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And I'm feeling good: effect of emotional sweat and perfume on others' physiology, verbal responses, and creativity

Stéphane Richard Ortegón[1,2], Arnaud Fournel[1], Olivia Carlos[2], Keith Kawabata Duncan[3], Kazue Hirabayashi[3], Keiko Tagai[3], Anne Abriat[4], Moustafa Bensafi[1], Bénédicte Race[2], Camille Ferdenzi[1,*]

[1]Lyon Neuroscience Research Center, CNRS UMR5292, INSERM U1028, University Claude Bernard Lyon 1, CH Le Vinatier, Bât. 462 Neurocampus, 95 boulevard Pinel, 69675 Bron Cedex, France
[2]Shiseido Europe Innovation Center, avenue du Général de Gaulle, 45150 Ormes, France
[3]Shiseido Co., Ltd MIRAI Technology Institute, 1-2-11 Takashima, Nishi-ku, Yokohama-shi, Kanagawa, 220-0011, Japan
[4]The Smell and Taste Lab, rue Cramer 6, Geneva 1202, Switzerland

*Corresponding author: Lyon Neuroscience Research Center, CNRS UMR5292, INSERM U1028, University Claude Bernard Lyon 1, CH Le Vinatier, Bât. 462 Neurocampus, 95 boulevard Pinel, 69675 Bron Cedex, France. Email: camille.ferdenzi@cnrs.fr

Abstract

Emotions can be communicated in social contexts through chemosignals contained in human body odors. The transmission of positive emotions via these signals has received little interest in past research focused mainly on negative emotional transmission. Furthermore, how the use of perfumed products might modulate this transmission remains poorly understood. To investigate human positive chemical communication, we explored the autonomic, verbal, and behavioral responses of receivers exposed to body odors of donors having undergone a within-subject positive or neutral mood induction procedure. These responses were compared with those obtained after exposure to the same body odors with added fragrance. Our findings suggest that positive emotions can be transmitted through body odor. They not only induced modifications at the physiological (heart rate) and verbal levels (perceived intensity and familiarity) but also at the behavioral level, with an improved performance on creativity tasks. Perfume did not modulate the physiological effects and had a synergistic effect on the positive body odor ratings (increased perceived differences between the neutral and positive body odor).

Key words: chemical communication, positive emotions, body odor, perfume, emotional contagion

Introduction

A growing body of evidence suggests that there is a communication of social information in humans via cues contained in their biological odors (i.e. chemical communication). This has been observed for information, such as gender (Penn et al. 2007), age (Mitro et al. 2012), health (Olsson et al. 2014), and even sexual arousal (Wisman and Shrira 2020). Information about emotional states can also be transmitted via this medium. For example, presenting the odor of stress collected on "donors" during first-time skydiving (Mujica-Parodi et al. 2009) and during academic examinations (Pause 2004) elicits stress-like responses in the "receivers" (e.g. amygdalin activation, facilitated subliminal perception of angry facial expressions).

However, the question of whether the transmission of positive emotional states is also possible has rarely been explored. Indeed, positive affect has traditionally been neglected in psychological studies (Seligman and Csikszentmihalyi 2000), perhaps because positive emotions are believed to be less differentiated, more idiosyncratic, and more difficult to elicit in laboratory settings. In addition, while negative emotions have an adaptive function for survival by modulating responses to threats, positive emotions are not likely to have such direct vital consequences (Pratto and John 1991). Yet, the impact of positive emotions on health and cognition is major: for example, happier people have more stable marriages, stronger immune systems, and are more creative (Lyubomirsky et al. 2005). The field of human chemical communication is no exception to this general trend, with the most studied emotions being negative ones (see de Groot and Smeets 2017 for a meta-analysis highlighting the capacity of humans to communicate fear, stress, and anxiety via body odor).

Only very few studies have explored "happy" sweat. In the first study, Chen and Haviland-Jones (2000) found that participants could discriminate happy sweat from fear sweat and blanks at an above-chance rate. Zhou and Chen (2009) found that ambiguous facial expressions (morphed face between happy and fearful) were rated as more fearful when

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exposed to the fear sweat, while happy sweat had no effect. They also showed that receivers could discriminate happy sweat from neutral control sweat, but that they were less accurate at doing so than when discriminating fear sweat from the control (Zhou and Chen 2011). Finally, de Groot et al. (2015) found that exposure to happy sweat elicited happier facial expressions and a more global processing style when compared with fearful sweat. This was the first study investigating not only the transmission of positive emotional information to receivers but also the replication of the donor state in the receiver (i.e. emotional contagion; Hatfield et al. 1993), a process that would favor communication between two individuals by achieving internal state synchronization (Semin 2007). Indeed, more global processing style has been robustly linked with positive affect (Isen et al. 1985, 1987; Ashby et al. 1999; Bolte et al. 2003). In sum, evidence for the existence of a chemical communication of positive emotions remains scarce and approaches poorly comparable (explicit vs. implicit).

Furthermore, the fact that in ecological situations body odors are rarely found alone (Allen et al. 2019) has never been considered before in emotional chemical communication studies. Body odors are an integral part of the sensory image we send to others, affecting our social interactions such as in mate choice (Franzoi and Herzog 1987; Sergeant et al. 2005). Trying to "control" these endogenous odors with exogenous ones has taken place almost universally since antiquity, with the use of fragrances, deodorants, or soaps. Fragrances could be chosen to complement our natural body odor and genetics (Milinski and Wedekind 2001; Lenochová et al. 2012), and our individual preferences could be the result of a culture-gene coevolution (Havlíček and Roberts 2013), enhancing some biologically evolved preferred traits. This is particularly relevant for the studies of positive emotions because perfumes are chosen by their wearers to generate positive feelings in themselves and in surrounding people. Perfumes could then act in synergy with endogenous odors to produce such states. However, some studies have also found that perfume addition alters negatively (although does not suppress) the perception of some traits advertised in body odors (Sorokowska et al. 2016). The cultural practice of wearing perfume could thus also have disrupting effects on biologically evolved signals. In sum, the combination between endogenous body odor and an exogenous fragrance may either have a synergic effect, by enhancing relevant characteristics of body odor, or a disruptive effect, by masking or altering them. Because humans usually emit a combination of biological and artificial odors, investigating their interaction is necessary to fully understand chemical communication.

In this study, the primary aim was to test whether positive emotions can be communicated through chemicals emitted by the body and whether they could take the form of emotional contagion. The secondary aim was to investigate to what extent the addition of perfume can modulate this. We collected sweat from male donors twice, once during a positive and once during a neutral mood induction procedure (MIP), and we presented them to female receivers. Although other studies included both a positive and a negative emotional condition (Chen and Haviland-Jones 2000; Zhou and Chen 2009; de Groot et al. 2015), we deliberately chose not to include a negative one in our design. Indeed, we wanted to avoid a potential contrast effect, where the processing of the negative stimuli would be prioritized over the processing of the positive one (negativity bias) and would thus prevent us from observing an effect of the positive condition. Receivers' responses were then monitored at three levels: verbal descriptions, peripheral nervous systems' responses, and performances in behavioral tasks. We hypothesized that the influence of emotional body odors is more likely to remain below the level of consciousness and should be measurable on physiological and/or behavioral responses as shown in previous studies (Li et al. 2007; Ferdenzi et al. 2016). At the behavioral level, we indirectly tested the transmission of positive emotions by using creative problem-solving and divergent thinking tasks. According to the "broaden-and-build" theory (Fredrickson 1998), positive emotions are expected to increase attentional scope and allow greater flexibility of thoughts. We hypothesized first that receivers' autonomic nervous system responses should differ in response to the positive versus the neutral odor, indicating a change in their emotional state (exploratory approach; see Kreibig 2010 for the difficulty to establish a prediction). Second, we hypothesized that if emotional contagion occurred, receivers should be more efficient in creative tasks after smelling the positive body odor than the neutral one. Third, we expected that positive body odors would elicit higher positive verbal ratings (pleasantness, well-being) and stronger and longer sniffs (Mainland and Sobel 2006), although it may very well not be the case because being produced in pleasant circumstances does not necessarily imply that a stimulus yields or possesses pleasant qualities in itself (see also de Groot et al. 2015, for an absence of pleasantness difference across conditions). Lastly, the literature on perfume effects is lacking in the field of chemical communication of emotions and our study thus remains exploratory on this question: perfume could either have no effect on chemical communication, erase it (by masking chemical cues), or enhance it due to a synergy between two emotionally positive messages.

Materials and methods

Odor donor part

Participants.

Donors were 21 males (mean age ± SD: 21.5 ± 2.7 years old), who declared being heterosexual, of European descent, and non-smokers. Male donors were preferred over female donors because they have larger apocrine glands (Doty et al. 1978) and might thus have the potential to produce more emotion-related chemicals. Sexual orientation and ethnicity were controlled because these parameters have been shown to influence body odor perception (Martins et al. 2005; Martin et al. 2010; Prokop-Prigge et al. 2016). All participants (donors and receivers hereafter) provided written informed consent before participation and received monetary compensation. This research was conducted in accordance with the Declaration of Helsinki and was approved by the local Lyon Sud-Est II ethical review board (2014 March 6).

Mood induction procedure.

All donors attended two emotion induction sessions (within-subject design), a positive and a neutral one in random order, 1 day apart. During each induction session, after having been equipped for body odor collection, donors entered a separate room where the experiment was conducted. Induction was performed using short film clips assembled to provide a 30-min sequence for each condition (for further details, see

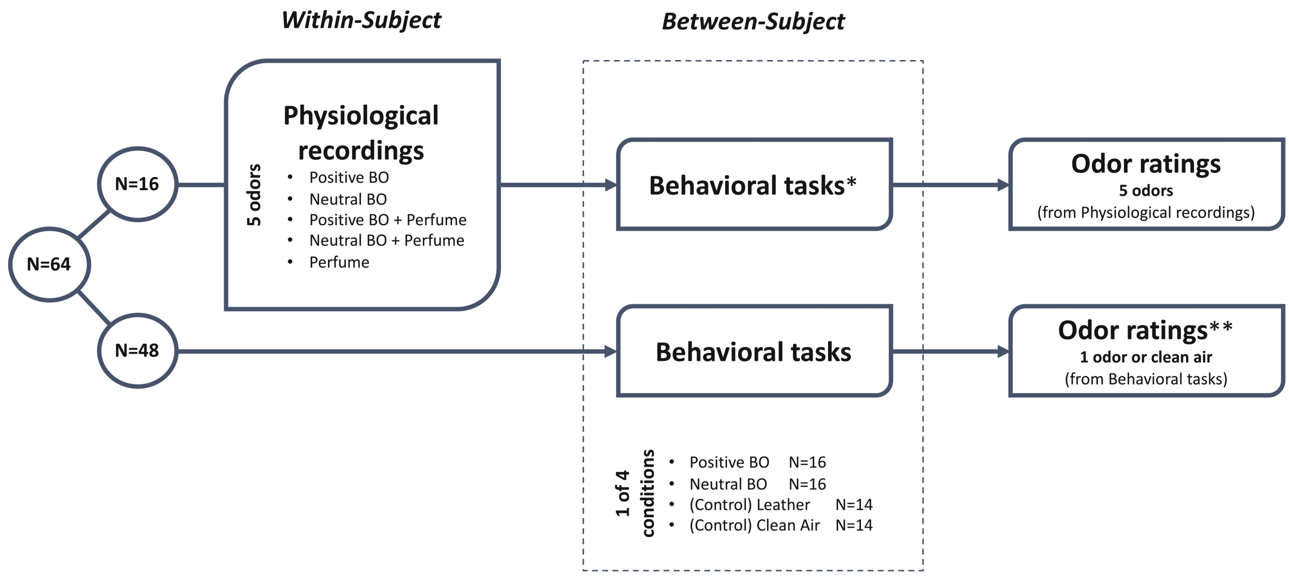

Fig. 1. Summary of the experimental procedure. Participants (*N* = 64) either took part in the physiological recordings followed by the behavioral creativity tasks and the verbal evaluations of odors or only did the behavioral tasks followed by the verbal evaluations. BO: body odor. The data of 4 (*) and 3 (**) participants were lost due to technical issues (Ns on the figure do not include these participants).

Supplementary Methods). Donors seated and watched the videos after the experimenters left the room. For the positive condition, donors were seated in groups of 3 which is believed to increase positive emotions thanks to the interaction and sharing of feelings (as seen in de Groot et al. 2015). They were also given a personalized present (perfume and chocolates) before the induction started (Isen et al. 1987). In the neutral condition, the same donors were seated alone in the room and did not receive any present. To measure the emotional response of the donors during the MIP, we asked them after each excerpt to rate how amused, afraid, happy, sad, surprised, disgusted, angry, neutral, and calm they felt during the clips using a paper-and-pencil 10-cm continuous scale from 0 (not at all) to 10 (extremely). Ratings were recorded in centimeters to the nearest 0.1 cm.

Body odor collection.

From 2 days before the first odor collection, donors followed a protocol to prevent odor contamination (details can be found in Supplementary Methods). On collection days, donors had to take a shower just before coming to the laboratory. Experimenters used odorless tape (Urgopore microporous, Urgo) to attach 10 × 10 cm sterile cotton gauze pads (Sylamed) under each donor's armpit, while wearing nitrile gloves. Donors were then asked to put on a cotton t-shirt (Decathlon, previously washed with a non-perfumed detergent) instead of their personal clothes to prevent odor contamination. At the end of the emotion induction procedure, pads were removed, cut into 1 × 3 cm strips taken from the central area of the pads, placed in aluminum foil, and then in one ziplock bag per donor and per emotion condition (Positive/Neutral), before being stored at −32°C.

Sample selection for odor presentation.

A selection of the samples was carried out before conducting the following step (presentation to the receivers) based on the emotional ratings provided by the donors after the video clips (see "Mood Induction Procedure" section). As we noticed that emotional induction was not equally efficient in all donors (i.e. average happiness ratings collected during the positive MIP ranged from 2.7 to 9.4 on a scale from 1 to 10), we selected only the body odor samples of the donors who were best responsive to the MIP, to maximize our chances of presenting a chemosignal of positive emotion. Eight individuals fitted the selection criteria of (i) average happiness ratings >5 in the positive MIP and (ii) average happiness ratings ≤5 in the neutral MIP and were thus selected. The samples of the remaining ones were not used in the following step of the experiment. Importantly, the fact that body odor samples were limited in quantity and not re-usable (due to their instability) constrained the number of receivers that we were able to include in the study.

Receiver part

Participants.

Receivers were females who declared being heterosexual, of European descent, non-smokers, and using hormonal contraception. They reported not suffering from any psychological, cardiac, respiratory, or olfactory diseases. Female receivers were preferred over male receivers because they have a better sense of smell and greater sensitivity to chemosignals of emotion (Brand and Millot 2001; de Groot et al. 2014). Sexual orientation and ethnicity were controlled for the same reasons as in donors, and hormonal contraception was also added to limit olfactory variations due to menstrual cycle in spontaneously ovulating women (Navarrete-Palacios et al. 2003). A total of 64 women took part (mean age ± SD: 21.6 ± 2.6 years old), either in both the physiological and behavioral tasks (*N* = 16 of them) or only in the behavioral task (*N* = 48 of them) (see distribution in Fig. 1). Physiological responses were recorded separately from the behavioral responses because for physiological recordings participants need to be motionless and calm to collect reliable measurements, which was not the case during the creativity tasks where they were standing and/or moving freely. Both groups did verbal evaluations of the odors they were exposed to either during the physiology session (5 odors) or during the behavioral session (1 odor). Note that some data were lost due to technical problems (see details in Fig. 1).

Olfactory stimuli.

In the physiological recording session, all receivers were presented with 5 odor stimuli: body odors sampled during the positive and neutral MIP with or without perfume added and perfume alone. The stimuli were presented 3 times each, in 3 blocks comprising the 5 stimuli in a pseudo-randomized order (interleaved with a clean air condition, never in first or last position, to limit olfactory fatigue). These 3 blocks were presented alternatively with blocks of other types of odors (non-body origin), used for another purpose, and not analyzed here.

In the behavioral tasks, receivers were exposed either to positive body odor samples, neutral body odor samples, or to the odor of leather (Firmenich SA) chosen because of its a priori perceptual similarities with human odor or clean air. As a between-subject design was used for the behavioral tasks, the number of different conditions to compare was limited. We therefore decided to include only the conditions related to our main hypothesis (positive vs. neutral body odor) and controls, not those related to our secondary question (effect of perfume). With the control odor of leather, we wanted to explore if the mere presence of an odor resembling human body odors could affect creativity performances. We did not do so in the physiological recordings, since the number of conditions was high and it is already known that the presence of an odor influences physiological parameters.

Preparation of the body odor samples was performed by putting the frozen 1 × 3 cm sweat pad strips obtained in donors at room temperature 1 h before the start of the receivers' session. To reduce the effects of interindividual variability, four strips from four different randomly selected donors, combining left or right armpits chosen at random (see Ferdenzi et al. 2009), were placed into a U-shaped Pyrex tube (VS technologies, France; volume: 10 mL; length: 50 mm; external diameter: 14 mm). Each positive composite body odor and neutral composite body odor was prepared twice, to allow the addition of 2 drops of a male perfume in one of the two samples. The perfume (concentrate of commercially available fine fragrance diluted in dipropylene glycol, 10% concentration) was chosen among other perfumes because it received the highest scores of pleasantness in a preliminary test ($N = 24$, 16 women). The "perfume alone" stimulus was obtained by putting 2 drops of the same perfume in a U-tube containing 4 clean 1 × 3 cm strips of gauze. The leather and clean air conditions were obtained by placing 2 mL solution (leather diluted in dipropylene glycol, 20% concentration, or dipropylene glycol alone from Sigma-Aldrich for the clean air condition) in U-tubes containing scentless polypropylene fabric (twice 1 × 6 cm; 3M, Valley, NE, USA). Olfactory stimuli were diffused at an airflow of 1.5 L/min using a computer-controlled olfactometer with time-controlled stimulus onset and were delivered to the participant's nose through a nasal cannula.

Physiological recordings.

Heart rate and skin conductance from 16 of the 64 receivers were measured with Equivital EQ02 + Lifemonitor system (Equivital, Cambridge, UK) and amplified by a Dual Bio Amp from AD Instruments (Dunedin, New Zealand). The acquisition software was LabChart v8.1.5 (AD Instruments, Dunedin, New Zealand). Signals were analyzed in a range of 10-s pre- and post-stimulus for the heart rate (as in Delplanque et al. 2009) and 10-s post-stimulus for the skin conductance (to get only the event-related responses occurring within a few seconds after the stimulus and not the non-specific ones; Dawson et al. 2007; Jacquot et al. 2018). High-pass and low-pass filters were added along with smoothing algorithms to eliminate artifacts. A local mean of the points during these 10-s windows was calculated using python scripts developed in-house. For *heart rate*, the mean values of the frequency were computed. For *skin conductance*, responses were detected using the algorithm described in Kim et al. (2004) and then counted in the 10-s post-stimulus window. The basic response basic peak was also measured, as the maximal value of the signal during the very same window. Sniffing behavior of the receivers was also recorded (as in Ferdenzi et al. 2014, 2015). This was performed by means of a nasal cannula positioned in both nostrils and connected to an airflow sensor (AWM720, Honeywell, France). This system was developed in-house to allow us (i) to synchronize odor delivery with the participants' respiration and (ii) to record sniffing behavior. The sniffing signal was amplified and digitally recorded at 256 Hz using LabVIEW software. The maximum airflow (highest point), the area under the airflow curve (volume inspired), and the duration of the sniff (time between the inhalation starting point and the point where the flow returned to zero) were computed for the first sniff following odor presentation.

Behavioral tests: creativity and problem-solving.

Almost all receivers took part in two behavioral tasks. The first task was the *Guilford's Alternate Uses Task* (Guilford 1967). In this test, the participants are asked to list as many non-obvious uses as possible for common objects in a limited time and their answers are given scores in terms of fluency, originality, elaboration, and flexibility (for details about scoring and examples, see Supplementary Methods). Here, receivers were given 2 min per object, which were: *brick*, *barrel*, *pencil*, *shoe*, *car tire*, *hanger*. The second task was *Duncker's Candle Problem* (Duncker 1945). The receivers were brought in front of a table where they could find a box of tacks, a candle, and a box of matches. They were asked to find a way to affix the candle to the wall with the available objects (on a corkboard) in such a way that it would burn without dripping wax on the table or on the floor. The problem was considered as solved if the receivers emptied the book of matches, used the tacks to nail the box to the corkboard, and made the candle stand inside the empty box. They were given 10 min to solve this problem and the time they spent to find the solution was scored in seconds. The participants who did not find the solution in the maximum allocated time were not taken into account in the time analysis.

Verbal measures.

At the end of the experiment (after the creativity tasks), the female receivers were asked to evaluate odors on 9-point Likert scales (1 = not at all, 9 = extremely) for how intense, pleasant, and familiar they were, and for the extent to which they caused well-being. These evaluations were required for the single odor to which receivers were exposed during the behavioral tasks (i.e. either the positive body odor, the neutral body odor, leather, or clean air). The 16 participants who underwent the physiological recording were asked to rate the five odors to which they were exposed (i.e. the positive body odor with and without perfume, the neutral body odor with and without perfume, perfume alone) and clean air.

Procedure.

The physiological recording session took part first (before the creativity tasks, for the 16 participants who took part in both types of tasks). The receivers were equipped with the measurement sensors and the nasal cannula and were seated in a comfortable chair in a quiet and well-ventilated room with standardized conditions of light (no windows) and temperature. They were also given white noise, sound-canceling headphones. The experiment started with 2 min of rest to provide a baseline, then the first odor was sent with the olfactometer for 5 s, on an expiration to ensure that it would enter the nostrils at the beginning of the next inspiration. The next 60 s were odorless to return to the baseline and to avoid olfactory adaptation. Then, the next odor was sent and so on (in a pseudo-randomized order) until all odors were sent (first block out of three). After a 5-min break, the behavioral tasks started. In the behavioral tasks, the odor condition was attributed randomly, the receivers being blind with regard to the nature of the odor. During the whole duration of the behavioral session, the odor (or clean air) was sent to the receivers' noses by the olfactometer through a nasal cannula, for 5 s every 30 s. Finally, the receivers rated the odor(s) on verbal scales and were thanked for their participation after a small brief about the purpose of the experiment.

Data analysis

Preparation of the data.

The receivers' physiological variables that we analyzed were: (i) mean heart rate difference between the 10-s post-stimulus window and the 10-s pre-stimulus window (beats per minute, post- minus pre-), (ii) log-transformed characteristics of the first sniff during odor presentation, namely sniff volume (area under the curve [AUC], arbitrary unit) and sniff duration in seconds (between inhalation starting point and the point where the sniff's flow returned to zero), (iii) characteristics of the skin conductance response, namely the log-transformed skin conductance (SC) basic peak (in microsiemens, maximum value of the signal during the 10-s post-stimulus window minus value of the signal at stimulus onset), and the number of SC responses (during the 10-s post-stimulus window). The odor ratings of intensity, pleasantness, familiarity, and well-being collected after stimulus presentation were used as such. Finally, we analyzed the receivers' performances in the creativity tasks, represented by Alternate Uses Task (AUT) scores of fluency, originality, elaboration, and flexibility (see "Behavioral tests: creativity and problem-solving" section) and time to solve the Candle Problem (in seconds). The AUT scores were attributed in a double-blind fashion by two independent judges. The scores of both judges on each variable were highly correlated ($r = 0.70$–0.98) and thus averaged.

There were missing data described as follows. Due to backup issues, 1 block (repetition) out of 3 was lost for 2 receivers (2 out of 48 blocks in total, 4.17%) for the physiological recordings. Due to technical issues, the responses of 4 out of 64 participants were lost for the behavioral tasks, and of 3 out of 48 participants for the odor ratings by the subgroup who only did the behavioral tasks (see Fig. 1).

Statistical analyses.

The physiological variables and verbal ratings made during the physiology session have been analyzed with linear mixed-effects models using the *lme4* package (Bates et al. 2015) in R (R Core Team 2019, RStudio version 3.6.1). Fixed factors were Condition (Positive/Neutral body odor) and Perfume (With/Without). Subject was used as a random factor. Repetition was also included as a random factor but not retained since it did not significantly improve the models. Model selection was used to select the best models, using the *anova* function. Visual inspection of residual plots did not reveal any obvious deviations from homoscedasticity or normality. *P*-values were obtained using Kenward–Roger approximation in the *anova* function of *lmerTest* package in R (Kuznetsova et al. 2017) and non-significant interactions were removed to keep only the best model including the main effects. Post hoc contrasts were performed using the *multcomp* function of the *emmeans* package in R (Lenth et al. 2020).

The number of SC responses was analyzed with three chi-square tests to evaluate the effect of Condition and Perfume (for all trials together, and for trials with and without Perfume separately). Because the size of some cells of the contingency table was <5, a Yates' correction was applied.

For both creativity tasks, we conducted one-tailed *t*-tests because a clear a priori hypothesis was postulated before data collection: smelling positive body odors is expected to increase positive affect and thereby creativity (Isen et al. 1987), compared with smelling neutral body odors. Our target comparison being the positive versus neutral conditions comparison, preliminary analysis comparing performances in the presence of the neutral body odor ($N = 16$) with those in the non-targeted conditions was conducted and revealed no significant differences: neither between neutral body odor and clean air ($N = 14$; AUT Fluency: $P = 0.328$; AUT Originality: $P = 0.412$; AUT Elaboration: $P = 0.910$; AUT Flexibility: $P = 0.439$; Candle Problem: $P = 0.144$) nor between neutral body odor and leather ($N = 14$; AUT Fluency: $P = 0.580$; AUT Originality: $P = 0.297$; AUT Elaboration: $P = 0.510$; AUT Flexibility: $P = 0.443$; Candle Problem: $P = 0.117$). Consequently, in the "Results" section, we focus only on the target comparison between positive ($N = 16$) and neutral body odor ($N = 16$). A chi-squared test was also conducted to compare the frequency of succeeded versus failed attempts during the Candle Problem in the positive versus the neutral condition.

Finally, the odor ratings made after the behavioral tasks (1 odor per participant) were analyzed using Kruskal–Wallis tests. It must be noted that the neutral body odor did not differ from leather or clean air on ratings of familiarity, pleasantness, and well-being (all *P*s > 0.05). Only leather intensity was rated higher than for all the other odors ($X^2(3) = 22.939$, $P < 0.001$).

Results

Physiological responses

After smelling the positive body odor, receivers had a decrease in mean heart rate (mean ± SD: −0.957 ± 2.85) which was not found after smelling the neutral body odor (−0.050 ± 2.81; Fig. 2), as shown by a significant effect of the Condition (Positive vs. Neutral: $P < 0.05$; 95% confidence interval

[CI] = [−1.67, −0.14]; Table 1). The log-transformed Skin Conductance basic peak was not found to be modulated by Condition (Positive: −0.860 ± 0.80; Neutral: −0.916 ± 0.78; $P > 0.05$, Table 1) or Perfume (With: −0.849 ± 0.79; Without: −0.949 ± 0.78; $P > 0.05$, Table 1). Neither was the number of SC responses (total neutral: N = 61/27/4/0 for 0/1/2/3 responses, respectively, and total positive N = 60/18/12/2; $X^2(3) = 7.808$, $P > 0.05$) even when analyses of only trials with perfume ($X^2(3) = 5.303$, $P > 0.05$) and without perfume ($X^2(3) = 3.302$, $P > 0.05$) were conducted. Regarding the olfactomotor responses, larger sniff volumes and longer sniff durations were found when body odors were presented with perfume (log-transformed volume: With perfume −0.35 ± 0.33 and Without −0.44 ± 0.30; $P = 0.002$; 95% CI = [0.03; 0.13]; log-transformed duration: With 0.27 ± 0.20 and Without 0.20 ± 0.14; $P < 0.001$; 95% CI = [0.04; 0.11]; Table 1), which is usually observed with more pleasant odors.

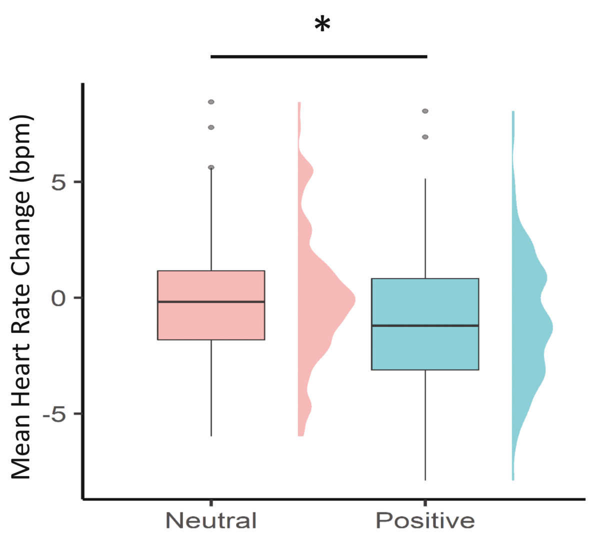

Fig. 2. Female receivers' autonomic responses during the presentation of male body odors collected during Positive and Negative mood induction (N = 16). Boxplot of mean heart rate change between the 10-s post-stimulus and the 10-s pre-stimulus window, in beats per minute (bpm) for the neutral and positive conditions (*$P < 0.05$, see statistics in Table 1).

Table 1. Physiological and olfactomotor responses as a function of Condition (Positive vs. Neutral body odor) and Perfume (With vs. Without) (N = 16).

Variable	Main effects and interactions	Statistics	
Heart rate	Condition	$F(1,166.03) = 5.496$	$\mathbf{P = 0.020}$
	Perfume	$F(1,166.03) = 0.334$	$P = 0.564$
	Condition × Perfume	–	–
Skin conductance basic peak	Condition	$F(1,61.237) = 0.044$	$P = 0.835$
	Perfume	$F(1,60.352) = 1.360$	$P = 0.248$
	Condition × Perfume	–	–
Sniff volume	Condition	$F(1,166) = 0.0004$	$P = 0.984$
	Perfume	$F(1,166) = 9.788$	$\mathbf{P = 0.002}$
	Condition × Perfume	–	–
Sniff duration	Condition	$F(1,166) = 0.028$	$P = 0.866$
	Perfume	$F(1,166) = 21.090$	$\mathbf{P < 0.001}$
	Condition × Perfume	–	–

Results of the linear mixed models with Condition and Perfume as fixed factors and Subject as random factor (intercept). For all variables, the best model was *Variable ~ Condition + Perfume* + (1|*Subject*); therefore, the effect of the interaction was not tested (see Materials and methods section). *P*-values <0.05 are in bold.

When asked to explicitly evaluate the stimuli they were exposed to during the physiological recordings, the participants rated the positive body odors as more intense than the neutral body odors (Positive: 4.09 ± 2.59, Neutral: 3.16 ± 2.11; Main effect of Condition: $P < 0.05$, 95% CI = [0.29; 1.58]; Table 2). The Condition × Perfume interaction was also significant ($P < 0.05$, Table 2) because positive body odors were rated as more intense only when combined with perfume (Fig. 3). They were also rated as more familiar (Positive: 4.5 ± 2.63; Neutral: 3.47 ± 2.17; Main effect of Condition: $P < 0.05$; 95% CI = [0.14; 1.92], Table 2; Fig. 3). Finally, when the stimuli were presented with perfume, they were perceived as more pleasant (With perfume: 4.91 ± 1.78; Without perfume: 3.50 ± 2.20; $P = 0.002$; 95% CI = [0.57, 2.25]; Table 2), more intense (With: 5.53 ± 1.83; Without: 1.72 ± 0.89; $P < 0.001$; 95% CI = [3.17, 4.46]; Table 2), more familiar (With: 5.25 ± 2.13; Without: 2.72 ± 2.08; $P < 0.001$, 95% CI = [1.64, 3.42]; Table 2), and tended to elicit higher levels of well-being (With: 4.46 ± 1.74; Without: 3.67 ± 2.22; $P = 0.06$; 95% CI [0.04, 1.67]; Table 2).

Behavioral responses

Receivers' responses in both behavioral tasks revealed consistent results. In the first task, the AUT, the group exposed

Table 2. Odor ratings as a function of Condition (Positive vs. Neutral body odor) and Perfume (With vs. Without) (N = 16).

Variable	Main effects and interactions	Statistics	
Pleasantness	Condition	$F(1,46) = 0.454$	$P = 0.504$
	Perfume	$F(1,46) = 11.340$	$\mathbf{P = 0.002}$
	Condition × Perfume	–	–
Well-being	Condition	$F(1,46) = 0.541$	$P = 0.466$
	Perfume	$F(1,46) = 3.657$	$P = 0.062$
	Condition × Perfume	–	–
Intensity	Condition	$F(1,45) = 8.508$	$\mathbf{P = 0.005}$
	Perfume	$F(1,45) = 140.710$	$\mathbf{P < 0.001}$
	Condition × Perfume	$F(1,45) = 5.445$	$\mathbf{P = 0.024}$
Familiarity	Condition	$F(1,45) = 5.476$	$\mathbf{P = 0.024}$
	Perfume	$F(1,45) = 32.992$	$\mathbf{P < 0.001}$
	Condition × Perfume	–	–

Results of the linear mixed models with Condition and Perfume as fixed factors and Subject as random factor (intercept). The effect of the interaction was tested only when the interaction was present in the best model (see Materials and methods section). *P*-values <0.05 are in bold.

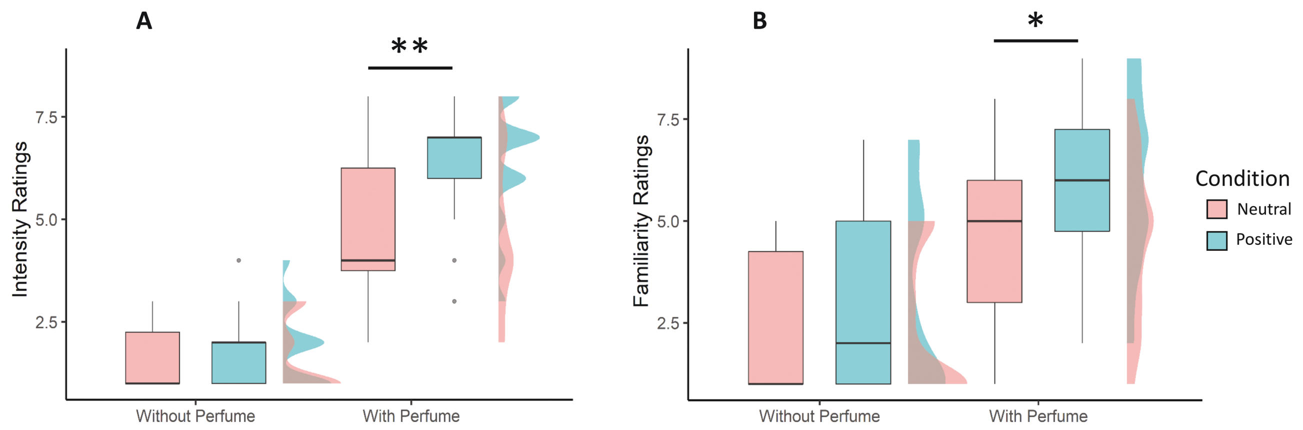

Fig. 3. Female receivers' verbal responses during the presentation of male body odors collected during Positive and Neutral mood induction ($N = 16$). (A) Boxplot of the intensity ratings (1–9) for neutral and positive body odors, without and with perfume (Condition × Perfume interaction: $P < 0.05$, see statistics in Table 1). (B) Boxplot of the familiarity ratings for neutral and positive body odors, with and without perfume. *$P < 0.05$, **$P < 0.01$, results of post hoc contrasts between Positive and Negative Conditions.

to positive body odors found significantly more alternative uses (higher Fluency) than the group receiving the neutral body odor (Positive: 24.37 ± 10.87 words, Neutral: 16.50 ± 5.83, $t(30) = 2.553$, $P = 0.008$, 95% CI = [1.58, 14.17]; Fig. 4A). They also displayed higher Flexibility, i.e. they used more varied categories of uses (Positive: 3.33 ± 1.23 categories, Neutral: 2.54 ± 0.78, $t(30) = 2.152$, $P = 0.018$; 95% CI = [0.04, 1.53]; Fig. 4B). Both groups did not differ on the Originality ($t(30) = 1.290$, $P = 0.103$; 95% CI = [−0.06, 0.27]) or Elaboration ($t(30) = 0.651$, $P = 0.260$; 95% CI = [−0.27, 0.14]) of their responses. In the second task, participants had to solve The Candle Problem in a limited time. Out of 16 participants in each group, 9 found the solution in the allowed time in the neutral condition (7 failed) and 7 in the positive condition (9 failed). This difference between the two observed frequencies was not significant ($X^2(1) = 0.125$, $P = 0.724$). Among the participants who did find the solution, those who were exposed to the positive body odor found the solution faster than those who smelled the neutral one (Positive: 230.43 ± 144.75 s, Neutral: 389.67 ± 177.22; $t(13.94) = 1.978$, $P = 0.037$; 95% CI = [−332.01, 13.53]; Fig. 4C). Let us recall that the effect of perfume was not investigated in these tasks.

When asked about their explicit evaluation of the odor they had just been exposed to, no differences were found between the positive and the neutral body odor regarding intensity, familiarity, pleasantness, and well-being (all *P*s > 0.05).

Discussion

The aim of this research was to explore whether positive emotions could be communicated between humans through body odors and if this transmission could take the form of an emotional contagion between an emitter and a receiver. We also explored for the first time whether perfume could modulate emotional contagion, since ecologically speaking body odors are uncommonly found alone. We showed that exposure to chemosignals of positive affect collected in donors impacted receivers' responses, in line with our hypotheses and previous work (Chen and Haviland-Jones 2000; de Groot et al. 2015). Moreover, there was concordant evidence that positive affect may transfer from one individual to another through this route (emotional contagion, Hatfield et al. 1993) since we recorded increased performances in two different creativity tasks in the presence of the positive body odor. Indeed, it has been extensively documented that performance on those tasks is affect-dependent and facilitated if one is experiencing positive affect (Isen et al. 1985, 1987). Finally, perfume increased stimuli pleasantness and had a synergic effect by revealing differences in perceived intensity between positive and neutral body odors that did not reach conscious perception in the absence of perfume.

At the physiological level, heart rate was modulated by the positive body odors compared with the neutral ones. There was a deceleration of the mean heart rate after participants smelled the positive body odor: such a decrease has been reported before with odors considered as pleasant (Alaoui-Ismaili et al. 1997; Bensafi et al. 2002). This may be related to the positive valence of the odor, even though it did not reach awareness since the positive odor did not receive higher pleasantness ratings. Heart rate deceleration has also been linked before to positive emotional states, through the measure of vagal tone. Vagal tone is a core component of the parasympathetic nervous system activity (Porges 1995); it decreases heart rate and predicts increases in positive emotions (Kok and Fredrickson 2010). Reciprocally, increases in positive emotions predict heightened vagal tone (Kok and Fredrickson 2010). This provides support to the fact that positive emotions have a role in countering the deleterious effects of negative emotions (e.g. increased blood pressure and heart rate in response to stressors) by acting as a brake and by allowing the organism to return to a physiological baseline (Steptoe et al. 2005; see also the "undo" effect of positive emotions: Fredrickson 1998). The fact that most participants (97%) reported not to smelling anything when presented with body odors alone and that no perceived differences were found in the "without perfume" condition (they were forced to provide ratings anyway) suggests that chemosignals of positive affect may alter physiology and cognition at a subliminal level. This is consistent with previous studies on human chemical communication, where body odors are consistently rated as very low in intensity, if not perceived at all (Mujica-Parodi et al. 2009), and have subliminal effects on perception and behavior.

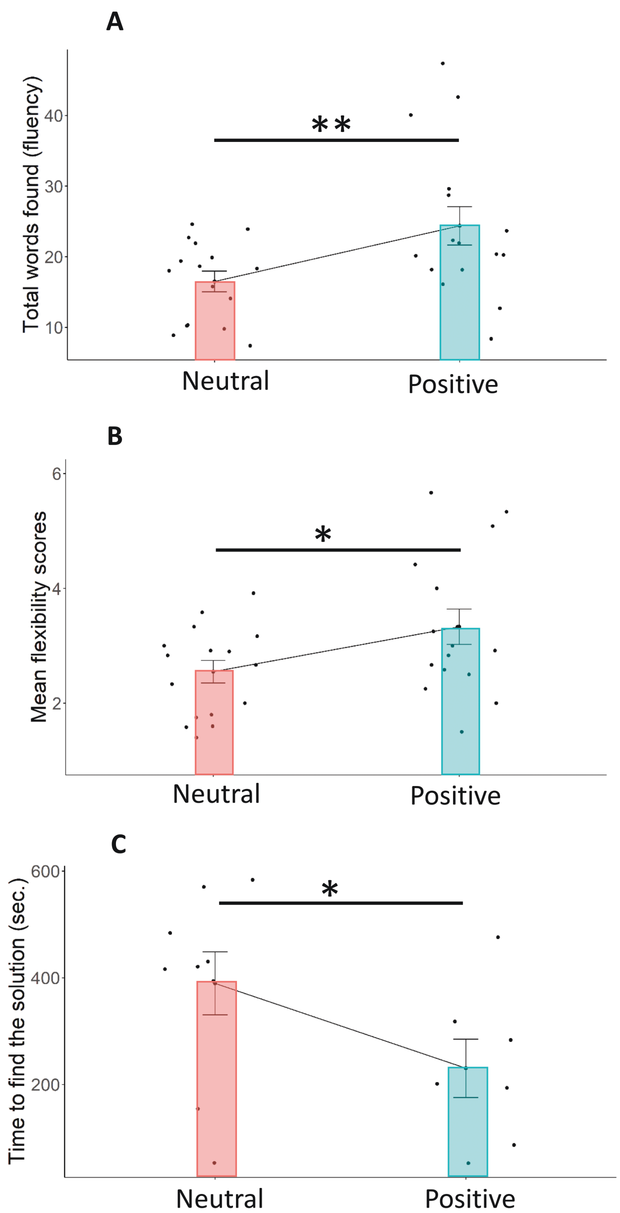

Fig. 4. Female receivers' behavioral responses in creativity tasks during the presentation of male body odors collected during either a Positive or a Neutral mood induction. (A) Total number of words found per participant in the Alternate Uses Test in the presence of the positive and neutral body odors ($N = 16$ per condition). (B) Mean flexibility scores for the AUT in the presence of the positive and neutral body odors ($N = 16$ per condition). (C) Mean time to find the solution to the Candle Problem, in seconds (in participants who successfully solved the problem: $N = 9$ out of 16 for the neutral condition, $N = 7$ out of 16 for the positive condition). Means ± SEM in all graphs. $^*P < 0.05$, $^{**}P < 0.01$.

Most importantly, when using creativity-related tasks as an indirect measure of positive affect transfer, we showed that the group smelling the positive body odor was significantly more efficient in these tasks than the neutral odor group. They had higher fluency and higher flexibility scores in the AUT and found the solution to the Candle Problem more quickly. Note that for the AUT, originality and elaboration scores remained unaffected by Condition, probably due to the time constraints, which can have detrimental effects on creativity (Amabile 1979). Also, participants in the positive group did not find the solution to the Candle Problem more often than the control group (perhaps because the allowed time—fixed for experimental reasons—might not have been sufficient to discriminate between them) but when they did find a solution, they were significantly faster. This has been observed before: after a positive emotional induction, medical students do not solve medical problems more often than the control group, but they do it faster and put more effort into solving them (Isen et al. 1991). Taken together, the physiological and behavioral results are consistent and suggest that emotional contagion may have occurred at two levels in the experimental setting, even though the design only provides indirect evidence of it. Respectively at the physiological and behavioral levels, low heart rate (Ekman et al. 1983) and better performances at creative problem-solving tasks (Isen et al. 1987) have been linked with experiencing happiness or positive affect. This is the first time an effect on creativity has been shown in receivers exposed to emotional body odors.

Regarding the role of fragrance that we tested only on ratings and physiological responses (not behavior), we found that adding perfume to body odors did not interfere with heart rate and skin conductance responses, but that it had a synergic effect with the positive emotion at the perceptual level. Indeed, perfume increased positive body odor intensity compared to the neutral body odor, while both odors were perceptually similar (and mostly not consciously perceived at all) when presented unperfumed. This suggests—for the first time in the context of emotional communication—that fragrance use may not be detrimental to chemical communication within human social networks, in accordance with previous findings on discrimination between individuals (Allen et al. 2015). This points out the fact that, even if the olfactory background changes, the emotional chemosignals contained in body odors may have such a relevance that they still remain effective. Additionally, our results show that perfume could even, in some cases, facilitate the perception of some characteristics inherent to the emotional body odor (at least with the particular perfume and concentration we used). This facilitating effect could be specific to the communication of positive states. Here, body odors received higher positive ratings (pleasantness, and a tendency for well-being) when mixed with perfume, which was corroborated by a more intense sniffing behavior (sniff duration and volume) than without perfume; therefore, the synergic effect we found might only take place if the intrinsic qualities of the exogenous (perfume) and endogenous (body) odors are consistent, allowing an easier discrimination by repetition of coherent information without redundancy. In the future, whether such a perceptual synergy would influence the behavioral outcomes we found in creativity tasks should be tested.

To conclude, this study constitutes a significant step forward in understanding the chemical communication of positive emotions in humans and on its modulation by exogenous fragrances. We provided evidence in favor of the presence of chemosignals of positive emotions in human body odor, of the modulation of receivers' physiology and behavior in response to these chemosignals and of a likely replication of the positive emotional state in the receivers. Future research is needed to confirm these conclusions. For example, because of technical constraints, our study had to be conducted in a single-blind fashion: although maximum precautions were taken to prevent observer-expectancy, a double-blind design is recommended in the future. In addition, as an initial approach of the question, we limited our study to female receivers responding to male odors of about the same age. Investigating other combinations of sex (and age) characteristics would provide a more ecologically valid picture. Sample sizes were quite small in our study, and future investigations should enhance statistical power by using larger sample sizes. Regarding perfume, investigating its effects on negative emotion communication could be useful, especially in situations where disruption of such a communication could be beneficial (e.g. stress contagion during examinations or in confined situations, etc.). Finally, future research could extend the investigation in social situations closer to real contexts, in which olfactory signals co-occur with other sensory stimuli and in which multisensorial integration takes place. While negative emotional contagion serves the adaptive function of alerting conspecifics about dangerous situations, positive emotional contagion also has adaptive advantages: it allows communities to build social interaction, inciting them to explore new approaches about situations and ideas, and promoting global communication. Sharing positive emotions helps us build resources and contributes to defining us as a social species.

Supplementary material

Supplementary material is available at *Chemical Senses* online.

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Author contributions

Conceptualization, SRO, CF, BR, and MB; methodology, SRO and CF; software, SRO and AF; validation, CF and MB; formal analysis, SRO; investigation, SRO; resources, CF, AF, OC, BR, and MB; data curation, SRO; writing—original draft preparation, SRO; writing—review and editing, CF, AF, OC, KKD, KH, KT, AA, MB, and BR; visualization, SRO and CF; supervision, CF, BR, and MB; project administration, CF and BR; funding acquisition, CF, MB. All authors have read and agreed to the published version of the manuscript.

Conflict of interest

All authors declare no conflicts of interest. This work results from a collaboration between the Lyon Neuroscience Research Center and the Shiseido company. The data collection and statistical analyses were exclusively led by the authors from the Lyon Neuroscience Research Center.

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