimenter was blind to the assigned conditions given to the participants. The first 37 male participants were exposed to the body odors of the first 23 women, while the next 26 were exposed to the body odors of the next 20 women. During the entire session, each man was exposed to one body odor stimulus, either from the high fertility condition or from the low fertility condition. At the beginning of each session, the men rated the odor they were exposed to in terms of intensity, pleasantness and familiarity (Frumin & Sobel, 2013). Subsequently, they performed the SOP task. In the second session, the participants underwent the same procedure while exposed to the other body odor condition. (If the stimulus presented in the first session was from the high fertility condition, the stimulus in the second session was from the low fertility condition and vice versa). The order of odor condition presentation was counterbalanced. At the end of the second session, participants were asked what they thought they were exposed to. None of the participants raised the possibility that they were exposed to body odors.

2.2. Experiment II

2.2.1. Participants

Sixty men (mean age 27.23, SD = 3.33) were recruited via advertisements posted at the University of Haifa and on social media. Participants completed an online screening questionnaire aimed to test their suitability for the experiment. Their reports met the same criteria mentioned in the first experiment. The experiment was approved by the University of Haifa Ethics Committee. Participants signed an informed consent form and were given payment or course credit for their time. We also collected data concerning the participants' emotion recognition (which will be reported elsewhere).

2.2.2. Compounds

The experimental stimulus comprised 2 M estratetraenol (Steraloid, Inc.) diluted in propylene glycol (Sigma Aldrich; purity 99%) with 1% eugenol (Sigma Aldrich; purity 99%) mask odor. Control solution was prepared by propylene glycol alone with an odor mask of 1% eugenol. Masking odor was used to prevent perceptual differences between EST and the control solutions. Similar stimuli were used in several previous studies (e.g., Jacob & McClintock, 2000). Due to the lack of previous behavioral effects and to ensure sufficient statistical power for obtaining existing effects, we used a pharmacological concentration of EST.

2.2.3. Experimental procedure

We used a double blind, within-subject design. Each participant underwent two experimental sessions within a one-week interval. The experimental procedure was identical to that described in Experiment I. During the entire session, men were exposed to one compound, either EST or the control solution. The compound was administered using a pre-prepared Band-Aid containing 100 μL of solution that was placed above the participant's upper lip. This type of administration ensures continuous presentation of the chemical signal throughout the

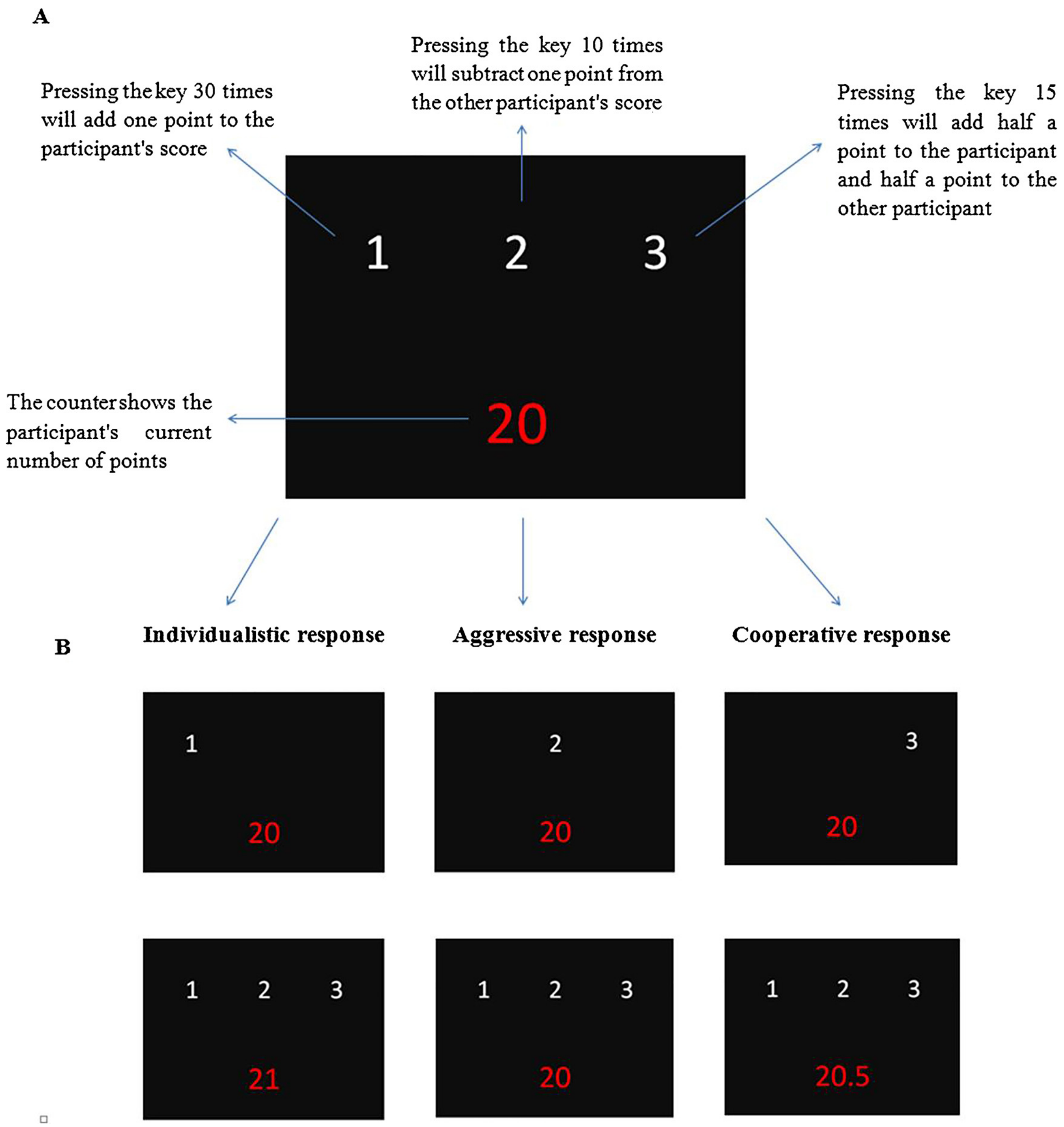

Fig. 1. Illustration of the SOP. The SOP is a monetary game that assesses three different behavior patterns. (A) The game begins with 20 points of credit; during each trial the participant is asked to choose one of three responses: individualistic, aggressive and cooperative. (B) Illustration of the three response patterns available in the SOP.

experimental session (as shown in Frumin & Sobel, 2013). Similar to Experiment I, at the beginning of each session the men rated the chemical signal to which they were exposed in terms of its intensity, pleasantness and familiarity (Frumin & Sobel, 2013). Subsequently, they performed the SOP task. The order of chemosignal administration was counterbalanced.

3. Results

3.1. Experiment I

3.1.1. Subjective ratings of odors

High and low fertility body odor stimuli did not differ in their perceived pleasantness [$t_{(62)} = .652$, p = .517, 95%CI(-.197, .381), Cohen's $d_Z = .08$] or in their perceived familiarity [$t_{(62)} = .361$, p = .719, 95%CI(-.425, .612), Cohen's $d_Z = .04$]. However, they differed in their perceived intensity [$t_{(62)} = -2.791$, p = .007, 95%CI(-.965, -.160), Cohen's $d_Z = .35$], with high fertility odor rated as more intense (M = 3.34, SD = 1.61) than low fertility odor (M = 2.78, SD = 1.45).

In order to preclude the possibility that the perceived intensity of the stimuli affected task performance, we conducted a Pearson correlation analysis between body odor ratings of intensity and task performance at all three response types. The analysis did not show the change in odor intensity (high fertility odor condition minus low fertility odor condition) to be significantly correlated with the change in the number of individualistic responses ($r = .088$, p = .494), the change in the number of aggressive responses ($r = .057$, p = .654) or the change in the number of cooperative responses ($r = .072$, p = .575).

3.1.2. The SOP task

A two-way repeated-measure ANOVA was conducted, with odor condition (low versus high fertility condition) and response type (individualistic, aggressive and cooperative response) as within-subject factors. The dependent variable was the number of times participants chose each response type.

For the response type main effect, Mauchly's test of sphericity indicated a violation of the assumption of sphericity (Mauchly's W = .67, $p < .000$), which was corrected according to Huynh-Feldt criteria (Epsilon = .770). The analysis revealed a significant main effect for response type [$F_{(1.54,95.42)} = 9.72$, p = .000, $\eta_p{}^2 = .14$]. Pairwise comparisons using Bonferoni correction indicated that the number of times the participants chose an individualistic response (M = 48.98, SD = 31.31) was significantly higher than the number of times they chose an aggressive response (M = 17.89, SD = 25.72; p = .000). Furthermore, the number of times the participants chose a cooperative response (M = 38.08, SD = 46.30) was significantly higher than the number of times they chose an aggressive response (p = .007). There was no significant difference between the number of times the participants chose individualistic versus cooperative responses (p = .22).

The main effect for odor condition was not significant [$F_{(1,62)} < 1$, p = .892, $\eta_p{}^2 = .000$], indicating that there was no overall effect of odor on the number of completed trails and that the number of completed trails was relatively similar across the low fertility odor condition (M = 104.40, SD = 29.07) and the high fertility odor condition (M = 102.64, SD = 29.79). For the interaction effect, Mauchly's test of sphericity indicated that the assumption of sphericity had not been violated (Mauchly's W = .95, p = .18). We found a significant two-way interaction between odor condition and response type [$F_{(2,124)} = 4.82$, p = .010, $\eta_p{}^2 = .072$].

Simple-effect analysis using paired-sample *t*-tests revealed a significant effect for odor condition on the number of times participants made an individualistic choice [$t_{(62)} = 2.21$, p = .031, 95%CI(.66, 13.18), Cohen's $d_Z = .28$], with fewer individualistic responses in the exposure to high fertility body odor condition (M = 45.52, SD = 31.78) than in the exposure to low fertility body odor condition (M = 52.44, SD = 32.00). The simple effect of odor condition on the number of times participants chose a cooperative choice was significant as well [$t_{(62)} = -2.52$, p = .014, 95%CI(-16.11, -1.86), Cohen's $d_Z = .32$], with more cooperative responses under exposure to the high fertility body odor condition (M = 42.57, SD = 50.69) than under exposure to the low fertility body odor condition (M = 33.59, SD = 44.43). The simple effect of odor condition on the number of times participants made an aggressive choice was not significant [$t_{(62)} = .88$, p = .383, 95%CI (-3.07, 7.90), Cohen's $d_Z = .11$] (Fig. 2).

To examine whether the order of the chemosignal presentation (high fertility body odor condition versus low fertility body odor condition in the first session) had an effect on the results, we analyzed the results once again by incorporating the order of odor presentation as an additional variable in the model. A three-way repeated-measure ANOVA was conducted, with odor-presentation order as an added between-subject independent variable. We found a significant three-way interaction between odor condition, response type and the presentation order [$F_{(2,122)} = 4.33$, p = .015, $\eta_p{}^2 = .066$] in addition to the still significant two-way interaction between odor condition and response type [$F_{(2,122)} = 5.35$, p = .006, $\eta_p{}^2 = .081$].

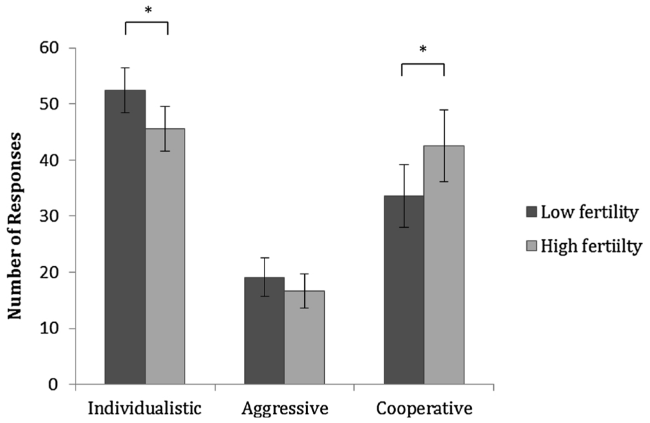

Fig. 2. Summary of the effects of odor condition on men's responses in the SOP. Mean (SEM) number of choices for each possible response type with respect to odor condition. A significant interaction between odor condition and response type was found (p = .010, $\eta_p^2 = .072$). We further found a significant increase in cooperative behavior (p = .014, Cohen's $d_Z = .32$) and a significant decrease in individualistic behavior (p = .031, Cohen's $d_Z = .28$) under exposure to the high fertility body odor condition. N = 63, * $p < .05$

Follow-up analysis using two-way repeated-measures ANOVA revealed a significant interaction between odor condition and response type for participants who underwent the high fertility body odor condition first [$F_{(1.67,\ 44.86)} = 6.42$, p = .006, $\eta_p{}^2 = .192$; corrected according to Huynh-Feldt criteria, Mauchly's W = .73, p = .018]. Simple-effect analysis using paired-sample *t*-tests revealed a significant effect of odor condition on the number of times participants made an individualistic choice [$t_{(27)} = 3.66$, p = .001, 95%CI(7.42, 26.36), Cohen's $d_Z = .69$], with fewer individualistic responses in exposure to high fertility odor condition (M = 40.54, SD = 26.11) than in the exposure to low fertility odor condition (M = 57.43, SD = 35.87). The simple effect of odor condition on the number of times participants chose a cooperative choice was not significant [$t_{(27)} = -1.39$, p = .18, 95%CI(-18.16, 3.52), Cohen's $d_Z = .26$] as was also the simple effect of odor condition on the number of times participants made an aggressive choice [$t_{(27)} = -1.33$, p = .195, 95%CI(-11.54, 2.47), Cohen's $d_Z = .25$] (Fig. 3a).

For participants who underwent the low fertility body odor condition first, we found a significant two-way interaction between odor condition and response type as well [$F_{(2,68)} = 3.30$, p = .043, $\eta_p{}^2 = .089$], with significantly more cooperative responses under the high fertility odor condition (M = 38.0, SD = 44.92) than under the low fertility odor condition (M = 27.69, SD = 36.52)[$t_{(34)} = -2.11$, p = .042, 95%CI(-20.24, -.39), Cohen's $d_Z = .36$]. The simple effect of odor condition on the number of times participants chose an aggressive behavior was significant as well [$t_{(34)} = 2.04$, p = .049, 95%CI(.026, 15.92), Cohen's $d_Z = .34$], with more aggressive responses under the low fertility odor condition (M = 21.54, SD = 29.71) than the high fertility odor condition (M = 13.57, SD = 24.52). The simple effect of odor condition on the number of times participants chose an individualistic response was not significant [$t_{(34)} = -.28$, p = .783, 95%CI (-8.79,6.67), Cohen's $d_Z = .05$] (Fig. 3b).

The pattern of aggressive behavior reactions is reversed with the different orders of chemosignal presentation. To examine whether this result can be attributed to a practice effect, we compared the overall number of responses made in each session. We found a non-significant trend [$F_{(1,61)} = 3.53$, p = .065, $\eta_p{}^2 = .055$] where the total number of responses was higher in the second (M = 37.30, SD = 13.15) compared to the first session (M = 33.13, SD = 11.76). We further found that while aggressive responses tended to be more frequent in the first session [$t_{(62)} = 2.44$, p = .017, 95%CI(1.17, 11.72), Cohen's $d_Z = .31$], cooperative and individualistic responses were more frequent in the second session [$t_{(34)} = -.66$, p = .509, 95%CI(-9.93, 4.98), Cohen's $d_Z = .08$ and $t_{(34)} = -2.62$, p = .011, 95%CI(-14.27, -1.92), Cohen's $d_Z = .33$, respectively].

3.2. Experiment II

3.2.1. Subjective ratings of compounds

EST and the control solution did not differ in their perceived intensity [$t_{(59)} = -.721$, p = .474, 95%CI(-.503, .237), Cohen's $d_Z = .09$], nor did they differ in their perceived pleasantness [$t_{(59)} = -.305$, p = .761, 95%CI(-.378, .278), Cohen's $d_Z = .04$] and familiarity [$t_{(59)} = .274$, p = .785, 95%CI(-.420, .554), Cohen's $d_Z = .03$].

3.2.2. The SOP task

A two-way repeated-measures ANOVA was conducted, with compound (EST versus placebo) and response type (individualistic,

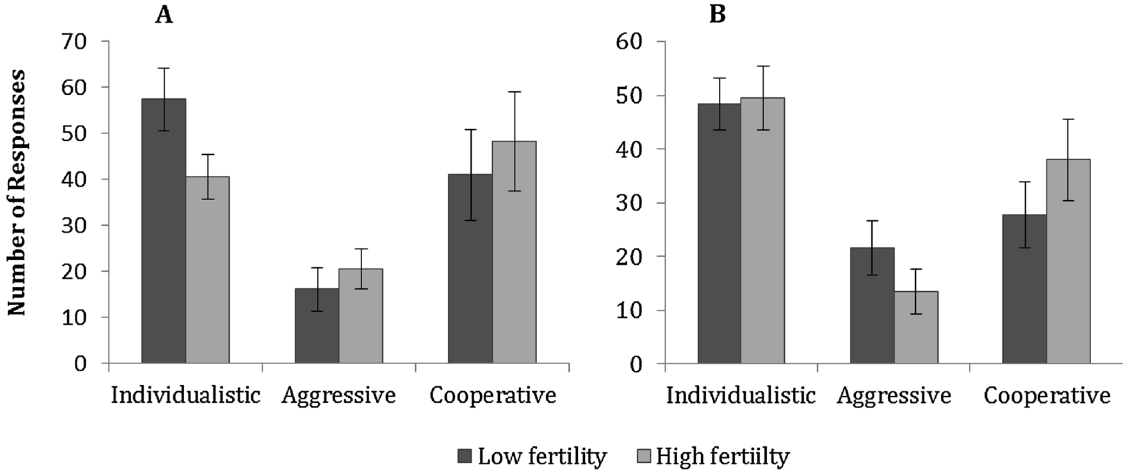

Fig. 3. Summary of the effects of odor condition on men's responses in the SOP with each odor presentation order. Mean (SEM) number of choices for each possible response type with respect to chemosignal exposure, for participants who were exposed to the high fertility body odor condition in the first session (A) and for those who were exposed to the low fertility body odor condition in the first session (B). A significant interaction between odor condition and response type was found in both. Exposure to the high fertility body odor in the first session significantly decreased individualistic responses, while exposure to this odor condition in the second session significantly increased cooperation and decreased aggression.

aggressive and cooperative response) as within-subject factors. The dependent variable was the number of times participants chose each response type.

For the response type main effect, Mauchly's test of sphericity indicated that the assumption of sphericity was violated (Mauchly's W = .67, p < .000); therefore a correction was made according to Huynh-Feldt criteria (Epsilon = .752). A significant main effect was found for response type [$F_{(1.52,90.52)} = 8.12$, p = .002, $\eta_p^2 = .12$]. Pairwise comparisons using Bonferoni correction indicated that the number of times participants chose an individualistic response (M = 50.30, SD = 34.79) was significantly higher than the number of times they chose an aggressive response (M = 20.41, SD = 29.12; p = .000). The number of times participants chose a cooperative response (M = 38.16, SD = 50.59) was higher than the number of times they chose an aggressive response and lower than the number of times they chose an individualistic response, though these differences were not significant (p = .072, p = .554, respectively). The main effect for the chemosignal was not significant [$F_{(1,59)} < 1$, p = .651, $\eta_p^2 = .004$], suggesting the compound had no overall effect on the number of completed trials in each experimental session. For the interaction effect as well, Mauchly's test of sphericity indicated a violation of the assumption of sphericity (Mauchly's W = .865, p < .05); therefore a correction was made according to Huynh-Feldt criteria (Epsilon = .906). We found a significant interaction between response type and presented compound [$F_{(1.81,106.96)} = 3.75$, p = .031, $\eta_p^2 = .060$].

Simple-effects analysis using paired-sample *t*-tests revealed that the presented compound had a significant effect on the number of times participants made a cooperative choice [$t_{(59)} = 2.17$, p = .034, 95%CI (.89, 22.14), Cohen's $d_Z = .28$], with more cooperative responses under exposure to EST (M = 43.92, SD = 53.45) than under exposure to the control solution (M = 32.40, SD = 47.33). The simple effect of odor condition on the number of times participants made an individualistic choice was marginally significant [$t_{(59)} = -1.76$, p = .084, 95%CI (-15.90, 1.03), Cohen's $d_Z = .23$], with fewer individual responses under exposure to EST (M = 46.58, SD = 34.31) than under exposure to the control solution (M = 54.02, SD = 33.04). The simple effect of chemosignal on the number of times participants made an aggressive choice was not significant [$t_{(59)} = -1.43$, p = .16, 95%CI(-12.77, 2.14), Cohen's $d_Z = .18$] (Fig. 4).

In order to investigate whether the order of the chemosignal presentation (EST versus control in the first session) had an effect on the results, we reanalyzed the results, including the order of odor presentation as an additional variable. A three-way repeated-measure ANOVA was conducted, with odor presentation order as the added between-subject independent variable. We found a significant three-way interaction between response type, the presented compound and presentation order [$F_{(1.65,97.38)} = 6.24$, p = .005, $\eta_p^2 = .096$; corrected according to Huynh-Feldt criteria, Mauchly's W = .74, p = .000] in addition to the still significant two-way interaction between odor condition and response type [$F_{(1.65,97.38)} = 4.039$, p = .027, $\eta_p^2 = .064$].

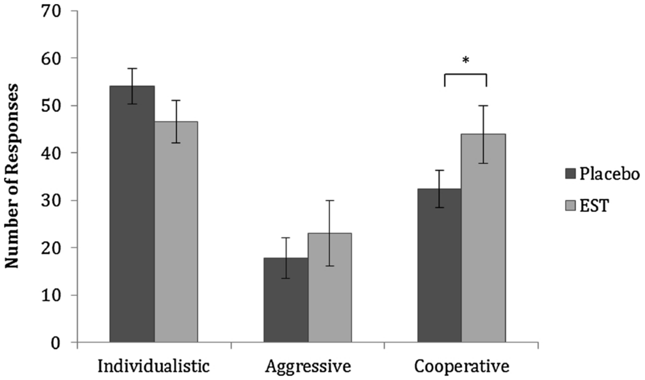

Fig. 4. Summary of the effects of EST on men's responses in the SOP. Mean (SEM) number of choices for each possible response type with respect to administered chemosignal. A significant interaction was found between exposure to the administered compound and response type (p = .031, $\eta_p^2 = .060$). We further found a significant increase in cooperative behavior (p = .034, Cohen's $d_Z = .28$) and a non-significant trend of decreased individualistic behavior (p = .084, Cohen's $d_Z = .23$) under exposure to EST, N = 60, * $p < .05$.

Follow-up analysis using two-way repeated-measures ANOVA revealed a significant interaction between compound and response type for participants who were administrated with EST in the first session [$F_{(1.3,37.64)} = 4.84$, p = .025, $\eta_p^2 = .143$; corrected according to Huynh-Feldt criteria, Mauchly's W = .42, p = .000]. Simple-effect analysis using paired-sample *t*-tests revealed a significant effect for compound on the number of times participants made an individualistic choice [$t_{(29)} = -3.15$, p = .004, 95%CI(-29.66, -6.34), Cohen's $d_Z = .58$], with fewer individualistic responses in the exposure to EST (M = 38.83, SD = 41.33) than in the exposure to the control solution (M = 56.83, SD = 31.46). The simple effect of compound on the number of times

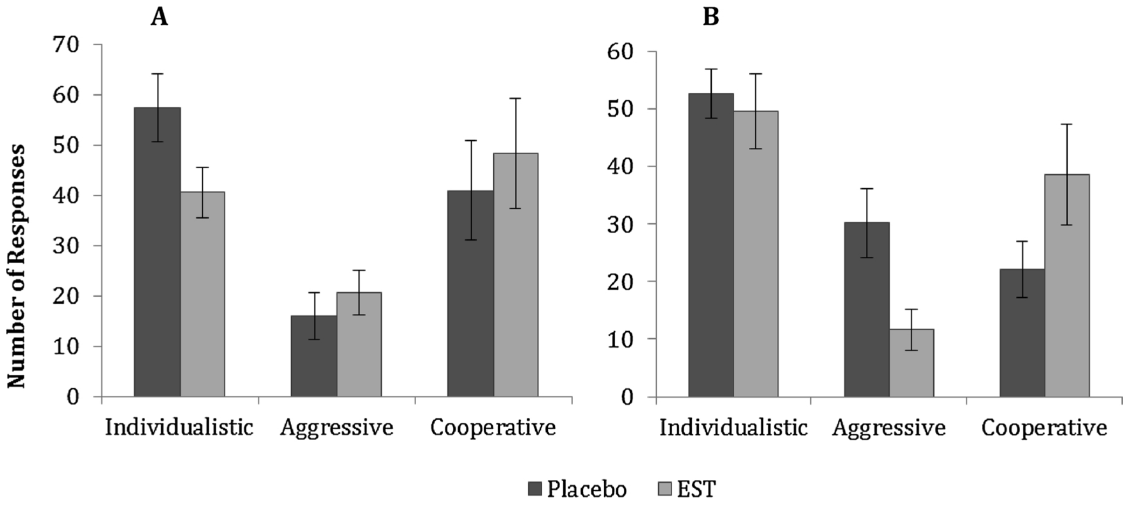

Fig. 5. Summary of the effects of EST on men's responses in the SOP with each odor presentation order. Mean (SEM) number of choices for each possible response type with respect to administered compound, for participants who were exposed to EST in the first session (A) and for those who were exposed to EST in the second session (B). A significant interaction between compound and response type was found in both cases. Exposure to EST in the first session significantly decreased individualistic responses and increased aggressive behavior, while exposure to EST in the second session significantly increased cooperation and decreased aggression.

participants chose an aggressive response was significant as well [$t_{(29)} = 3.13$, $p = .004$, 95%CI(2.95, 14.05), Cohen's $d_Z = .57$], with more aggressive responses during the exposure to EST ($M = 24.1$, $SD = 35.12$) than with exposure to the control solution ($M = 15.6$, $SD = 25.02$). The simple effect of compound on the number of times participants chose a cooperative choice was not significant [$t_{(29)} = .824$, $p = .42$, 95%CI(-8.79, 20.66), Cohen's $d_Z = .15$] (Fig. 5a).

For participants who were administrated with the control solution in the first session, a significant two-way interaction was found between compound and response type as well [$F_{(2,60)} = 5.41$, $p = .007$, $\eta_p{}^2 = .15$], with significantly more cooperative responses with exposure to EST ($M = 38.61$, $SD = 48.84$) than with exposure to the control solution ($M = 22.06$, $SD = 27.05$)[$t_{(30)} = 2.19$, $p = .036$, 95%CI(1.12, 31.97), Cohen's $d_Z = .39$]. The simple effect of compound on the number of times participants chose an aggressive behavior was significant as well [$t_{(30)} = -3.18$, $p = .003$, 95%CI(-30.42, -6.61), Cohen's $d_Z = .57$], with more aggressive responses resulting from exposure to the control solution ($M = 30.16$, $SD = 33.21$) than from EST ($M = 11.65$, $SD = 19.98$). The simple effect of compound on the number of times participants chose an individualistic response was not significant [$t_{(30)} = .549$, $p = .587$, 95%CI(-8.25, 14.32), Cohen's $d_Z = .098$] (Fig. 5b).

To examine whether the results can be attributed to a practice effect, we compared the overall number of responses made in each session. We found a non-significant trend [$F_{(1,59)} = 3.18$, $p = .080$, $\eta_p{}^2 = .051$] according to which the total number of responses was higher in the first ($M = 38.77$, $SD = 14.58$) compared to the second session ($M = 34.10$, $SD = 14.35$). We once again found that the overall number of aggressive responses was significantly higher in the first session [$t_{(60)} = 4.14$, $p = .000$, 95%CI(7.02, 20.16), Cohen's $d_Z = .53$], while cooperative and individualistic responses were more frequent in the second session [$t_{(60)} = -1.02$, $p = .311$, 95%CI(-16.25, 5.67), Cohen's $d_Z = .13$ and $t_{(60)} = -2.56$, $p = .013$, 95%CI(-18.50, -2.87), Cohen's $d_Z = .33$, respectively].

4. Discussion

In this study we investigated the effect of women's chemosignals of fertility on men's tendency to adopt a cooperative strategy. We used a large sample of odor donors and created pooled odor stimuli in order to avoid recipients' preferences for individual donors. We further explored the role of the chemosignal estratetraenol in producing similar effects. In line with our hypothesis, we found that exposure to women's chemosignals of high fertility increases men's tendency to apply a cooperative strategy and decreases their tendency to apply an individualistic strategy while interacting with another unfamiliar man. In the second experiment, we similarly found that EST administration increases men's tendency to implement a cooperative strategy in the same environment.

In both experiments, within-subject differences in behavior could not be attributed to differences in perceptual qualities of the odors. Nevertheless, it is important to note that failure to detect differences in women's body odor pleasantness across the menstrual cycle phases is inconsistent with previous findings suggesting that women's body odor during ovulation is more pleasant than during other phases (Havlíček et al., 2006; Kuukasjärvi et al., 2004). One possible explanation for this discrepancy is methodological differences in odor presentation. Previous studies presented men with several different odors successively, that is, with women's body odors from several menstrual cycle phases in each experimental session. Such presentation allows participants to compare odors and experience minor differences in their perceptual quality. Presenting odors from different menstrual cycle phases in different sessions, as in the current study, prevents participants from such comparison and thus from detecting subtle changes in the odors' pleasantness.

From an evolutionary standpoint, the human ability to function adequately in a social environment is crucial. Evolutionary research contends that humanoid ancestors that were not appropriately integrated within social groups were unable to survive or reproduce (Buss & Kenrick, 1998). In line with this contention, studies suggest that cooperative behavior is perceived as representing an individual's attractive traits (Farrelly et al., 2007). Thus, in the context of mating motivation, pro-social cooperative qualities offer a significant advantage, in accordance with Zahavi's (1995) handicap principle. As previous studies support the notion that exposure to women's chemosignals of fertility enhances mating motivation (Miller & Maner, 2011; Oren & Shamay-Tsoory, 2017), we suggest that such enhanced motivation further influences men's behavior by causing them to act in a way that highlights their attractive qualities by adopting a cooperative approach.

Previous findings obtained using the Social Orientation Paradigm demonstrate that participants' performance may vary significantly due to the context in which the task is presented. For example, under administration of oxytocin, which is known to enhance the social salience of stimuli in the environment (Shamay-Tsoory & Abu-Akel, 2016), participants reacted to aggressive provocations by choosing an aggressive strategy significantly more often than under administration of placebo (Ne'eman et al., 2016). In a different study in which participants performed the SOP task while being exposed to androstadienone, a putative chemosignal that signals dominance, participants more frequently chose an individualistic response while choosing a cooperative response less frequently. This finding was interpreted as an increase in social avoidance (Banner et al., 2018). In the present study, participants followed a more pro-social rather than anti-social course of action under exposure to women's chemosignals of fertility and under exposure to EST. It is possible that exposure to these chemosignals induces a different context in which mating motivation is more dominant, while provocations and competition become less salient.

As participants were exposed to women's fertility cues, they increased their cooperation with the other participant. Such behavior can be considered pro-social approach behavior. It is possible that the presented chemosignals implied the presence of women during the experiment. Such presence could be interpreted either that a woman is present in the room or that the other player against whom the participant is playing is a woman. In both cases, since pro-social behavior is considered to be attractive (Farrelly et al., 2007), increased cooperation following exposure to signals of fertility may stem from an attempt to impress and from increased mating motivation. Our findings are in line with those of Tan and Goldman (2015), who used a simple approach-avoidance task to demonstrate that exposure to women's chemosignals of fertility increases men’s preference to sit in closer proximity to women, a preference that was interpreted as a stronger tendency to approach other women.

It is important to note that exposure to women's chemosignals of fertility may hypothetically lead to increased aggressive behavior. This is in line with primate research suggesting that aggression between males is more frequent during females' estrus days (Fruth & Hohmann, 2003). However, the findings of the current study demonstrate a different pattern, in which exposure to women's chemosignals of fertility increased cooperative rather than aggressive behavior. As previously mentioned, it is possible that exposure to such signals created a sense of presence of a woman, which in turn decreased aggressive behavior. It is further possible that such presence influenced participants' perceptions of the other player with whom they were playing, intimating that they were playing with a woman rather than a man. As male aggression toward females is rare and infrequently followed by mating (Fruth & Hohmann, 2003), it is unlikely that men would behave aggressively toward someone they believe to be a woman.

The results from the two aforementioned experiments that found similar effects for chemosignals of high fertility and EST under a similar environment support the hypothesis that EST may serve as a possible biological mediator for the effects of women's chemosignals of fertility on men's behavior. EST has previously been identified as a putative human chemosignal (Verhaeghe et al., 2013) as it has been linked to sexual arousal (Bensafi et al., 2004) and gender communication (Zhou et al., 2014). Further support for the compound's role in sexual communication is apparent by its selective influence on men's electrical potential at cells that were considered a part of the vomeronasal system, while not producing such electrical changes in women or in other olfactory epithelium cells (Monti-Bloch & Grosser, 1991). It should be noted that EST may be only one compound among others present in women's body odor at high fertility. Therefore it is possible that exposure to EST only partially explains the effects of women's body odor on men's behavior. Furthermore, similar to several previous studies involving putative human chemosignals (Verhaeghe et al., 2013), in this study we used a pharmacological concentration of EST in order to ensure the detection of any possible effect. Future studies examining effects of biological concentrations on behavior are warranted. It is important to note that EST has not yet been found in women's axillary sweat (Wyatt, 2015), and that several studies using EST and other putative chemosignals of the same family produced conflicting effects (Ferdenzi et al., 2016; Hare et al., 2017; Pause, 2004). Therefore the results should be interpreted with caution.

Another limitation of the current study is that no measures of psychological and/or biological factors were included, thus precluding us from relating our findings to such factors. The current study provides the first evidence of the influence of chemosignals of fertility on cooperative behavior, and to the possible involvement of the chemosignal EST. Further studies exploring the biological and psychological mechanisms of the behavioral changes found in men's cooperative behavior are needed. Furthermore, in the current study we were not able to see whether chemosignals of low fertility affect men's behavior, as we only examined these chemosignals compared with chemosignals of high fertility. In order to explore that and to determine the unique contribution of EST in fertility signaling, we suggest future studies to use a three-group comparison design, incorporating exposure to both chemosignals of fertility and EST. In such study, comparing a control solution to chemosignals of low-fertility (non-ovulation) may reveal whether low-fertility chemosignals also affect men’s behavior, and comparison of low-fertility chemosignals to low-fertility chemosignals with EST may reveal whether EST has a role in modifying men's behavior, similarly to that found here for chemosignals of high fertility.

It is important to note that in both experiments we found an interaction between the presented chemosignal, response type and presentation order of chemosignals. This finding may reflect a practice effect. As previously suggested by Banner, Frumin and Shamay-Tsoory (2018), this pattern may result from higher familiarity with the task in the second session, and from a possibly more efficient decision-making process. This is in line with several previous studies which used the SOP or similar tasks (Banner et al., 2018; Cherek, 1981; Ne'eman et al., 2016), all of which found differences in participants' reactions across the experimental sessions, regardless of treatment. Further examination of the pattern of results and effect sizes in the present study’s two experiments, reveals that aggressive behavior was particularly subjected to a practice effect as it decreased systematically in the second session. This was accompanied by an increase in individualistic and cooperative responses in the second session. Such a decrease in aggressive behavior may result from participants understanding the monetary expectancies of each response. As both individualistic and cooperative responses hold a positive monetary value, aggressive reactions are not beneficial. Namely, it is possible that in the second session, participants had learned that in order to maximize their earnings they should avoid using aggressiveness and consequently the frequency of such reactions decreased. The monetary expectancy of individualistic and cooperative responses are positive and equal, therefore differences in the frequency of these reactions cannot be attributed to a learning effect. Increased frequency of these responses in the second session may result from higher levels of motivation and by an attempt to maximize earnings in this later session (Banner et al., 2018). Most importantly, the fact that despite these potential practice effects, we found a significant interaction effect between the presented chemosignal and the participants' response in both sessions, supports the role of chemosignals in regulating behavior.

5. Conclusions

In conclusion, our findings show that women's chemosignals of fertility affect men's tendency to adopt a cooperative strategy toward others. The increased mating motivation occurring after exposure to signals of high fertility encourages men to cooperate with others in order to highlight qualities considered attractive. Our study is the first to test the influence of estratetraenol, a human putative chemosignal, in a natural social environment. We demonstrated that similar to exposure to women’s chemosignals of fertility, exposure to EST causes a significant increase in cooperative behavior frequency, implying a potential role of EST in mediating the behavioral influences of body odor. This role should be examined in further studies by analyzing auxiliary sweat chemical composition. These findings extend the knowledge regarding the involvement of chemosignals in human social behavior and represent initial steps in establishing the biological mechanism underlying human chemosignals.

Declarations of interest

none

References

Arnocky, S., Piché, T., Albert, G., Ouellette, D., Barclay, P., 2017. Altruism predicts mating success in humans. British Journal of Psychology 108 (2), 416–435. https://doi.org/10.1111/bjop.12208.

Banner, A., Frumin, I., Shamay-Tsoory, S.G., 2018. Androstadienone, a Chemosignal Found in Human Sweat, Increases Individualistic Behavior and Decreases Cooperative Responses in Men. Chemical Senses 43 (3), 189–196. https://doi.org/10.1093/chemse/bjy002.

Bensafi, M., Brown, W., Khan, R., Levenson, B., 2004. Sniffing human sex-steroid derived compounds modulates mood, memory and autonomic nervous system function in specific behavioral contexts. Behavioural Brain Research 152 (1), 11–22. https://doi.org/10.1016/j.bbr.2003.09.009.

Bhogal, M.S., Galbraith, N., Manktelow, K., 2016. Sexual selection and the evolution of altruism: males are more altruistic and cooperative towards attractive females. Letters on Evolutionary Behavioral Science 7 (1), 10–13. https://doi.org/10.5178/lebs.2016.42.

Bowles, S., Gintis, H., 2003. Origins of human cooperation. In: Hammerstein, P. (Ed.), Genetic and cultural evolution of cooperation. MIT press, pp. 429–443.

Boyd, R., Richerson, P.J., 2009. Culture and the evolution of human cooperation. Philosophical Transactions of the Royal Society of London B: Biological Sciences 364 (1533).

Brown, R.E., Macdonald, D.W., 1985. Social odours in mammals. Clarendon Press.

Buss, D., Kenrick, D., 1998. Evolutionary social psychology. In: Gilbert, D.T., Fiske, S.T., Lindzey, G. (Eds.), The handbook of social psychology, 4th ed. Oxford University Press, New York pp. 982–1026.

Cavigelli, S.A., Pereira, M.E., 2000. Mating Season Aggression and Fecal Testosterone Levels in Male Ring-Tailed Lemurs (Lemur catta). Hormones and Behavior 37, 246–255. https://doi.org/10.1006/hbeh.2000.1585.

Cerda-Molina, A.L., Hernández-López, L., de la, O.C.E., Chavira-Ramírez, R., Mondragón-Ceballos, R., 2013. Changes in Men's Salivary Testosterone and Cortisol Levels, and in Sexual Desire after Smelling Female Axillary and Vulvar Scents. Frontiers in Endocrinology 4, 159. https://doi.org/10.3389/fendo.2013.00159.

Chen, D., Haviland-Jones, J., 1999. Rapid mood change and human odors. Physiology & Behavior 68 (1), 241–250. https://doi.org/10.1016/S0031-9384(99)00147-X.

Cherek, D.R., 1981. Effects of smoking different doses of nicotine on human aggressive behavior. Psychopharmacology 75 (4), 339–345. https://doi.org/10.1007/BF00435849.

Cornwell, R.E., Boothroyd, L., Burt, D.M., Feinberg, D.R., Jones, B.C., Little, A.C., Pitman, R., Whiten, S., Perrett, D.I., 2004. Concordant preferences for opposite–sex signals? Human pheromones and facial characteristics. Proceedings of the Royal Society of London B: Biological Sciences 271 (1539), 635–640. https://doi.org/10.1098/rspb.2003.2649.

Doty, R.L., 1986. Odor-guided behavior in mammals. Experientia 42 (3), 257–271. https://doi.org/10.1007/BF01942506.

Farrelly, D., 2011. Cooperation as a signal of genetic or phenotypic quality in female mate choice? Evidence from preferences across the menstrual cycle. British Journal of Psychology 102 (3), 406–430. https://doi.org/10.1348/000712610X532896.

Farrelly, D., Lazarus, J., Roberts, G., 2007. Altruists Attract. Evolutionary Psychology 5 (2), 313–329. https://doi.org/10.1177/147470490700500205.

Ferdenzi, C., Delplanque, S., Atanassova, R., Sander, D., 2016. Androstadienone's influence on the perception of facial and vocal attractiveness is not sex specific. Psychoneuroendocrinology 66, 166–175. https://doi.org/10.1016/j.psyneuen.2016.01.016.

Fisher, R., Smith, W.P., 1969. Conflict of interest and attraction in the development of cooperation. Psychonomic Science 14 (4), 154–155. https://doi.org/10.3758/BF03332761.

Frumin, I., Sobel, N., 2013. An Assay for Human Chemosignals. In: Touhara, K. (Ed.), Pheromone Signaling: Methods and Protocols. Humana Press, Totowa, NJ, pp. 373–394. https://doi.org/10.1007/978-1-62703-619-1_27.

Fruth, B., Hohmann, G., 2003. Intra- and Inter-Sexual Aggression By Bonobos in the Context of Mating. Behaviour 140 (11), 1389–1413. https://doi.org/10.1163/156853903771980648.

Gintis, H., Smith, E., Bowles, S., 2001. Costly Signaling and Cooperation. Journal of Theoretical Biology 213 (1), 103–119. https://doi.org/10.1006/jtbi.2001.2406.

Goldberg, T.L., 1995. Altruism towards panhandlers: Who gives? Human Nature 6 (1), 79–89. https://doi.org/10.1007/BF02734137.

Hamilton, W.D., 1964. The genetical evolution of social behaviour. Journal of Theoretical Biology 7 (1), 17–52.

Hare, R.M., Schlatter, S., Rhodes, G., Simmons, L.W., 2017. Putative sex-specific human pheromones do not affect gender perception, attractiveness ratings or unfaithfulness judgements of opposite sex faces. Royal Society Open Science 4 (3). https://doi.org/10.1098/rsos.160831. 160831.

Havlíček, J., Dvořáková, R., Bartoš, L., Flegr, J., 2006. Non-Advertized does not Mean Concealed: Body Odour Changes across the Human Menstrual Cycle. Ethology 112 (1), 81–90. https://doi.org/10.1111/j.1439-0310.2006.01125.x.

Huoviala, P., Rantala, M.J., 2013. A Putative Human Pheromone, Androstadienone, Increases Cooperation between Men. PLoS ONE 8 (5). https://doi.org/10.1371/journal.pone.0062499. e62499.

Iredale, W., Van Vugt, M., Dunbar, R., 2008. Showing Off in Humans: Male Generosity as a Mating Signal. Evolutionary Psychology 6 (3), 386–392. https://doi.org/10.1177/147470490800600302.

Jacob, S., McClintock, M.K., 2000. Psychological State and Mood Effects of Steroidal Chemosignals in Women and Men. Hormones and Behavior 37 (1), 57–78. https://doi.org/10.1006/hbeh.1999.1559.

Jensen, N.H., 2013. Male mating signaling in social dilemma Games. Journal of Evolutionary Psychology 11 (3), 131–150. https://doi.org/10.1556/JEP.11.2013.3.3.

Kuukasjärvi, S., Eriksson, C.J.P., Koskela, E., Mappes, T., Nissinen, K., Rantala, M.J., 2004. Attractiveness of women's body odors over the menstrual cycle: the role of oral contraceptives and receiver sex. Behavioral Ecology 15 (4), 579–584. https://doi.org/10.1093/beheco/arh050.

Lotem, A., Fishman, M.A., Stone, L., 2003. From reciprocity to unconditional altruism through signalling benefits. Proceedings. Biological Sciences 270 (1511), 199–205. https://doi.org/10.1098/rspb.2002.2225.

Maestripieri, D., Henry, A., Nickels, N., 2017. Explaining financial and prosocial biases in favor of attractive people: Interdisciplinary perspectives from economics, social psychology, and evolutionary psychology. Behavioral and Brain Sciences 40, e19. https://doi.org/10.1017/S0140525X16000340.

Manson, J., 1994. Male aggression: a cost of female mate choice in Cayo Santiago rhesus macaques. Animal Behavior 48 473–175.

Marlowe, F.W., Berbesque, J.C., 2012. The human operational sex ratio: Effects of marriage, concealed ovulation, and menopause on mate competition. Journal of Human Evolution 63 (6), 834–842. https://doi.org/10.1016/j.jhevol.2012.09.004.

Maynard-Smith, J., 1964. Group Selection and Kin Selection. Nature 201 (4924), 1145–1147. https://doi.org/10.1038/2011145a0.

Mesterton-Gibbons, M., Dugatkin, L.A., 1992. Cooperation Among Unrelated Individuals: Evolutionary Factors. The Quarterly Review of Biology 67 (3), 267–281. https://doi.org/10.2307/2830649.

Miller, G., Tybur, J.M., Jordan, B.D., 2007. Ovulatory cycle effects on tip earnings by lap dancers: economic evidence for human estrus? Evolution and Human Behavior 28 (6), 375–381. https://doi.org/10.1016/j.evolhumbehav.2007.06.002.

Miller, S.L., Maner, J.K., 2010. Scent of a woman: men's testosterone responses to olfactory ovulation cues. Psychological Science 21 (2), 276–283. https://doi.org/10.1177/0956797609357733.

Miller, S.L., Maner, J.K., 2011. Ovulation as a male mating prime: Subtle signs of women's fertility influence men's mating cognition and behavior. Journal of Personality and Social Psychology 100 (2), 295–308. https://doi.org/10.1037/a0020930.

Monti-Bloch, L., Grosser, B.I., 1991. Effect of putative pheromones on the electrical activity of the human vomeronasal organ and olfactory epithelium. The Journal of Steroid Biochemistry and Molecular Biology 39 (4), 573–582. https://doi.org/10.1016/0960-0760(91)90255-4.

Mujica-Parodi, L.R., Strey, H.H., Frederick, B., Savoy, R., Cox, D., Botanov, Y., Tolkunov, D., Rubin, D., Weber, J., 2009. Chemosensory Cues to Conspecific Emotional Stress Activate Amygdala in Humans. PLoS ONE 4 (7). https://doi.org/10.1371/journal.pone.0006415. e6415.

Ne'eman, R., Perach-Barzilay, N., Fischer-Shofty, M., Atias, A., Shamay-Tsoory, S.G., 2016. Intranasal administration of oxytocin increases human aggressive behavior. Hormones and Behavior 80, 125–131. https://doi.org/10.1016/j.yhbeh.2016.01.015.

Oren, C., Shamay-Tsoory, S.G., 2017. Preliminary evidence of olfactory signals of women's fertility increasing social avoidance behavior towards women in pair-bonded men. Scientific Reports 7 (11056). https://doi.org/10.1038/s41598-017-11356-0.

Pause, B.M., 2004. Are androgen steroids acting as pheromones in humans? Physiology & Behavior 83 (1), 21–29. https://doi.org/10.1016/j.physbeh.2004.07.019.

Perach-Barzilay, N., Tauber, A., Klein, E., Chistyakov, A., Ne'eman, R., Shamay-Tsoory, S.G., 2013. Asymmetry in the dorsolateral prefrontal cortex and aggressive behavior: A continuous theta-burst magnetic stimulation study. Social Neuroscience 8 (2), 178–188. https://doi.org/10.1080/17470919.2012.720602.

Prehn-Kristensen, A., Wiesner, C., Ole Bergmann, T., Wolff, S., Jansen, O., Maximilian Mehdorn, H., Ferstl, R., Lauwereyns, J., 2009. Induction of Empathy by the Smell of Anxiety. PLoS ONE 4 (6), e5987. https://doi.org/10.1371/journal.pone.0005987.

Raihani, N.J., Smith, S., 2015. Competitive Helping in Online Giving. Current Biology 25 (9), 1183–1186. https://doi.org/10.1016/j.cub.2015.02.042.

Roney, J.R., Simmons, Z.L., 2012. Men Smelling Women: Null Effects of Exposure to Ovulatory Sweat on Men's Testosterone. Evolutionary Psychology 10 (4), 703–713. https://doi.org/10.1177/147470491201000404.

Savic, I., Berglund, H., Gulyas, B., Roland, P., 2001. Smelling of Odorous Sex Hormone-like Compounds Causes Sex-Differentiated Hypothalamic Activations in Humans. Neuron 31 (4), 661–668. https://doi.org/10.1016/S0896-6273(01)00390-7.

Shamay-Tsoory, S.G., Abu-Akel, A., 2016. The Social Salience Hypothesis of Oxytocin. Biological Psychiatry 79 (3), 194–202. https://doi.org/10.1016/j.biopsych.2015.07.020.

Singh, D., & Bronstad, P. M. (2001). Female body odour is a potential cue to ovulation. The Royal Society, 268(1469), 797–801. https://doi.org/10.1098/rspb.2001.1589.

Smith, T.D., Laitman, J.T., Bhatnagar, K.P., 2014. The shrinking anthropoid nose, the human vomeronasal organ, and the language of anatomical reduction. The Anatomical Record 297 (11), 2196–2204. https://doi.org/10.1002/ar.23035.

Solnick, S.J., Schweitzer, M.E., 1999. The Influence of Physical Attractiveness and Gender on Ultimatum Game Decisions. Organizational Behavior and Human Decision Processes 79 (3), 199–215. https://doi.org/10.1006/obhd.1999.2843.

Stoléru, S., Ennaji, A., Cournot, A., Spira, A., 1993. LH pulsatile secretion and testosterone blood levels are influenced by sexual arousal in human males. Psychoneuroendocrinology 18 (3), 205–218.

Strom, J.O., Ingberg, E., Druvefors, E., Theodorsson, A., Theodorsson, E., 2012. The female menstrual cycle does not influence testosterone concentrations in male partners. Journal of Negative Results in BioMedicine 11 (1), 1. https://doi.org/10.1186/1477-5751-11-1.

Tan, R., Goldman, M.S., 2015. Exposure to female fertility pheromones influences men's drinking. Experimental and Clinical Psychopharmacology 23 (3), 139–146. https://doi.org/10.1037/pha0000016.

Thornhill, R., Gangestad, S.W., 1999. The Scent of Symmetry: A Human Sex Pheromone that Signals Fitness? Evolution and Human Behavior 20 (3), 175–201. https://doi.org/10.1016/S1090-5138(99)00005-7.

Thornhill, R., Gangestad, S.W., Miller, R., Scheyd, G., McCollough, J.K., Franklin, M., 2003. Major histocompatibility complex genes, symmetry, and body scent attractiveness in men and women. Behavioral Ecology 14 (5), 668–678. https://doi.org/10.1093/beheco/arg043.

Thysen, B., Elliott, W.H., Katzman, P.A., 1968. Identification of estra-1,3,5 (10), 16-tetraen-3-ol (estratetraenol) from the urine of pregnant women. Steroids 11 (1), 73–87. https://doi.org/10.1016/S0039-128X(68)80052-2.

Trivers, R.L., 1971. The Evolution of Reciprocal Altruism. The Quarterly Review of Biology 46 (1), 35–57.

Tuomela, R., 2011. Cooperation as joint action. Analyse & Kritik 33 (1), 65–86.

Van Vugt, M., Iredale, W., 2013. Men behaving nicely: Public goods as peacock tails. British Journal of Psychology 104 (1), 3–13. https://doi.org/10.1111/j.2044-8295.2011.02093.x.

Verhaeghe, J., Gheysen, R., Enzlin, P., 2013. Pheromones and their effect on women's mood and sexuality. Facts, Views & Vision in ObGyn 5 (3), 189–195.

West, S.A., Griffin, A.S., Gardner, A., 2007. Social semantics: altruism, cooperation, mutualism, strong reciprocity and group selection. Journal of Evolutionary Biology 20 (2), 415–432. https://doi.org/10.1111/j.1420-9101.2006.01258.x.

Wyatt, T.D., 2015. The search for human pheromones: the lost decades and the necessity of returning to first principles. Proceedings of the Royal Society Biological Sciences 282 (1804). https://doi.org/10.1098/rspb.2014.2994. 20142994.

Zahavi, A., 1995. Altruism as a Handicap: The Limitations of Kin Selection and Reciprocity. Journal of Avian Biology 26 (1), 1–3. https://doi.org/10.2307/3677205.

Zhou, W., Yang, X., Chen, K., Cai, P., He, S., Jiang, Y., 2014. Chemosensory Communication of Gender through Two Human Steroids in a Sexually Dimorphic Manner. Current Biology 24, 1091–1095. https://doi.org/10.1016/j.cub.2014.03.035.