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The smell of cooperativeness: Do human body odours advertise cooperative behaviours?

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Abstract

Several physical features influence the perception of how cooperative a potential partner is. While previous work focused on face and voice, it remains unknown whether body odours influence judgements of cooperativeness and if odour-based judgements are accurate. Here, we first collected axillary odours of cooperative and uncooperative male donors through a public good game and used them as olfactory stimuli in a series of tasks examining whether and how they influence cooperative decision-making in an incentivized economic game and ratings of cooperativeness. Our results show that having access to the donor's body odours provided a strategic advantage to women during economic decisions (but not to men): with age, women were more likely to cooperate with cooperative men and to avoid interacting with uncooperative men. Ratings of cooperativeness were nonetheless unrelated to the donors' actual cooperativeness. Finally, while men with masculine and intense body odours were judged less cooperative, we found no evidence that donors' actual cooperativeness was associated with less masculine or less intense body odour. Overall, our findings suggest that, as faces and voices, body odours influence perceived cooperativeness and might be

Hopfensitz and Ferdenzi jointly supervised this work.

used accurately and in a non-aware manner as olfactory cues of cooperativeness, at least by women.

KEYWORDS
body odours, chemosensory cues, economic games, partner choice

INTRODUCTION

Many human interactions necessitate judging strangers and whether to cooperate with them or not. The results of such judgements strongly affect if individuals will initiate an interaction with others (Cosmides & Tooby, 1992). In addition to information on past interactions and reputation, cooperativeness judgements are based on a variety of cues across multiple sensory modalities. For example, people readily form judgements of others' cooperativeness based on how they look and sound (e.g., Bonnefon et al., 2017; Knowles & Little, 2016). In this paper, we will explore a so far understudied type of cue, namely body odours.

Human olfaction has been mistakenly considered as very poor for decades, but recent studies have highlighted that humans actually have very fine olfactory abilities (McGann, 2017). In addition, humans can communicate, through chemosensory cues, socially relevant information, including sickness (e.g., Olsson et al., 2014), emotional state (fear, stress, happiness) (de Groot et al., 2015, 2020; Mujica-Parodi et al., 2009), or personality traits (Sorokowska, 2013a, 2013b; Sorokowska et al., 2012). To which degree chemosensory cues influence cooperativeness judgements and whether these judgements are accurate remain to be determined.

In this study, we experimentally tested the existence of a chemosensory cooperativeness cue in humans. Specifically, we examined whether having access to the body odours of counterparts provides a strategic advantage to participants when making cooperative decisions. To that aim, we quantified the cooperativeness of men (donors) by means of an incentivized economic game: a public good game, while also collecting their axillary odours. We then used the olfactory samples of the most and least cooperative donors as olfactory stimuli in a main experiment where participants (players) had to decide whether they wish to cooperate or not with partners represented solely by their body odours. This game was incentivized in a way that players maximized their monetary payoff by cooperating with cooperative partners and by not cooperating with uncooperative partners. Players were also asked to rate the cooperativeness of each partner based on their body odour. If complex body odours contain cues of cooperativeness, we would predict that players' decisions and ratings would be modulated by donors' actual cooperative behaviour advertised solely by their body odours.

Indeed, a recently growing literature has been exploring whether various traits are reliable indicators of male social behaviours, with a focus on facial and vocal features. In fact, there is evidence supporting the possibility that facial and vocal features, such as facial height-to-width ratio or voice pitch, may represent valid cues to behavioural trustworthiness or cooperativeness (Bonnefon et al., 2017; De Neys et al., 2017; Stirrat & Perrett, 2010; Tognetti et al., 2013; Tognetti et al., 2019; O'Connor & Barclay, 2017; Little et al., 2013; see also Jaeger et al., 2020; Schild et al., 2020). Phenotypic features, like facial width-to-height ratio and voice pitch, as well as social behaviour, like trustworthiness and cooperativeness, have been discussed to have the same biological basis in that all of them are reported to be influenced by testosterone levels. Hence, a pleiotropic effect of testosterone has been proposed as a proximal mechanism explaining the validity of facial and vocal cues of cooperativeness (O'Connor & Barclay, 2017; Stirrat & Perrett, 2010; Tognetti et al., 2013).

Olfactory cues might provide an alternative channel to transmit such information. Indeed, some olfactory studies that have used indirect approaches by focusing on a particular compound of human body odour, androstadienone, indicate that smelling this compound influences behavioural responses during cooperative interactions (see below). Androstadienone is derived from testosterone (Kwan et al.,

1997) and its concentration in human fluids (axillary sweat, plasma) appears to be sexually dimorphic (Brooksbank et al., 1972; Jackman & Noble, 1983). This androgen compound is a likely cue of dominance and threat in men (Banner & Shamay-Tsoory, 2018; Frey et al., 2012) and is therefore expected to influence inter-personal decision-making including decisions to cooperate or not with a potential partner (Banner & Shamay-Tsoory, 2018). In line with this hypothesis, it has been found that in a competitive context, smelling androstadienone, compared to a placebo, increased men's individualistic responses while it decreased their cooperative response. In other words, it elicits behavioural avoidance and social withdrawal tendencies (Banner & Shamay-Tsoory, 2018). In a cooperative context, studies using experimental economic games showed that smelling androstadienone, compared to a placebo, increases women's but not men's generosity (monetary donations) when playing a Dictator Game (Huoviala & Rantala, 2013; Perrotta et al., 2016). Finally, in an Ultimatum Game, smelling androstadienone, compared to a placebo, reduces the minimum acceptable offer that men would accept from their partner, that is, increases their willingness to cooperate with their partner even when the latter proposes a low (and unfair) offer (Huoviala & Rantala, 2013). Although these findings suggest that body odours likely influence an individual's decision to cooperate or not, it is yet unclear whether complex natural body odours enable perceivers to extract cues regarding their partners' cooperativeness and whether it influences their cooperative decisions.

Our study thus aims at testing whether smelling body odours of counterparts provides a strategic advantage to participants when making cooperative decisions, specifically, whether olfactory stimuli enable participants to cooperate more with cooperative partners and to avoid uncooperative partners. We further examined the possible perceptual mechanisms underlying cooperativeness detection, by relating participants' ratings of intensity, masculinity, pleasantness, and familiarity of the odours of their partners with decisions and ratings regarding cooperativeness.

METHODS

The study was conducted in accordance with the Declaration of Helsinki and experimental procedures were approved by the ethical committee of the Toulouse School of Economics and the Institute for Advanced Study in Toulouse (#2016-10–001). Written informed consent was obtained from all participants, who received monetary compensation for their participation (see below).

Odour donors

Participants

The body odours were collected during a larger study testing the relationship between male acoustic traits and cooperative behaviours (see Tognetti et al., 2019). During this previous study, we recruited 81 male participants (average age was 21.3 ± 3.2 SD) from the student population at the University of Montpellier, France. Students were invited via the ORSEE software, from a pool of more than 4,000 volunteers, to participate in an experiment at the Laboratory of Experimental Economics in Montpellier (LEEM, University of Montpellier, France).

Procedure

Eighty-one male participants (from now-on called 'odour donors') played a public good game at the LEEM (none of them had participated in a public good game before). All sessions were conducted from November 2016 to February 2017 and started at 2 p.m. All donors sat in individual cubicles in which they fastened cotton-wool pads under their armpits to collect their axillary odours (they also performed other tasks and filled out a demographic questionnaire that are not detailed here but are presented elsewhere (Tognetti et al., 2019)).

Collection of body odours

Upon arrival at the laboratory, odour donors were invited to sit in individual cubicles and were instructed about how to collect axillary odours. Instructions were given both orally and by using an illustrated instruction sheet provided with the required material. Axillary odours were collected on oval cotton pads, fastened by the participants themselves onto their axilla with surgical Micropore tape and using odourless gloves. Once the pads fastened, they had to wear a cotton t-shirt pre-washed using fragrance-free detergent, to avoid pad contamination with unwanted odours possibly coming from the participants own clothes. Odour donors had been instructed to refrain from drinking alcohol, eating strong foods that could affect their body odours (e.g., curry, chilli, and other spices, garlic, onion, pepperoni, blue cheese, cabbage, and asparagus), smoking, and spending time in locations with strong odours of food or smoke, from the day before their participation. On the evening preceding the experiment, they were required to shower and not to use any scented products such as antiperspirants, deodorants, perfumes, or colognes afterwards. They also were instructed to avoid sexual intercourse, sleeping next to someone, or being close to an animal during the night preceding the experiment. Finally, they were instructed not to shower, practice exercise, or use any scented products from the morning of their participation, and to wear unworn and washed clothes.

Odour donors kept the pads and t-shirt during the entire experimental session. On average, the pads were worn during 2.8 h ($SD = 0.22$). At the end of the session, they packed each pad separately in aluminium foil, identified them as left or right armpit, and placed them in a zip-lock bag. All samples were then kept in a cooler box for transportation to the laboratory where each pad was cut into two equal pieces, packed separately in aluminium foil, and stored in a −80°C freezer until testing.

The public good game

To quantify the odour donors' cooperativeness, we used what has become the benchmark for experimental research on social dilemmas: the public good game (Ledyard, 1995). The public good game represents a stylized model of a community in which each individual's well-being depends on own and others' contributions. Individually, each member is best off if he contributes nothing and relies on others' effort to create social benefits by behaving cooperatively. The external validity of the public good game was previously demonstrated by linking individual's contributions to the public good with cooperative behaviours in naturally occurring situations (Fehr & Leibbrandt, 2011; Rustagi et al., 2010).

The public good game was run on a computer network. To prevent visual contact, each participant was seated in an individual cubicle containing a computer terminal. Communication between participants was not allowed. At the beginning of each session, participants received a written copy of the instructions (for details see the Supplementary Material, SM). To implement common knowledge of the game and the task, the principal investigator (AT) also read the instructions aloud. Questions were allowed and were answered privately. We checked participants' understanding of the instructions by a computerized questionnaire. To guarantee experimenter–subject and subject–subject anonymity, a subject number was assigned to each participant.

During 12 sessions, odour donors were randomly assigned into pairs to play a one-shot public good game (note that we did not select a public good game with multiple rounds as we aimed to measure a donor's cooperativeness independent of his randomly assigned partner's cooperativeness) followed by a conditional contribution in the same game (we followed procedures of Fischbacher et al. (2001); for details see the SM). The one-shot public good game is classically used to measure cooperativeness and has the advantage to provide a continuous measure of cooperativeness but does not control for the participants' beliefs. Conditional contributions do control for individual's beliefs and allow the categorization of individuals either as *conditional cooperators* (the more others contribute to a public good, the more these individuals are willing to contribute) or *free riders* (individuals who do not contribute to a public good, whatever the others' contributions), which are the two most represented categories (for details see Fischbacher et al. (2001); see also Figure S1 in the SM).

The game began once all donors had fastened their pads and had read the instructions on how to play the game. At the beginning of the game, each donor received an initial endowment of 20 tokens. Then, each donor independently decided how to allocate his endowment between a private and a public account. Allocation decisions yielded payoffs that the donor received in euros from the experimenter at the end of the game. Each token allocated by a donor to his private account paid off €1.50 to himself while the public account paid off €0.90 to each member of the pair (marginal per capita return, MPCR = 0.6). It was made clear that each token allocated to the public account would provide exactly the same payoff to each member of the pair regardless of the contributor. From these parameters, it follows that the utilitarian optimum and the efficient symmetric outcome is for all group members to contribute their entire endowments to the public account. However, even under these specifications, it still remains in each individual's self-interest to contribute zero. The number of tokens allocated to the public account is therefore considered as a measure of cooperativeness.

After the one-shot public good game, donors were asked how much they would contribute if they could condition their contributions on their partner's contribution (conditional choice) allowing us to characterize them as free riders (donors who contributed 0 tokens to the public account, whatever the others' contributions) or conditional cooperators (donors for which the number of tokens allocated to the public account was positively correlated to the other's contributions).

Odour donors were informed about their final payoff at the end of the entire experimental session to avoid any potential influence on body odour collection. Average earnings were €32 (SD = 5.60) and each subject was paid in private.

Donor selection for the main experiment

A selection of olfactory stimuli to be used in the main experiment was made as follows. First, to avoid potential confounding factors influencing the composition and perception of axillary body odours (e.g., Ferdenzi et al., 2009; Parma et al., 2019; Prokop-Prigge et al., 2016), we selected the samples of the donors who reported being non-smokers, not having used scented products on the day of the experiment, and who reported being born in France, having parents born in France and European grandparents.

Second, we maximized the variability in cooperativeness of the donors by selecting the body odours of the donors displaying the most and the least cooperative behaviours in the public good game. To this aim, we combined the outcomes of both tasks (one-shot public good game and conditional contributions), which we believe provide a more accurate description of the donors' cooperativeness. Namely, the donors who did not contribute at all to the public good both during the one-shot public good game (i.e., who allocated 0 tokens) and in their conditional contributions (i.e., free-riders, for more details see Figure S1 in the SM), were selected as the 'low cooperative' donors (N = 8 men). In contrast, the donors who allocated their entire endowment in the public good (i.e., who allocated 20 tokens) during the one-shot public good game and who were categorized as conditional cooperators (see Figure S1 in the SM) were selected as the 'high cooperative' donors (N = 9 men). To have a balanced set of olfactory samples from both categories (N = 8), we excluded the olfactory samples of one high-cooperative man on the basis of his conditional contributions: he was the only one who had not contributed his entire endowment when his partner did. Both groups did not differ in age (high: 22.0 ± 3.3 SD, low: 21.4 ± 2.9 SD, Wilcoxon rank-sum test: U (N = 16) = 36.5, p = .67).

Main experiment

Participants

We recruited 58 male and 58 female participants from the student population at the University of Montpellier, France. Students were invited via the ORSEE software, from a pool of more than 4,000 volunteers, to participate in an experiment at the Laboratory of Experimental Economics in Montpellier (LEEM, University of Montpellier, France). None of the participants had participated in a public good game experiment before. There was no significant age difference for men or women (Student's t-test: $t(112.24) = -1.82, p = .07$) although men (on average 23.1 ± 6.1 SD) tended to be older than women (on average 21.8 ± 4.1 SD). Sociodemographic information was obtained through a questionnaire at the end of each session. We notably collected self-report on sense of smell (normal or impaired during the day of their participation) in order to exclude from analyses the participants who reported to have an impaired sense of smell ($N = 6$ women, $N = 6$ men).

Procedure

In order to test the existence of olfactory cues of cooperativeness, we presented body odours of the male donors with contrasted levels of cooperativeness (chosen as detailed in section *Donor selection for the main experiment)* to our newly recruited participants. We conducted 12 experimental sessions during 1 week at the LEEM in May 2018. During each session, only same-sex participants participated. Each session took place in a computer laboratory where participants (from 6 to 12 participants simultaneously) were seated in individual cubicles.

To control for the integrity of the olfactory stimuli, each body odour stimulus was only used once and only up to 4 h. Three 1-h sessions were thus conducted, in quick succession, every morning in a week. Each morning, eight stimuli from four high- and four low-cooperative male donors were used. Each set of eight stimuli was presented to both men and women. The olfactory stimuli were presented to the participants using glass jars with glass lids (Weck, 160 ml). Each jar was identified by a unique number and contained two halves of cotton pads from the same donor (from the right and left armpit, to avoid possible side-related differences). An experimenter placed each jar one by one on a desk in front of each participant while s/he was seated in his/her cubicle. All participants manipulated the jars with gloves and they were instructed to shake the jar before removing the lid, to smell the jar during a few deep breaths while neither touching the jar aperture with their nose nor blowing on it, and to put the lid back on immediately afterwards. After smelling a sample, the participants were asked to wait at least 15 seconds before smelling the next one.

Each session comprised three tasks. In task 1, participants' cooperativeness was quantified by using a one-shot public good game (see *Task 1*: *Players' baseline cooperativeness* below). In task 2, we examined whether they were able to assess cooperativeness through body odour cues by playing an incentivized game during which they smelled the body odours of a series of partners of contrasted levels of cooperativeness (see *Task 2*: *Players' cooperativeness depending on partner body odour* below). Specifically, we examined whether the participants preferentially selected high-cooperative partners and preferentially avoided low-cooperative partners based on body odours only. At the start of this task, we informed each participant that s/he will successively smell the body odours of eight male donors with whom s/he would have the possibility to interact during an incentivized game similar to the one s/he just played (task 1). We also informed him/her that these 8 male donors previously participated in a similar experiment where they played a one-shot public good game and that we selected specifically the body odours of the male donors who allocated either 0 or 20 tokens to the public good during their previous participation. The third task (see *Task 3*: *Odour ratings* below) consisted in evaluating each stimulus for donor's selfishness and for perceptual odour characteristics (intensity, masculinity, pleasantness, familiarity). Communication between participants was not allowed at any time.

Task 1: Players' baseline cooperativeness

In order to quantify participants' cooperativeness and improve their understanding of the context in which the olfactory stimuli were obtained, they played an incentivized one-shot public good game (see description of the task in section *The public good game* above) in randomly chosen pairs.

Task 2: Players' cooperativeness depending on partner body odour

The participants were presented with a total of eight body odour samples (four samples from each category of donors, in a pre-determined randomized order) representing their game partners. No information regarding the proportion of each category of donors was given to them. After smelling the first odour sample, they had to predict their partners' cooperativeness which was framed as a choice between two options: either to cooperate with the man whose odour they had just smelled or not to cooperate. This procedure was then repeated for the seven other odour samples. This game was incentivized in a way that participants increased their monetary payoff by cooperating with the high cooperative partners and by avoiding the low cooperative partner. Indeed, they received €4.80 when cooperating with a high cooperative man and when avoiding a low cooperative man, while they received only €2.40 otherwise. In another word, they maximized their payoff when they correctly predicted the strategy adopted by the male donor whose body odour they have just smelled. Note that we did not use a standard one-shot public good game, since in this game it remains in each individual's self-interest to contribute zero regardless of their partner's cooperativeness. Hence, it would not allow us to disentangle whether people can assess cooperativeness through olfactory cues.

The game was performed through a computer interface, displaying the odour sample identification number and recording the participant's decisions. Participants had been informed that their payoff to this specific task would be the payoff earned during one of the eight interactions selected randomly.

Task 3: Odour ratings

Finally, the participants had to smell again each of the same eight stimuli (identified with a new code), in a randomized order. For each odour, they were asked to evaluate the selfishness of the donor by answering the question '*if you would have to assess this man based on his body odour, how selfish/individualistic do you think that he is?'* (in French) using a 9-point scale ranging from 1 (not at all selfish) to 9 (extremely selfish). We used 'selfish/individualistic' because these two words have a clearer and more self-understanding definition in the everyday language in French compared with 'cooperative'. They also evaluated the stimuli for intensity, masculinity, pleasantness, and familiarity on 9-point scales ranging from 1 (not at all) to 9 (extremely).

Final payoff

Participants' total earnings were the sum of the payoff earned during tasks 1 and 2. Participants were informed about their payoffs at the end of the entire experimental session only. Average earnings were €8.0 (SD = 1.5) plus a show-up fee and each participant was paid in private.

Statistical analyses

Statistical analyses were performed using R, version 3.6.0 (R Core Team, 2017). Following the recommendations found in Schielzeth (2010), we centred every continuous variable in all the models in order to make the effects more easily biologically interpretable. The significance of each variable was tested with likelihood ratio tests comparing the full model to those without the term of interest and the α-level was set to 0.05.

Effect of odour donor cooperative behaviours on players' cooperative decisions

In order to examine whether the actual cooperative behaviour of the donors influenced participants decisions to cooperate or not through olfactory cues, we used a Bayesian Generalized Linear Mixed-Effects Model (*bglmer* function in the *blme* R package) with a binomial error structure for men and women separately (the *bglmer* function applies a weak prior (Wishart) over the random effects to avoid singularity). Our dependent variable was the 'Cooperative Decision' by a participant (0 when he/she did not cooperate, 1 otherwise) for each of the eight olfactory stimuli. Our explanatory variable 'Donor Cooperativeness' represented the two categories of the olfactory stimuli (high- vs. low-cooperative donors). We included the variable 'Age' of the participants and its interactions with the explanatory variable into the model to examine whether the accuracy to predict cooperative intent increases with age as previously shown with faces (De Neys et al., 2015; Salvia et al., 2020). We also included the variable 'Own Cooperativeness' corresponding to the contribution allocated to the public good by each participant as a controlling variable. Finally, we included a random intercept for each participant's and odour donor's ID (respectively, 'ParticipantID' and 'OdourID') and random slopes for Donor Cooperativeness by participant. In other word, the model was: Cooperative Decision ~Donor Cooperativeness + Age + Own Cooperativeness +Donor Cooperativeness:Age + (1 | OdourID) + (1 + Donor Cooperativeness | ParticipantID). We included all the main effects and interaction term in the initial model, which was then simplified by removing the non-significant interaction term to achieve the minimal adequate model.

Effect of odour donor cooperative behaviours on players' selfishness ratings

In order to examine whether the actual cooperative behaviour of the donors influenced participants ratings of selfishness, we used a similar Bayesian Linear Mixed Model (see above) with the evaluation of selfishness ('Selfishness Ratings') as dependent variable, for men and women separately (Selfishness Ratings ~Donor Cooperativeness + Age + Own Cooperativeness + Donor Cooperativeness:Age + (1 | OdourID) + (1 + Donor Cooperativeness | ParticipantID)).

Perceptual mechanisms underlying cooperativeness detection

First, we used a Bayesian Generalized Linear Mixed Model with a binomial error structure to examine how the perceptual characteristics of body odours (Task 3) influenced participants' cooperative behaviour in Task 2. The dependent variable was 'Cooperative Decision' (a participant's decision to cooperate (1) or not (0) with the male smell donor) and the explanatory variables were the ratings of intensity, masculinity, pleasantness, and familiarity. We included a random intercept for each participant identity and each odour sample identity. The final model was: Cooperative Decision ~Intensity + Masculinity + Pleasantness + Familiarity + (1| ParticipantID) + (1| OdourID). We ran the analyses separately for both sexes.

Second, we used a similar model to examine how these four perceptual characteristics (explanatory variables, Task 3) affected the odour-based evaluation of donor selfishness (dependent variable, Task 3). A Bayesian Linear Mixed Model was used with random intercepts for each participant identity and odour sample identity. Analysis was conducted on both sexes separately. The final model was: Selfishness Ratings ~Intensity + Masculinity + Pleasantness + Familiarity + (1| ParticipantID) + (1| OdourID).

Because perceptual characteristics are intercorrelated (see descriptive statistics Table S1), we checked for multicollinearity by calculating the variance inflation factor (VIF) for all explanatory variables. We ruled out potential bias from multicollinearity as all variables demonstrated a low value of VIF for both models (all VIF<2.86).

Perceptual differences between the body odour of high and low cooperative men

We used a Bayesian Linear Mixed Model to examine whether the body odours of the two donor categories were perceived differently. We used three separate models, one for each perceptual characteristic rated. The dependent variable was either the ratings of intensity, masculinity, or pleasantness. Our explanatory variable was 'Donor Cooperativeness' that represented the two categories of the olfactory stimuli (high- vs. low-cooperative donors). Finally, we included a random intercept for each participant's and odour donor's ID (respectively, 'ParticipantID' and 'OdourID') and random slopes for Donor Cooperativeness by participant. In other word, the model was: Perceptual ratings ~Donor Cooperativeness + (1 | OdourID) + (1 + Donor Cooperativeness | ParticipantID). Because the perceptual ratings of men's body odour are likely to differ between men and women, we ran the analyses separately for both sexes.

RESULTS

Effect of odour donor cooperative behaviours on players' cooperative decisions and selfishness ratings

The minimal adequate models that were run to obtain the results reported below were obtained by removing the non-significant interaction term between Age and Donor Cooperativeness, in all models ($.062 < p < .439$) except the model testing the effect Donor Cooperativeness on women's Cooperative Decisions.

Male players

Donor Cooperativeness did neither influence men's Cooperative Decisions ($\beta = -0.23$, $SE = 0.38$, $X^2 = 0.37$, df = 1, $p = .545$, Table S2A) nor Selfishness Ratings ($\beta = 0.18$, $SE = 0.33$, $X^2 = 0.30$, df = 1, $p = .586$, Table S2B).

Female players

The interaction between women's Own Age and Donor Cooperativeness was significantly associated with their Cooperative Decisions ($\beta = 0.16$, $SE = 0.07$, $X^2 = 5.37$, df = 1, $p = .020$, Table S3) and indicated that with age women were more likely to cooperate with the high cooperative men and less likely to cooperate with the low cooperative men (Figure 1). The significance of the interaction survived even after the exclusion of two women who were much older (35 and 41 years old; >2.5 S.D) than the other participants ($\beta = 0.51$, $SE = 0.14$, $X^2 = 12.66$, df = 1, $p = .0004$). Post-hoc analyses testing the robustness of this finding to exclusion of the control variable and the inclusion of the women who reported to not have had a normal sense of smell yield similar results (see Table S3). Finally, Donor Cooperativeness did not significantly affect the Selfishness Ratings ($\beta = -0.14$, $SE = 0.34$, $X^2 = 0.18$, df = 1, $p = .673$, Table S4).

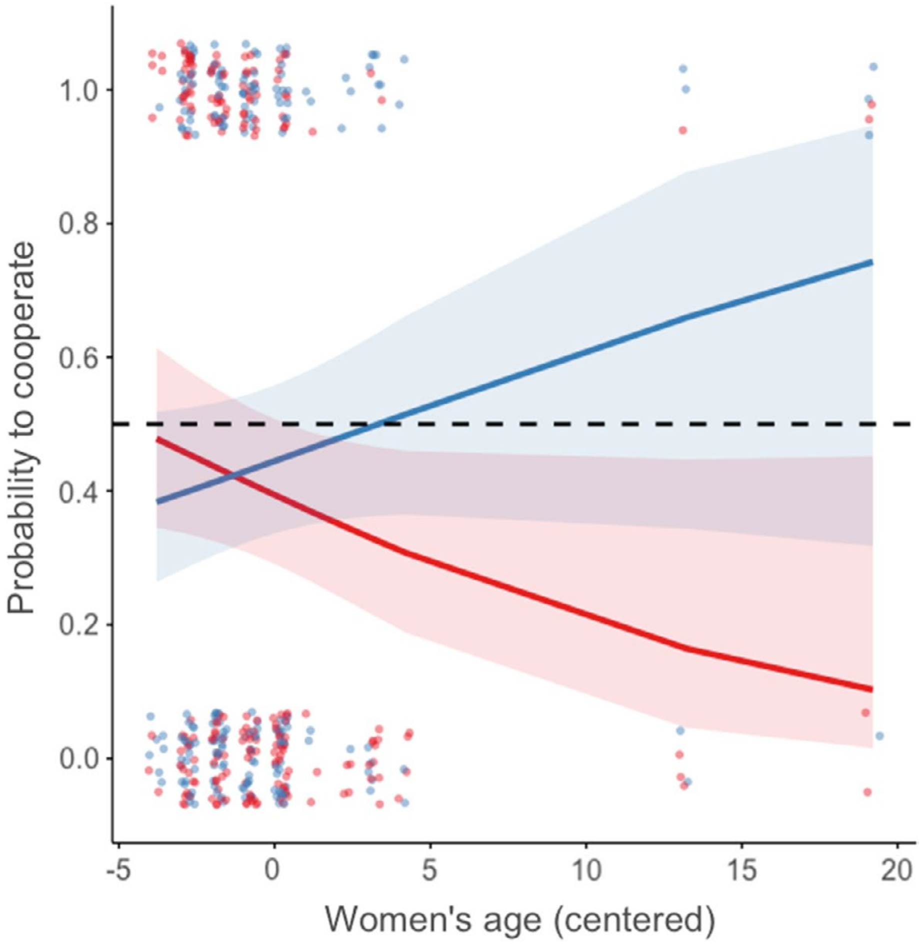

FIGURE 1 Predicted probabilities of women's decisions to cooperate or not with the high- (blue line) and the low-cooperative male donors (red line) as a function of women's age. Dots represent individual decisions to cooperate (1) or not (0) (N = 416) with the high- (blue) and low-cooperative men (red) as well as 95%CI are shown. The dotted black line represents random choice (50%). Note that following the recommendations found in Schielzeth (2010), we centred women's age (on average 21.8 ± 4.1 SD, range: 18–41 years). A Bayesian Generalized Linear Mixed-Effects Model indicates that the interaction between women's age and donor's cooperativeness was significantly associated with women's decisions to cooperate or not ($\beta = 0.16$, $SE = 0.07$, $X^2 = 5.35$, df = 1, $p = .020$)

Perceptual mechanisms underlying cooperativeness detection

Male players

Both men's Cooperative Decisions and Selfishness Ratings were influenced by the masculinity of the olfactory stimuli: higher perceived masculinity tended to decrease men's decisions to cooperate with the donor ($\beta = -0.16$, $SE = 0.08$, $X^2 = 3.75$, df = 1, $p = .053$, Table S5A) and significantly increased men's ratings of donor selfishness ($\beta = 0.18$, $SE = 0.07$, $X^2 = 5.57$, df = 1, $p = .018$, Table S5B). Intensity, pleasantness, and familiarity did not influence men's Cooperative Decisions or Selfishness Ratings (all $p > .188$, Table S5).

Female players

Women's Cooperative Decisions and Selfishness Ratings were influenced by the intensity of the olfactory stimuli: higher perceived intensity significantly decreased women's decisions to cooperate with the donor ($\beta = -0.13$, $SE = 0.06$, $X^2 = 4.17$, df = 1, $p = .041$, Table S6A) and significantly increased the ratings of selfishness ($\beta = 0.15$, $SE = 0.06$, $X^2 = 7.21$, df = 1, $p = .007$, Table S6B). As for men, masculinity significantly influenced women's ratings of selfishness ($\beta = 0.12$, $SE = 0.06$, $X^2 = 3.91$, df = 1, $p = .048$, Table S6B) but did not influence decisions to cooperate ($\beta = -0.003$, $SE = 0.07$, $X^2 = 0.002$, df = 1, $p = .969$, Table S6A). Finally, neither pleasantness (all $p > .083$, Table S6) nor familiarity affected women's probability to cooperate or selfishness ratings (all $p > .189$, Table S6).

Perceptual differences between the body odour of high and low cooperative men

None of the models found evidence that high and low cooperative men smell differently in term of intensity, masculinity, or pleasantness whether rated by men (all $p > .284$, Table S7) or women players (all $p > .233$, Table S8).

DISCUSSION

Previous research has investigated whether social traits can be accurately assessed by phenotypical cues, such as face and voice (Bonnefon et al., 2017; De Neys et al., 2015; Little et al., 2013; Schild et al., 2020; Stirrat & Perrett, 2010; Tognetti et al., 2013, 2019), based on the idea that both behavioural and phenotypic traits are influenced by common physiological mechanisms. Specifically, cooperative behaviours and facial and vocal characteristics have been discussed to be associated in men through a pleiotropic effect of testosterone levels (O'Connor & Barclay, 2017; Stirrat & Perrett, ; Tognetti et al., 2013, 2019). Although the composition of human body odours is influenced by androgens and although several studies showed that androstadienone, a chemical compound derived from testosterone, influence an individual's decision to cooperate or not (Banner & Shamay-Tsoory, 2018; Huoviala & Rantala, 2013; Perrotta et al., 2016), whether natural body odours are a valid cue of cooperative behaviour has never been tested so far in humans. This study fills this gap by investigating whether body odours represent a cue to men's cooperative behaviour. Our findings are mixed: while donors' cooperativeness does not affect how men and women rated cooperativeness, nor the cooperative decisions by men, we found that donor's cooperativeness influences cooperative decisions by women depending on age. With age, women were more likely to cooperate with the high cooperative men and more likely to avoid interacting with the low cooperative men.

This suggests that, somehow, women are able to assess who is cooperative and who is not based on olfactory cues of cooperativeness and resulting of processes that are likely to be beyond the scope of attention. Interestingly, women's cooperative decisions become increasingly accurate with age. Both women's better performance over men and the influence of age on the performance at detecting cooperative traits was previously demonstrated in studies using facial pictures (De Neys et al., 2015; Salvia et al., 2020). Taken together, these findings suggest a development of cooperativeness detection across multiple sensory modalities. According to the redundant signal hypothesis (Moller & Pomiankowski, 1993), these multiple cues of cooperativeness across different sensory modalities might improve the assessment of cooperative behaviour when considered simultaneously and future studies should explore this possibility.

Although this result needs to be considered with caution, as the variability of women's age in our sample was relatively low, several explanations emerge. First, it seems that women are better at avoiding low cooperative partners rather than cooperating with high cooperative partners. Indeed, from approximately 24 years old, women avoid interacting with low cooperative partners above chance expectation (95%CI does not overlap 0.5, see Figure 1), whereas the probability of cooperating with high cooperative partners do not differ from chance expectation at any age of our sample (95%CI overlaps 0.5, see Figure 1). This finding is in line with the cheater detection module, a cognitive mechanism that would help people to detect cheaters (Cosmides, 1989; Cosmides & Tooby, 1992). Indeed, several experimental studies demonstrated for example an enhanced recognition of cheaters (Verplaetse et al., 2007; Yamagishi et al., 2003) and that people remember faces of known cheaters better than those of known cooperators (Mealey et al., 1996; Oda, 1997; but see Barclay, 2008).

Second, only women, and not men, were able to use men's body odours to correctly assess men's cooperativeness. This sex-specific effect may partly be explained by the existence of sex differences in olfaction. Indeed, it has been repeatedly shown that women outperform men in many aspects of olfactory abilities (identification, discrimination, memory) (Hummel et al., 2007; Larsson et al., 2003; Sorokowski et al., 2019), including the processing of human chemosignals (individual recognition, response to the emotional content of human body odour) (Ferdenzi et al., 2010; Pause et al., 2010; Schleidt et al., 1981). An (non-exclusive) alternative explanation could be linked to the relative difference between men and women in terms of cost-benefit ratio of detecting men cooperativeness. Indeed, it has been hypothesized that low cooperative men exhibit low parenting quality (Farrelly, 2013; Miller, 2007). While parental investment is a crucial resource for human children (Sear & Mace, 2008), paternal investment is facultative and shows larger inter-individual variations than maternal investment (Geary, 2000; Sear & Mace, 2008). Hence, the ability to detect and avoid low-cooperative mates before reproducing could be an adaptive strategy specifically for women (although we cannot exclude the possibility that men are not able to detect women's cooperativeness through body odours, or are not responsive to it). An effect of women's age is thus likely to be observed if the ability to detect cooperativeness through body odour requires to be learned. We can also speculate that, because of its likely costs (e.g., cognitive costs), this detection ability should vary with women's reproductive age: the onset of detection should arise before age at first birth and the ability to detect should decrease after menopause. In our study, women avoided interacting with low cooperative partners above chance from approximately 24 years old, which is consistent with the mean age at first birth in several pre-industrial populations with natural fertility (between 26 and 27 years old, see Dribe (2004), Käär et al. (1996), and Nitsch et al. (2013)). Since age at first birth differ between populations and cultures (Clark, 2008), one way to test this conjecture would be to explore whether the onset of cooperativeness detection varies between populations and thus with age at first birth. However, it remains highly speculative and replication of this effect is necessary before drawing any strong conclusions.

Reading cooperativeness or trustworthiness from faces appears to improve when people do not consciously try to assess it. Indeed, cooperativeness detection is not always accurate (Jaeger et al., 2020) and it seems that people perform better when information is limited or participants are distracted (Bonnefon et al., 2013, 2017; De Neys et al., 2017; Reinhard et al., 2013). As a result, the actual decisions whether to cooperate or not with unknown individuals are more accurate than the explicit beliefs about whether unknown individuals are cooperative (Bonnefon et al., 2013, 2017). This could potentially explain why we observe that donors' cooperativeness influences women's cooperative decisions but not selfishness ratings.

The chemical compounds involved in the detection of cooperative behaviours remain to be determined. Compounds derived from androgens could be involved (Banner & Shamay-Tsoory, 2018; Huoviala & Rantala, 2013; Perrotta et al., 2016) and future studies should investigate whether the composition of body odours between cooperative and non-cooperative men varies in terms of chemical compounds derived from androgens. In addition to the possibility that body odours represent a cue of an individual's cooperative tendencies (such as high versus low cooperative individuals), body odours may also represent a cue of the cooperative behaviour itself (Gerber et al., 2020). Both possibilities are not mutually exclusive and it seems that both exist in non-human animals (Gerber et al., 2020; Tognetti et al., 2018). In our study, we cannot disentangle whether women detect cues of cooperative action or cues of cooperativeness as we only collected axillary body odours while the participants played a cooperative task. In addition, as altruistic actions trigger positive emotions in the individuals performing them (Nelson et al., 2016), it cannot be excluded that women responded to chemical cues of donor's emotion (de Groot et al., 2015) rather than cues of cooperativeness or cooperative action. These questions should be explored in future studies.

Finally, our results show that the more the odour is perceived as masculine and intense, the less the donor is judged as cooperative. These perceptual differences are however not related to the donor's actual cooperativeness as there is no evidence that high and low cooperative donors smell differently in terms of intensity or masculinity. The influence of masculinity on perceived cooperativeness is in line with what was previously found with faces and voices in both the economic and mating contexts: wider faces and lower pitched voices decrease how cooperative (Knowles & Little, 2016; Little et al., 2013; Stirrat & Perrett, 2010; Tognetti et al., 2013) or trustworthy (O'Connor & Barclay, 2017; Schild et al., 2020) a male partner is judged. Because men with relatively high testosterone levels report lower cooperativeness (Harris et al., 1996), exploit more their partner's trust (Takagishi et al., 2011), act more punitively with other players in economic games (Burnham, 2007), and report a higher number of extra-pair sex partners (Booth & Dabbs, 1993; Fisher et al., 2012), using sexually dimorphic traits (such as face, voice, or body odour) as a cue of cooperativeness and trustworthiness could allow avoiding the potential fitness costs associated with uncooperative and untrustworthy mates or social partners. However, the relationships among testosterone, masculinity and, cooperativeness and trustworthiness, are context-dependent (O'Connor & Barclay, 2017; Reimers & Diekhof, 2015; Schild et al., 2020; Stirrat & Perrett, 2012). Similarly, the influence of olfactory, masculinity, or intensity on cooperativeness judgements is likely to be context-dependent and further investigations are needed to better understand how body odour influences cooperativeness ratings across contexts.

Although this study has a number of strengths, it is also subject to several limitations. First, our sample size of donors is relatively small. Nevertheless, it should be noted that we used state-of-the-art methodology in economics to quantify and categorize individuals according to type (Fischbacher et al., 2001) and we maximized the variability of cooperativeness by selecting the body odours of the donors displaying the most and the least cooperative behaviours in the public good game. Selecting the extremes of cooperation could be nonetheless problematic as the link between cooperation and odour could differ at the extremes compared to the whole sample and future studies should use donors' samples characterized by a more continuous distribution of cooperativeness. In addition, we used only male donors and future investigations should be extended to women. Finally, although our sample size of participants was relatively high ($N = 116$), it should be noted that their age range was limited, precluding any firm conclusion about the effect of women's age on the ability to detect cooperativeness based on men body odours.

To conclude, this study suggests that men's body odours influence perceived cooperativeness and might be used as a valid cue to men's cooperativeness, at least by women and probably in a non-aware manner (since it is unrelated with odour perceptual ratings). Although the replication of our result is needed, our findings pave the way for future investigations examining which chemical compounds are involved, whether women body odours could also be used as cues of cooperation, and whether body odour is a cue of cooperative behaviour itself or of an individual cooperative tendency. Finally, our study suggests that multiple cues of cooperativeness are present in different sensory modalities and that considering them simultaneously might improve the assessment of cooperative behaviour.

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CONFLICTS OF INTEREST

All authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

Melissa Barkat-Defradas (Investigation; Resources; Writing – review & editing) Astrid Hopfensitz (Conceptualization; Funding acquisition; Writing – review & editing) Camille Ferdenzi (Conceptualization; Methodology; Writing – original draft; Writing – review & editing) Arnaud Tognetti, PhD (Conceptualization; Formal analysis; Funding acquisition; Investigation; Methodology; Project administration; Supervision; Visualization; Writing – original draft) Valerie Durand (Investigation; Resources) Dimitri Dubois (Investigation; Resources; Software; Writing – review & editing).

DATA AVAILABILITY STATEMENT

The data and the R script that support the findings of this study are openly available at https://doi.org/10.6084/m9.figshare.16578797.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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