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Different armpits under my new nose: Olfactory sex but not gender affects implicit measures of embodiment☆

Marte Roel Lesur [a,e,g,*], Yoann Stussi [b,c], Philippe Bertrand [d,e], Sylvain Delplanque [c], Bigna Lenggenhager [a,f,*]

[a] Department of Psychology, University of Zurich, Zurich, Switzerland
[b] Department of Psychology, Harvard University, Cambridge, MA, USA
[c] Swiss Center for Affective Sciences, University of Geneva, Geneva, Switzerland
[d] Institute of Psychology, Faculty of Humanities and Social Sciences, Université de Paris, France
[e] BeAnotherLab, Spain
[f] Department of Psychology, University of Konstanz, Konstanz, Germany
[g] Department of Computer Science and Engineering, Universidad Carlos III de Madrid, Spain

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ABSTRACT

Conflicting multisensory signals may alter embodiment to produce self-identification with a foreign body, but the role of olfaction in this process has been overlooked. We studied in healthy participants how sex (male and female sweat odors) and gender (male and female cosmetic scents) olfactory stimuli contribute to embodiment. Participants saw, on a head mounted display, the first-person perspective of a sex mismatching person. Synchronous visuotactile stimulation was applied to enhance illusory embodiment. Simultaneously, they smelled either sex- or gender- congruent or incongruent stimuli. We assessed implicit (skin conductance responses to visual threats) and explicit (questionnaire) measures of embodiment. Stronger responses to threat were found when participants smelled the sex-congruent compared to the sex-incongruent odor, while no such differences were found for the cosmetic scents. According to the questionnaire, embodiment did not differ between conditions. Post-experimental assessment of the presented cues, suggest that while both sweat odors were considered generally male, cosmetic scents were not. The presented scents were generally not associated with the embodied body. Our results suggest that sex-related body odors influence implicit but not explicit aspects of embodiment and are in line with unique characteristics of olfaction in other aspects of cognition.

1. Introduction

We often seem to disregard the role of olfaction when scientifically studying human self-identity. This contrasts with evidence from nonhuman animals. For instance, dogs, while not passing the well-known mirror-self recognition task (Gallup, 1970), have been shown to recognize their own scent in an olfactory equivalent of the task (Horowitz, 2017). As is the case with canines, odors are an integral part of animal interactions and guide behavior across species. In animal research, it has been long accepted that odors mediate basic behaviors such as kin recognition, or sexual identification and attraction (Russell, 1976). By comparison, human capacity to extract biological and social cues from body odors has long been dismissed outright (Lundström & Olsson, 2010). Yet, we permanently produce and process body odors, even if largely on a subconscious level (Perl et al., 2020; Prehn et al., 2006; Zhou & Chen, 2008, 2009). These odors seem to play a role in the perception of self and others and in self-other distinction (Perl et al., 2020). Humans can indeed distinguish their own body odor from that of other persons'. Body as compared to non-body odors in humans are linked to specific neural substrates including multisensory integration areas like the angular gyrus (Lundström et al., 2008), a network associated with bodily self-perception (Blanke et al., 2002, 2004). One's own body odor is considered a quite stable and unique "signature" of the bodily self (Lundström & Olsson, 2010), and it has been argued that

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* Correspondence to: 14, Box 9, Zurich 8050, Switzerland.
E-mail addresses: marte.roel@psychologie.uzh.ch (M.R. Lesur), bigna.lenggenhager@uni-konstanz.de (B. Lenggenhager).

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humans partake in self-smelling behaviors as a way of reassuring the self (Perl et al., 2020). In fact, human body odors deliver a great range of information, from individual/kin identity, age, illness, reproductive state, attraction, to transient emotional states (Chen & Haviland-Jones, 2000; Ferdenzi et al., 2020; Mallet & Schaal, 1998; Porter, 1998, 1998; Semin & Groot, 2013, for a review).

It seems reasonable to assume that one's own body odor is integrated with other senses (e.g., visual, tactile, motor, auditory, interoceptive, vestibular) to create and maintain a coherent sense of a bodily self. Bodily self-consciousness is thought to depend on a continuous integration and updating of signals from various modalities and prior beliefs (Apps & Tsakiris, 2014; Blanke et al., 2015). It has been studied by providing participants with spatiotemporally congruent multisensory signals, which are mediated by top-down associations with the embodied object. Stimulation to both their hidden own and a seen virtual or fake full-bodies or body parts results in illusory embodiment of the foreign body or limb despite clear morphological differences from the own body (Botvinick & Cohen, 1998; Kilteni et al., 2015). While an existing debate on the exact nature of embodiment exists in the cognitive science (Blanke et al., 2015; de Vignemont, 2011; Longo et al., 2008), we here refer to this concept when an object, body, or body part is reported to feel as part of the own body (body ownership or self-identification) or when physiological and behavioral responses are consistent with such feeling (e.g., a greater physiological response to threat compared to a control condition in which self-identification with the object is lower or absent). To study this, most research has relied on a/synchrony between signals from different combinations of sensory modalities (Aspell et al., 2013; Ehrsson et al., 2005; Macauda et al., 2014; Tajadura-Jiménez et al., 2012; Tsakiris et al., 2006), however the contribution of bodily smells to illusory embodiment has, to our knowledge, not been addressed. Recent studies showed that (a) visuo-olfactory congruent cues increase embodiment of an arbitrary object (a grapefruit) seen in the position of the own body (Roel Lesur et al., 2020), and (b) the feeling of bodily lightness/heaviness was modulated by a concurrent scent (Brianza et al., 2019), thereby suggesting that prior associations of odors might influence bodily self-consciousness.

We here investigated the effects of sex- and gender-congruent/incongruent body-related odors on illusory embodiment. Differences between sexes in the composition of sweat are supported by distinct chromatographic profiles of volatile compounds (Penn et al., 2007), non-volatile odor-precursors (Troccaz et al., 2009), and varying amounts of axillary skin microflora (Jackman & Noble, 1983). This evidence is in line with research suggesting that bodily chemical compounds signal sex-specific cues (Gustavson et al., 1987; Lundström et al., 2006; Olsson et al., 2006; Wyart et al., 2007). While sex-specific compositions of odors are at least partially biologically-driven given their dependency on genetic and anatomical factors (Jackman & Noble, 1983; Savelev et al., 2008), cultural associations also determine certain scents in a gender-specific manner, as has been stereotyped by cosmetics (Donna, 2009; Lindqvist, 2013).

Participants were blindly exposed to sex- (female/male sweat artificial odor; corresponding to body odors) or gender- (female/male stereotypical cosmetic odor; corresponding to cosmetic scents) congruent or incongruent smells in an embodied virtual reality (VR) setup. While exposed to these compounds, they saw from the perspective of a sex-mismatched person in a head mounted display (HMD) and experienced congruent visuo-proprioceptive and visuo-tactile stimulation, which have been consistently used to induce embodiment illusions (see Kilteni et al., 2015) including embodiment of different genders (Bertrand et al., 2014; Bolt et al., 2021; Petkova & Ehrsson, 2008; Tacikowski et al., 2020). At different moments, a visual threat was presented to the seen body, and electrodermal response to threat was measured for each of these events (Armel & Ramachandran, 2003; Preuss & Ehrsson, 2019). Explicit illusory embodiment was assessed through a questionnaire after each condition. We expected stronger self-identification as measured by explicit and implicit measures in the visuo-olfactory congruent (i.e., same sex/gender for the seen body and the smell) as compared to the incongruent conditions (i.e., different sex/gender for the seen body and the smell). Further explorative measures were taken to assess odor perception in a second experimental block where participants smelled different stimuli and answered an odor perception questionnaire.

2. Methods

2.1. Participants

Based on sample sizes from similar studies on virtual-reality based bodily illusions (Lenggenhager et al., 2007; Maselli & Slater, 2013; Slater et al., 2009), 24 participants without any history of psychiatric or neurological disorders were recruited at the University of Zurich and received either university credits or a financial compensation (20 CHF) for their participation. They provided written informed consent. Our protocol was approved by the Ethics Committee of the Faculty of Arts and Social Sciences at the University of Zurich (Approval Number 17.12.15) and followed the ethical standards of the Declaration of Helsinki. Two participants interrupted the procedure and thus their data was removed from subsequent analyses, with the final sample consisting of 22 participants (12 females) ranging between 18 and 42 years old ($M = 28.8$, $SD = 7.5$). Electrodermal activity data from two additional participants was discarded due to data loss and from an additional participant due to lack of skin conductance responses (SCR; see *Implicit embodiment measure: skin conductance response to threat* in the *Measures* section), resulting in a sample size of 19 participants for this measure (N = 19; 9 females; age $M = 29.5$, $SD = 7.5$).

2.2. Apparatus

2.2.1. Visuotactile stimulation

An Oculus CV1 HMD was used for stimulation. The software was designed using Unity 2018.2.8 for displaying a 235-degree prerecorded video portraying the first-person perspective of a male or female sex person that were previously filmed using a monoscopic Kodak SP360 4 K camera at a resolution of 2160 × 2160 pixels at 30 frames per second. The sex and gender of the seen person was expected to be distinguished from the HMD based on stereotypical associations (see *Limitations, considerations, and outlook* section), such as clothing, more prominent hair, and distinct body shapes. Another sex-matched person was recorded allocentrically interacting with them, this person synchronized their movements and actions to a previously recorded set of audio instructions to achieve consistent timing between videos. The same audio was heard by the experimenter during the stimulation procedure to imitate the movements in synchrony with the video, which was further facilitated by visual monitoring on a screen (see Fig. 2). This protocol is based on a method developed by BeAnotherLab and widely used in diverse settings (Bertrand et al., 2014) including several scientific studies (e.g. Bertrand, 2021; Roel Lesur et al., 2020). The questionnaires were displayed on the HMD and answered by looking at a fixed position with a virtual pointer for a period of 1 s

2.2.2. Olfactory stimulation

Three different compounds [MSH (3-methyl-3-sulfanylhexan-1-ol), HMHA (3-hydroxy-3-methylhexanoic acid), and M2HA (3-methyl-2-hexenoic acid)] were used to create two synthesized sweat mixtures that respect sexual dimorphism observed for real sweat (Troccaz et al., 2009). Female synthesized sweat was composed of 80 % HMHA, 10 % M2HA and 10 % MSH and diluted 1000 times in triacetin (female sweat odor). Male synthesized sweat was composed of 80 % HMHA and 20 % M2HA and diluted 100 times in triacetin (male sweat odor). A typically feminine scent (Chloé eau de Parfum at 10 % in dipropylene glycol; DIPG; female gender cosmetic scent), and masculine scent (Hugo Deep Red at 10 % in DIPG; male gender cosmetic scent) were used as pleasant body-related scents. Two extra scents were used for the odor perception block (mushroom 10 % in DIPG and rose 10 % in DIPG, respectively), these were previously selected as a rather negative scent and rather positive scent based on tests from a small-scale sample (see Supplementary Materials). All compounds were provided by Firmenich, S.A. The solutions (3 ml) were injected into the tampon of cylindrical felt-tip pens (14-cm long, inner diameter 1.3 cm). The use of these devices (provided by Burghart, Germany) avoids contamination from the environment.

2.2.3. Skin conductance recordings

Threat-evoked SCRs were measured using two Ag-AgCl electrodes (6 mm diameter contact area with a 1.6 mm cavity for electrode gel) mounted in individual polyurethane housings attached to the palmar side of the middle phalanges of the first and second digits of the participants' right hand. Skin conductance was recorded with a Biopac MP150 system and an EDA100C amplifier (Biopac Systems Inc., USA) at a 500 Hz sampling rate running in an additional computer.

2.3. Procedure

See Fig. 1 for an overview of the experimental design.

2.4. Preparation

Participants were first informed about the experimental procedure before signing the informed consent form. They were told that they would see from the perspective of another body in VR and that they would be touched on the arms, feet, and knees. Also, that a virtual threat would be presented without any real threat to their bodies. After providing written informed consent, the electrodes for the electrodermal activity were placed on the corresponding position and participants were helped to put on the HMD and sit down. There was no reference to the odors at this stage. A single test question was presented to confirm that participants understood how to answer the questionnaire on a visual analogue scale (VAS).

2.4.1. Embodiment

Before beginning the stimulation, for each condition, a pen with synthesized odor was fixed on to the headset just below the nose (see Fig. 2). This pen contained one of four synthesized odors, namely male or female (gender) cosmetic scent, or male or female (sex) sweat odor. Participants then saw a sex-mismatching body from a first person-perspective on the headset. The decision to expose participants exclusively to a sex-mismatched body was for experimental simplicity. This allowed us to test the olfactory-visual congruency in a simple design while only modulating the presented odors but not the seen body. Before playing the video, they were required to put their hands on their laps and their feet on the ground to match their posture to that seen on the HMD (see Fig. 2).

The videos started with the experimenter grabbing the left arm seen from the participants' perspective and taking the elbow close to the nose (this was intended as a simile to smelling the armpit). Other than this passive movement directed by the experimenter (Fig. 2, 2a), participants were sitting still with their hands on their laps (Fig. 2, 2c). A series of eight visuotactile stimuli (to enhance embodiment) and seven visual threats (to measure implicit embodiment; see Fig. 2, 2b) were presented during each video. The order of visuotactile non-threatening stimuli was interleaved with that of the threatening stimuli (see Fig. 1b). To avoid expectation, this was done in a way that a threatening stimulus would not always follow a non-threatening one, but a mix of subsequent kinds of stimuli. The first two stimuli were always non-threatening tactile stimuli to strengthen embodiment (Fig. 2; 1b, 2a). For both male and female participants, there were two sex-mismatched videos with differing orders for the stimuli intended to minimize potential order effects (each order was presented twice to every participant).

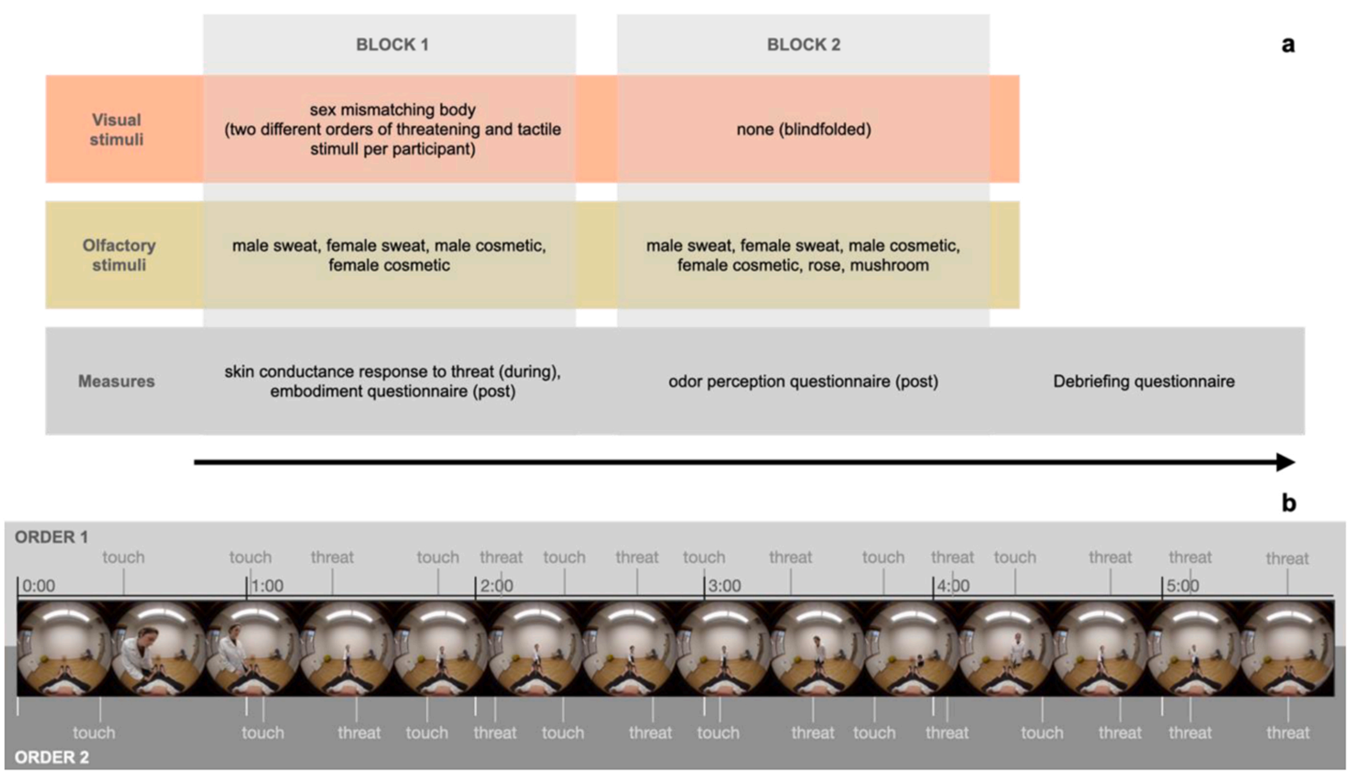

Fig. 1. (a) Visually depicts the experimental design including the two blocks, their corresponding visual and olfactory stimuli (presented sequentially in a counterbalanced manner), and the associated measures. 1b depicts the different orders and approximate timing of the visual stimuli (tactile and threatening) for the female video. The order for the male stimuli was the same, and the timing for each stimulus did not differ for more than 1 s compared to the female.

Fig. 2. 1a) Illustrates a male participant wearing the HMD with an olfactory pen attached to it while receiving tactile stimulation from the experimenter. The experimenter wears headphones where the timing for the tactile stimulation is presented while at the same time visually monitoring the gestures. 1b) depicts what is seen at this moment by the male participant on the HMD. 2a, 2b and 2c depict zoomed-in frame captures from the immersive videos presented on the HMD to female participants. The first illustrates the initial gesture of their own arm being brought towards their nose, the second shows a threat (a syringe pinching the hand), and the third depicts the static sitting position.

In total, participants underwent four conditions, one for each odor. The conditions were presented in a semi-counterbalanced manner, and each was followed by an embodiment questionnaire.

2.4.2. Odor perception

In a following block, participants were blindfolded before being presented each of the six smells in a counterbalanced manner. The stimuli were the female and male (gender) cosmetic scents and sweat (sex) odors from the previous block, plus two extra scents: mushroom and rose. The additional two scents were included as control items, and one was as rather negative (mushroom), while the other as rather positive (rose) in a small naive sample (see Supplementary Materials). Participants were instructed to smell each of the scents for 10 s, while they were blindfolded. A questionnaire followed to assess the recognition, pleasantness, and gender-association of each scent. This questionnaire included items for *gender attribution, certainty of gender attribution, recognition, typicality, liking, intensity,* and *familiarity* (see Table S1). A subsequent debriefing questionnaire consisting of 5 questions followed.

2.5. Measures

2.5.1. Explicit embodiment measure: questionnaire

The embodiment questionnaire (Table 1) was adapted from previous studies (Botvinick & Cohen, 1998; Dobricki & Rosa, 2013; Gonzalez-Franco & Peck, 2018). The items were grouped into the subscales of *self-identification, agency,* and *control* according to the literature; a general *embodiment* score was calculated by integrating items belonging to the categories of *self-identification, agency,* and an item for *presence* ("Sometimes it felt like I was in the middle of the action"; adapted from Dobricki & Rosa, 2013). We further included items for *referral of touch* and *bodily threat* (Gonzalez-Franco & Peck, 2018), *perceived multisensory synchrony* (Roel Lesur et al., 2020), *bodily gender identity* (adapted from Bolt et al., 2021). The latter item ("Sometimes it felt like I had a male/female body") was changed between participants so that those embodying a female sex body would be asked the question according to a female body and those embodying a male sex body would be asked according to a male body. Newly included items for *valence* were also grouped into a subscale. The questionnaire was answered on a VAS ranging from *strongly disagree* (0) to *strongly agree* (1) on the HMD.

2.5.2. Implicit embodiment measure: skin conductance response to threat

For synchronizing the visual stimulation and physiological recordings, serial triggers were sent from the stimulation computer to the Biopac. These were timed to match when each visual threat appeared on the screen. A total of 7 threats to the body were included per condition. These were: a knife stabbing the leg, a syringe injecting the arm, a hammer hitting the foot, and a ball being thrown at the belly. The first three of these were repeated twice, once on the left and once on the right limb so that two subsequent threats would not be on the same side or limb. The ball thrown at the belly was presented once. These threatening gestures were inflicted to the seen body using dummy instruments, i.e., a fake but visually realistic knife touching the seen body (Petkova & Ehrsson, 2008), a dummy syringe whose tip would contract upon pressing (Avenanti et al., 2010); the hammer was used softly on the actors' feet, and the ball was a soft plastic ball. Prior exploratory piloting with members of the lab ensured that these gestures generated SCRs.

Specific SCRs were measured in microSiemens (μS) and analyzed offline using Ledalab (v3.4.9, Benedek & Kaernbach, 2010). For each trial, SCRs were scored as the peak-to-peak amplitude difference in skin conductance of the response falling within − 2 s to 5 s of the trigger onset. The minimal response criterion was set as 0.01 μS and only trials where there was a single response in the temporal window of interest were included. To improve the characteristics of the amplitude

Table 1
Results of ART ANOVAs for the embodiment questionnaire (N = 22).

	Congruency					Odor Type					Interaction				
Item				90 % CI					90 % CI					90 % CI	
	F (df)	*p*	η_{π}^{2}	low	high	*F* (df)	*p*	η_{π}^{2}	low	high	*F* (df)	*p*	η_{π}^{2}	low	high
Self-identification	**0.06 (1,21)**	**0.81**	**0.00**	**0.00**	**0.11**	**0.02 (1,21)**	**0.89**	**0.00**	**0.00**	**0.07**	**2.41 (1,21)**	**0.14**	**0.10**	**0.00**	**0.33**
Sometimes the body I saw when looking down felt like a stranger	2.6 (1,21)	0.12	0.11	0.00	0.34	0 (1, 21)	0.98	0.00	0.00	0.00	2.64 (1, 21)	0.12	0.11	0.00	0.34
Sometimes the body I saw felt like my own	2.78 (1,21)	0.11	0.12	0.00	0.35	0.04 (1, 21)	0.85	0.00	0.00	0.00	1.4 (1, 21)	0.25	0.06	0.00	0.28
Agency	**0.01 (1,21)**	**0.92**	**0.00**	**0.00**	**0.00**	**0 (1,21)**	**0.97**	**0.00**	**0.00**	**0.00**	**0.09 (1,21)**	**0.76**	**0.00**	**0.00**	**0.13**
Sometimes it felt like I could control the seen body like my own.	0.23 (1,21)	0.63	0.01	0.00	0.17	0.45 (1, 21)	0.51	0.02	0.00	0.20	0.28 (1, 21)	0.60	0.01	0.00	0.18
Sometimes I felt as if I could move the seen body	0 (1,21)	0.96	0.00	0.00	0.00	1.12 (1, 21)	0.30	0.05	0.00	0.26	0.03 (1, 21)	0.87	0.00	0.00	0.09
Valence	**1.27 (1,21)**	**0.27**	**0.06**	**0.00**	**0.27**	**0.59 (1,21)**	**0.45**	**0.03**	**0.00**	**0.22**	**0 (1,21)**	**0.97**	**0.00**	**0.00**	**0.00**
I felt good in my body	1.73 (1,21)	0.20	0.08	0.00	0.30	0.93 (1, 21)	0.35	0.04	0.00	0.25	0.01 (1, 21)	0.93	0.00	0.00	0.03
I felt comfortable in the room	0.33 (1,21)	0.57	0.02	0.00	0.19	0.01 (1, 21)	0.94	0.00	0.00	0.01	0.13 (1, 21)	0.73	0.01	0.00	0.15
Control															
Sometimes it felt like I was wearing different clothes than before the experiment	1.91 (1,21)	0.18	0.08	0.00	0.31	0.31 (1, 21)	0.58	0.02	0.00	0.18	1.18 (1, 21)	0.29	0.05	0.00	0.26
Sometimes it felt as if the body I saw was like my own in terms of shape or skin color or appearance	1.51 (1,21)	0.23	0.07	0.00	0.28	2 (1, 21)	0.17	0.09	0.00	0.31	0.06 (1, 21)	0.81	0.00	0.00	0.11
Other items															
Sometimes it felt as if the touches I felt were caused by the ones I saw	0.7 (1,21)	0.41	0.03	0.00	0.23	0.11 (1, 21)	0.74	0.01	0.00	0.14	0.17 (1, 21)	0.68	0.01	0.00	0.16
Sometimes it felt like I was in the middle of the action.	0.39 (1,21)	0.54	0.02	0.00	0.19	0.31 (1, 21)	0.58	0.02	0.00	0.18	0.59 (1, 21)	0.45	0.03	0.00	0.22
Sometimes I had the feeling that I could be threatened by what I saw	0.23 (1,21)	0.64	0.01	0.00	0.17	0.09 (1, 21)	0.77	0.00	0.00	0.13	0.1 (1, 21)	0.75	0.01	0.00	0.01
Sometimes it felt like I had a male/female body	0.6 (1,21)	0.45	0.03	0.00	0.22	0.88 (1, 21)	0.36	0.04	0.00	0.24	0.8 (1, 21)	0.38	0.04	0.00	0.24
In general, the touches I saw and felt were synchronous	0.05 (1,21)	0.82	0.00	0.00	0.11	1.69 (1, 21)	0.21	0.07	0.00	0.29	1.31 (1, 21)	0.27	0.06	0.00	0.27

distributions, we applied a natural logarithmic transformation (i.e., transformed SCR = log(SCR+1)) to the raw SCR scores (Boucsein, 2012). Because the inclusion of zero responses (i.e., using SCR magnitude) is subject to confounds between the response strength and the frequency (Dawson et al., 2016; Preuss & Ehrsson, 2019; Prokasy & Raskin, 1973) and the large number of stimuli and repetitions in our setup, we excluded zero responses from analysis (i.e., using SCR amplitude). This was implemented given our interest in assessing threat-related responses, which are a standard measure in the investigation of bodily illusions (Armel & Ramachandran, 2003; Petkova & Ehrsson, 2008; Preuss & Ehrsson, 2019) but are well known to be reduced after several repetitions (Dawson et al., 2016; Preuss & Ehrsson, 2019). Such measure of SCR amplitude has been used as an indicator of illusion strength in related research (e.g., Preuss & Ehrsson, 2019).

2.5.3. Odor perception

An 8-item questionnaire (Table S1) with interleaved forced choice and VAS items was included after participants smelled each stimulus. The period between stimulus was not measured but it corresponded to the duration between removing the olfactory pen and responding to the eight questions on the HMD.

2.5.4. Debriefing

A final debriefing questionnaire was answered on a VAS ranging from *strongly disagree* (0) to *strongly agree* (1). The items listed in the Results section, were responded using a computer and a mouse.

2.6. Statistical analyses and data processing

Aligned rank transform (ART) ANOVA, binomial tests, linear mixed models, Cronbach's alpha (reported in the Supplementary Materials), descriptive statistics and data preprocessing were conducted in R version 3.5.1 (R Core Team, 2020) and inspected for normality through visual inspection and Shapiro-Wilk tests. Two-tailed comparisons are reported. Additional Bayesian statistics were performed using JASP 0.11.1 (JASP Team). The data can be found on https://osf.io/3k86r/.

VAS data were analyzed with aligned rank transformation ANOVAs using the package ARTool (Kay & Wobbrock, 2020) for each item. We used ART ANOVAs because of their robustness for nonparametric analyses (Wobbrock et al., 2011). Significant findings were followed up with multiple Bonferroni-corrected Wilcoxon signed-rank for the comparisons of interest. We report median and interquartile range (IQR) as descriptive statistics for nonparametric data, as well as partial eta-squared (η_p^2) as an estimate of effect size together with the corresponding 90 % confidence intervals (CI; see Steiger, 2004 for a discussion on CI for η_p^2). For the embodiment questionnaire, besides comparisons for the individual items, we averaged responses to create the subscales of *self-identification*, *agency*, *valence*, *control* and *embodiment* (see Table 1). For the *self-identification* and *embodiment* subscales, the question "Sometimes the body that I saw felt like a stranger" was inverted before averaging (i.e., *1 - response*). The forced choice dichotomous items from the odor perception questionnaire (Table S2) were analyzed using binomial tests to assess whether the ratio of yes/no responses was different from chance (50 %).

To confirm whether SCR amplitude (excluding zero-responses) could be used for subsequent analyses, we assessed whether the frequency of zero-responses between conditions of interests was not statistically different. A Bayesian analysis of variance (ANOVA) was performed with congruency (congruent vs. incongruent; i.e., respective to the body seen on the HMD) and odor type (sweat odor vs. cosmetic scent) as within-participant factors. Using this statistical method, we calculated a two-sided Bayesian Factor (BF_{01}) indicating the strength of the evidence for the null hypothesis (i.e., no differences between conditions) using a default Cauchy prior distribution with a width of 0.5 (Rouder et al., 2012). A BF_{01} between 3 and 10 is indicative of moderate evidence, while a greater value is typically considered strong evidence (van Doorn et al., 2021).

Comparisons for SCR amplitude were performed by means of a general linear mixed-effects (LME) model using the lme4 (Bates et al., 2015) and lmerTest (Kuznetsova et al., 2017) packages. We entered the within-participants factors congruency (congruent vs. incongruent) and odor type (sweat odor vs. cosmetic scent) and their interaction as fixed effects. As random effects, we modeled random intercepts for participants and by-participant random slopes for congruency and odor type. The by-participant random slope for the interaction was not included in the random-effects structure, as its inclusion led to model singularity, indicating overfitting (Bates et al., 2018). A principal component analysis of the random-effects covariance matrix estimates (Bates et al., 2018) confirmed that the inclusion of the by-participant random slope for the interaction led to overfitting in returning four principal components, whereas three were sufficient to account for 100 % of the variance explained (i.e., the fourth component explained 0 % of the random-effects variance). The final model was built as follows (in lme4 syntax):

*sqrtSCR ~ (congruency * odor.type) + (1 + congruency + odor.type| participant).* We used the ‘bobyqa’ optimizer and set the number of model iterations to 200′000 to fit the model. Follow-up comparisons were computed with the emmeans (Lenth, 2020) package when appropriate and Bonferroni correction was applied to correct for multiple testing. We report Cohen’s *d* for LME models (see Brysbaert & Stevens, 2018; Westfall et al., 2014) as an estimate of effect size and their 95 % CI. Complementary analyses using robust linear mixed effects were computed to ensure that our results were not biased by outliers, these are reported in the Supplementary Materials (section: Robust Linear Mixed Effects Model for the Skin Conductance Responses).

3. Results

3.1. Embodiment questionnaire

The ART ANOVA performed for the embodiment questionnaire data revealed no statistically significant differences between conditions for any of the items or (sub)scales (see Table 1 for results, Table S2 for descriptive statistics). Similarly for the embodiment subscale, no statistically significant differences were found for the factors congruency ($F(1, 21) = 0$, $p = .988$, $\eta_p^2 = .0$, 90 % CI [0,0]), odor type ($F(1, 21) = 0$, $p = .952$, $\eta_p^2 = .0$, 90 % CI [0,0]) nor their interaction ($F(1, 21) = 0.89$, $p = .356$, $\eta_p^2 = .04$, 90 % CI [0, 0.24]). To assess the internal validity of our subscales, we report Cronbach’s alpha values on Table S3.

3.2. Skin conductance response to threat

A Bayesian analysis of variance (ANOVA) using JASP version 0.11.1 (JASP Team) showed moderate evidence for a similar repartition of the zero responses across the various conditions of the congruency ($BF_{01} = 3.88$) and the odor type ($BF_{01} = 3.52$) factors, along with their interaction ($BF_{01} = 14.15$). This suggests that there were no differences in the proportion of zero responses across the experimental conditions.

Results from the LME model conducted on the SCR data are reported in Table S4. In line with our prediction that visuo-olfactory sex congruence modulates threat-evoked SCRs as an implicit measure of embodiment (Fig. 3), we found a statistically significant main effect of congruency, indicating that participants showed higher SCR amplitude to threat when they were exposed to a sex- or gender-congruent odor ($M = 0.28$, $SE = 0.04$) than to a sex- or gender-incongruent odor ($M = 0.16$, $SE = 0.04$), $b = .06$, 95 % CI [.007,.12], $p = .023$, $d = 0.514$, 95 % CI [0.053, 0.975]. The main effect of odor type conversely did not yield statistical significance $b = .02$, 95 % CI [− .03,.06], $p = .337$, $d = 0.174$, 95 % CI [− 0.227, 0.575].

Importantly, the main effect of congruency was qualified by the higher-order interaction between congruency and odor type, $b = .05$, 95 % CI [.02,.08], $p = .002$, $d = 0.764$, 95 % CI [0.245, 1.280]. Follow-up comparisons revealed that participants exhibited higher SCR amplitude to threat when exposed to a sex-congruent ($M = 0.35$, $SE = 0.06$) than a sex-incongruent ($M = 0.13$, $SE = 0.04$) sweat odor, $t(34.8) = 3.44$, $p = .003$, $d = 0.896$, 95 % CI [0.361, 1.431]. By contrast, no such difference emerged when participants were exposed to a gender-congruent ($M = 0.22$, $SE = 0.04$) versus gender-incongruent cosmetic scent ($M = 0.18$, $SE = 0.05$), $t(29.6) = 0.53$, $p > .99$, $d = 0.132$, 95 % CI [− 0.375, 0.638]. This suggests that participants’ implicit embodiment, as measured with threat-evoked SCR amplitude, increased specifically for the sex-congruent sweat odor compared to the sex-incongruent sweat odor, but not when they were exposed to gender-congruent and incongruent cosmetic scents.

3.3. Odor perception questionnaire

For each of odor perception questionnaire items (Table S1), an ART ANOVA was performed including the single factor condition with six levels, each corresponding to each of the presented odors. Statistically significant differences were found for the *gender attribution* ($F(5, 105) = 9.06$, $p < .001$, $\eta_p^2 = .302$, 90 % CI [0.16, 0.39]), *liking* ($F(5, 105) = 18.46$, $p < .001$, $\eta_p^2 = .468$, 90 % CI [0.34, 0.55]) and *intensity* ($F(5, 105) = 3.07$, $p = .013$, $\eta_p^2 = .127$, 90 % CI [0.02, 0.2]) ratings of the odors, but not for the *familiarity* ratings ($F(5, 105) = 0.41$, $p = .84$, $\eta_p^2 = .019$, 90 % CI[0.00, 0.029]). Bonferroni-corrected multiple comparisons between the relevant odors for the significant items are reported in Table S5. Results from the binomial tests assessing whether the proportion of *yes/no* responses was different from chance for the dichotomous items are presented in Table 2.

3.4. Debriefing

Each of the debriefing questions yielded the following scores: *1) I thought that the odor was coming from the body that I saw in my position* (Median = 0.19, IQR = 0.35)*; 2) During the VR film I paid attention to the smells* (Median = 0.41, IQR = 0.55); *3) The smell changed the way I felt about the body that I saw in my position* (Median = 0.21, IQR = 0.51); *4) I thought the smell was coming from the experimenter or the room I saw in the video* (Median = 0.54, IQR = 0.41); *5) The smell changed my mood* (Median = 0.36, IQR = 0.38). For items *1)* and *4)* we additionally calculated these scores excluding three participants that reported not recognizing any of the presented smells (Median = 0.24, IQR = 0.4 and Median = 0.51, IQR = 0.43, respectively).

4. Discussion

We used an immersive video portraying the first-person perspective of a sex mismatching body together with synchronous visuo-tactile stimulation for eliciting illusory embodiment of the seen body (Bertrand, 2021; Bertrand et al., 2014; Bolt et al., 2021; Petkova & Ehrsson, 2008; Tacikowski et al., 2020). Simultaneously, participants were

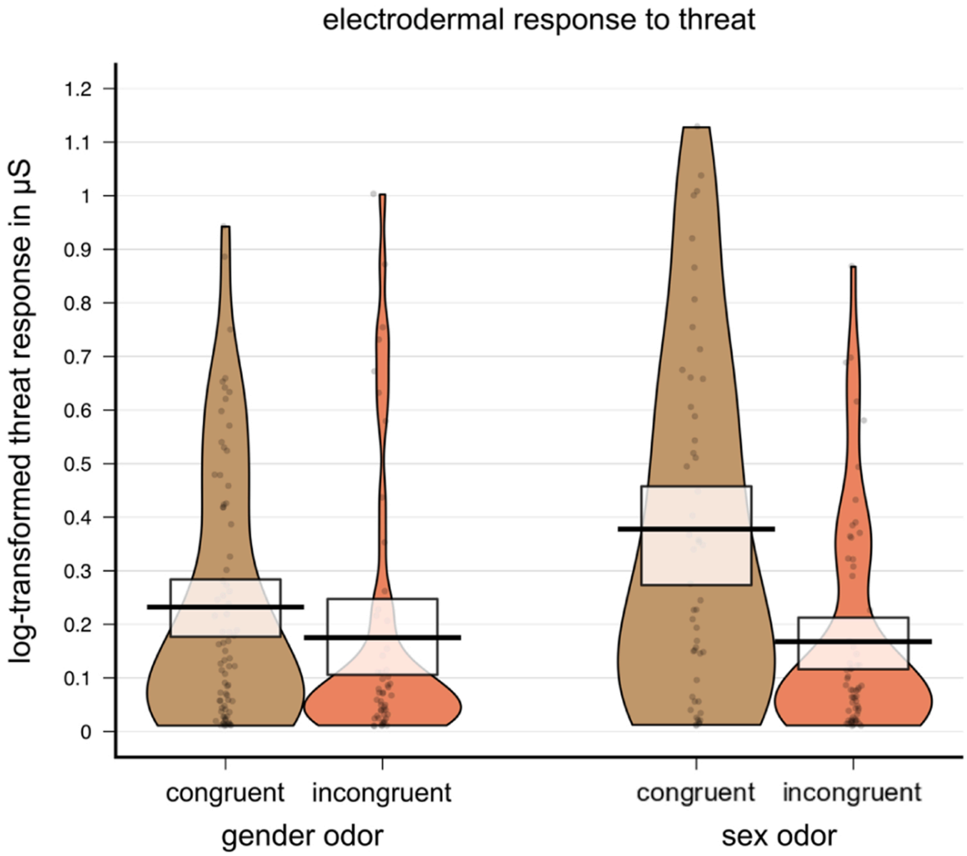

Fig. 3. SCR values after natural logarithmic transformation, central tendencies and distribution of skin conductance responses grouped by congruency and odor type.

Table 2
Multiple binomial tests for the forced choice items of the odor perception questionnaire with a hypothesized proportion of 50 %.

	Gender				Certainty				Recognition				Typicality			
	95 % CI				95 % CI				95 % CI				95 % CI			
Condition	low	high	% female	*p*	low	high	% yes	*p*	low	high	% yes	*p*	low	high	% yes	*p*
female odor	17.2 %	59.3 %	36.4 %	0.286	28.2 %	71.8 %	50.0 %	1	28.2 %	71.8 %	50.0 %	1	32.2 %	75.6 %	54.5 %	0.832
female cosmetic	65.1 %	97.1 %	86.4 %	0.001	65.1 %	97.1 %	86.4 %	0.001	65.1 %	97.1 %	86.4 %	0.001	0.0 %	15.4 %	0.0 %	<.001
male odor	5.2 %	40.3 %	18.2 %	0.004	28.2 %	71.8 %	50.0 %	1	36.4 %	79.3 %	59.1 %	0.523	49.8 %	89.3 %	72.7 %	0.052
male cosmetic	40.7 %	82.8 %	63.6 %	0.286	54.6 %	92.2 %	77.3 %	0.017	36.4 %	79.3 %	59.1 %	0.523	2.9 %	34.9 %	13.6 %	0.001
other negative	36.4 %	79.3 %	59.1 %	0.523	13.9 %	54.9 %	31.8 %	0.134	5.2 %	40.3 %	18.2 %	0.004	0.1 %	22.8 %	4.5 %	<.001
other positive	28.2 %	71.8 %	50.0 %	1	45.1 %	86.1 %	68.2 %	0.134	20.7 %	63.6 %	40.9 %	0.523	0.1 %	22.8 %	4.5 %	<.001

Note. Statistically significant deviations from the hypothesized proportions are marked in bold.

presented with gender- (cosmetic scents) and sex-related (sweat odors) olfactory stimuli that were either congruent or incongruent with the sex of the seen body. We aimed to evaluate the contribution of body smells to illusory embodiment through explicit (questionnaire) and implicit (SCR) assessment. The former showed no differences between odor conditions; however, our implicit measure yielded stronger reactions for the congruent sweat odors (when the seen and smelled avatar were sex-congruent), compared to both cosmetic scents and incongruent sweat odors. A subsequent questionnaire on odor perception showed some important findings. First, there were differences in gender-associations for the cosmetic scents (with the female scent being judged as more feminine), but no differences between the sweat odors (both judged as rather male). Second, though a large majority of participants reported recognizing the female cosmetic scent from the stimulation procedure, this was not the case for the other olfactory stimuli. Lastly, most participants did not attribute the smell as emanating from the seen body. Although we cannot provide a final conclusion why our implicit and explicit measures of embodiment differ, we do offer some hypotheses based on prior research.

4.1. Bodily self-identification and odors

Despite the relative lack of research addressing the role of smell in human bodily self-consciousness, it has been argued that we engage in subconscious self- or other-smelling behaviors as a process of reassuring the self (Perl et al., 2020). Self-smelling could be considered an analog of self-touch, which has been reckoned elemental for the healthy maintenance of our bodily self-consciousness (Husserl, 1952; Roel Lesur et al., 2021). In our study, no differences in our explicit measure of embodiment were found. However, when participants smelled the sex (sweat odor) but not gender (cosmetic scents) congruent stimuli, they showed stronger physiological reactions to threat. SCR to a bodily threat is a common measure in the study of alterations of embodiment, where arguably our physiological responses are extended to a fake or virtual limb or full body when we self-identify with it (e.g. Armel & Ramachandran, 2003; Petkova & Ehrsson, 2008; Preuss & Ehrsson, 2019). This process is considered involuntary and subconscious (Armel & Ramachandran, 2003), and as such it is a relevant measure in practically all areas of psychology (Dawson et al., 2016). Our combined findings suggest no evident differences in explicit self-identification with the seen body, but differences in our implicit measure mediated by the concurrent odor. At this stage, we cannot conclusively attribute this modulation as a clear measure of embodiment nor subconscious processing of the odors (see e.g., Shanks et al., 2021), however further research might clarify the processes underlying our observations.

It remains a possibility that congruent bodily odors played no effect in implicitly altering embodiment but merely affected electrodermal responses to threat. A potential interpretation could be that the presence of such odors congruent with the observed body could increase empathy towards that body, which would be observed in increases in electrodermal responses to threats.[1] An important theoretical link has been established between empathy and embodying others' emotional, motor, and cognitive processes (de Waal & Preston, 2017; Singer & Lamm, 2009). While in principle related, however, empathy and embodiment are distinct. Instead of suggesting an increased stress response to threat towards the self-identified body, our findings could alternatively point at an increased empathic response to the seen body beyond bodily self-identification. Studies addressing potential links between olfaction and empathy have yielded mixed results, with some of them reporting a positive relationship (e.g., Lübke et al., 2014; Spinella, 2002) while others did not find such a relationship (see e.g., Gamsakhurdashvili et al., 2021). At this stage, it would thus be highly speculative to relate our observations with such literature. Running the same experiment but with asynchronous visuotactile stimulation (or another cue to break illusory embodiment) might elucidate whether the changes in SCR with the presented odors are sustained despite lack of self-identification. This would allow to better disentangle the specific influence of bodily odors on embodiment, as opposed to other factors such as empathy.

Several studies have shown that visual dominance is a very strong cue for inducing illusory embodiment (Maselli & Slater, 2013; Roel Lesur et al., 2018). Given the strength of observing a proprioceptively matching body from a first-person perspective with contingent head-related cues, the lack of explicit modulation of embodiment in our work is not surprising. In fact, research on olfactory contributions to embodiment (Roel Lesur et al., 2020) reported explicit self-identification with an arbitrary object (a grapefruit) seen in VR when there was a smell that was congruent with it (grapefruit scent) compared to an incongruent smell (strawberry scent). The reasons between explicit modulations of embodiment in the cited study and the lack of modulation here reported is unknown. Perhaps, in contrast to the grapefruit study, the olfactory stimuli presented here were not as notable given that they are usual smells emanating from humans, compared to the fruity scents. Alternatively, it could be that, in the case of the grapefruit, the object seen in the location of the own body (i.e., the grapefruit) triggered no prior associations related to a human body, thus forcing participants to shift their attention to senses other than vision (i.e., smell) for grounding their sense of body. While in the cited study (Roel Lesur et al., 2020), the smells were identifiable (by a different experimental sample, as citric and strawberry, respectively), here the olfactory stimuli that yielded significant differences in SCRs (female and male sweat odors) were not judged as different in terms of the measured categories (gender, liking, recognition, and intensity). Furthermore, a previous study in a large sample showed that the bodily compounds used for this study were not explicitly distinguished by participants (Ferdenzi & Delplanque, 2021). Our integrated findings suggesting differences in explicit (odor-distinction and self-identification) and implicit measures might reflect a characteristic feature of olfaction that we discuss below.

4.2. Unconscious processing of odors and implicit differences

Contrasting evidence between explicit and implicit measures has been often reported in the literature on bodily self-consciousness (e.g. de Haan et al., 2017; Roel Lesur et al., 2021; Rohde et al., 2011; Rohde et al., 2013). Such divergent outcomes may seem surprising for stimulation through other modalities; nonetheless, in the context of olfaction, this might be in line with specific characteristics of the sense of smell. Olfactory processing in humans has been highlighted due to unique features in comparison with the other major senses. Amongst these, the conscious access to smells in terms of involuntary habituation, conscious content, attentional control, post-perceptual processing, and memory, seem to contrast other senses (Arshamian et al., 2020; Köster, 2002; Stevenson & Attuquayefio, 2013; Zucco, 2003). The subconscious processing of smells has been noted for its capacity to shift behavior (Gustavson et al., 1987; Holland et al., 2005; Mas et al., 2019; Olsson et al., 2006). Several studies have shown correct recollection behaviors without explicit recognition (Degel et al., 2001; Degel & Köster, 1999; Köster, 2002; Olsson & Cain, 2003) and findings suggest that odors alter cognition and behavior largely at a subconscious level (Prehn et al., 2006; Wisman & Shrira, 2015; Ye et al., 2019; Zhou et al., 2014; Zhou & Chen, 2008). Regarding self-other distinction, a study showed that participants were able to distinguish their own and their friends' odors in a three-alternative forced choice task, but only with strikingly low confidence (Lundström et al., 2008). Another study showed no explicit recognition of one's own body odor when compared to others in an experimental setting; however, disgust ratings were lower for the own odor (Übel et al., 2017). This supports the notion that despite a lack of clear direct identification, indirect psychological reactions support implicit olfactory self-other distinction. Following this, it does not seem implausible that despite the lack of changes in explicit self-identification, body odors did play a role in altering physiological responses related to embodiment (or at least empathy, which is thought of as a way of simulating others' states; (de Waal & Preston, 2017; Singer & Lamm, 2009), as our findings might suggest. However, at this stage this is merely speculative and future studies should attend these questions in more detail.

A similar exclusive modulation of implicit embodiment measures has previously been found in other less attended senses like the vestibular system (Macauda et al., 2014). Our findings showed stronger SCRs for sex-congruent compared to sex-incongruent sweat odors, but this was not the case between gender-congruent and incongruent cosmetic scents. The reason behind this is not clear. However, this might suggest a potential implicit association to biologically determined chemical compounds related to sex, which might be rooted in our cognitive system beyond cultural conceptions of gender. Alternatively, a hedonic bias triggering self-odor associations only for negatively perceived odors might explain these findings. One could imagine that when smelling sweat, a concern that this odor might emanate from oneself could trigger self-reassuring processes that are not activated for positive scents. At this point, these lines of reasoning remain purely speculative and further research is needed to pinpoint the underlying causes.

[1] We thank one of the reviewers for suggesting this interpretation.

4.3. Sex and gender associations of odors and embodiment illusions

Gender is of course a cultural construct, and cosmetic scents with specific gender associations are culturally bound and reinforced by branding (Lindqvist, 2013; Zellner et al., 2008). However, the different chemical constitutions of body (sweat) odors between biological sexes might be more genetically determined, though gender-related cultural habits might indeed play a role in the chemical constitution of body odors (Havlicek & Lenochova, 2008). As mentioned in the introduction, there are differences between sexes in the composition of sweat (Penn et al., 2007), axillary skin microflora (Jackman & Noble, 1983), and non-volatile odor-precursors (Troccaz et al., 2009). While there are environmental factors playing a role in body odors (Havlicek & Lenochova, 2008), it has been argued that genetics are the primary source of such determinants (Havlicek & Lenochova, 2008; Porter, 1998; Porter et al., 1985). However, the full composition of human body volatiles is inconclusive due to methodological differences between studies (Dormont et al., 2013), and our capacity to discriminate sex through body odors remains elusive (Mutic et al., 2016). Still, this distinction between more genetically determined versus more culturally determined factors might underlie the differences between gender cosmetic scents and sex sweat odors in our study. To further support this distinction, it has been argued that body odors are of functional relevance in some cultures due to the linguistic diversity referring to such odors (Arshamian et al., 2020); by contrast, in Western culture people rather seek to hide these body odors (Perl et al., 2020). Indeed, our measures suggest that participants found significantly different gender associations between the cosmetic scents, but no differences between the sweat odors, which indeed follows culturally determined associations. It has been suggested that stronger and less pleasant body odors tend to be related to a male sex category (Doty et al., 1978), which may explain why both male and female axillary sweat have been explicitly associated with rather masculine scents (see Mutic et al., 2016).

Interestingly, no differences between conditions were found for the item regarding the gender of the own body (i.e., *Sometimes it felt like I had a male/female body*). A recent study showed that by embodying a different sex body, participants' own gender identity is modulated in the direction of the gender associated with the embodied body (Tacikowski et al., 2020). However, a more recent study showed no modulation of the gender identity by a similar intervention, but, in contrast to our study, it did show relatively high responses regarding the feeling that they embodied the gender associated with the embodied avatar (Bolt et al., 2021). Notably, we did not assess how participants rated the gender-identity of their own bodies at baseline but only between conditions, preventing us from assessing whether there was any variation from the usual gender identification of their body. However, their ratings were relatively neutral overall (see Table 1), which might suggest a change from their general gender identity towards a more neutral one. Furthermore, we only addressed explicit gender identification but not implicit gender associations. There is evidence that olfactory cues implicitly communicate sex-related information of a seen body (Ye et al., 2019; Zhou et al., 2014), and future studies are encouraged to also assess implicit measures of gender identity associated with embodiment and the sense of smell. It should be noted, however, that our question on gender identity could have been interpreted in terms the visual features of the seen body rather than in terms of the identity of the own body. Lastly, depicting a sex-matching instead of a sex-mismatching body on the HMD could have increased embodiment. As mentioned before, we used a sex-mismatching body for experimental viability. However, future studies might include a sex-matching body as an additional experimental factor or to assess whether the effect of the olfactory cues remains (or changes in magnitude) despite the gender-matching illusory embodiment.

4.4. Limitations, considerations, and outlook

We included a gesture so that participants approached their skin to their nose for accentuating the association of the smell to the seen body. However, it did not seem to help participants associate the odors with the egocentrically seen body nor to attend the odors. Participants overall did not recall feeling that the smells emanated from their own bodies, despite our inclusion of the armpit sniffing part, but rather from the experimenter or the environment. However, this question was only asked after the embodiment procedure. In fact, participants recollection of having smelled the odors during the procedure was not above chance except for the female gender cosmetic scent. A vast amount of literature suggests that explicit recollection of odors is not as good as are implicit behaviors suggesting recollection (Degel & Köster, 1999; Herz & Engen, 1996; Zucco, 2003). As a result, such responses might be related to poor memory retrieval. It remains unclear whether the perceived source of the odors would make a strong difference, particularly given the arguably that we only found differences in embodiment at an implicit level. Future studies might want to ensure that the presented odors appear to emanate from the own (or seen) body, e.g., by repeating such body movements to the nose and only present the odor time-locked to the movement using an olfactometer rather than continuously as done in our study. Time locking the olfactory cues to actions might improve this effect since temporal synchrony of multisensory cues has shown to be fundamental for embodiment (Botvinick & Cohen, 1998; Roel Lesur et al., 2021; Shimada et al., 2014). Furthermore, enhancing the visual stereotypical gender cues through for example clothing of the seen body (e.g., Bolt et al., 2021) might enhance the modulation of gender identity and potentially its link to the stereotypical cosmetic scents.

We found differences using reconstructed sweat odors (only three compounds), based on the results of Troccaz et al. (2009). However, this is only a first approach because the content of sweat is much richer (Starkenmann, 2017) and it is likely that other compounds are involved in sexual dimorphism of sweat odors. Using a more ecological approach, it might be interesting to address this issue using real sweat samples collected from humans to confirm our results. However, it remains important to disentangle the basic components influencing sex-related processes to elucidate the biological mechanisms our results.

It is worth noting that the way in which we studied stereotypical gender- and sex-congruencies (i.e., using certain cosmetics typically associated with the male/female sex) does not truthfully reflect the richness of gender expression and its dissociation from sex. Our reliance on such typical associations was for the purpose of experimental simplicity, and we by no means want to perpetuate these as normative associations.

5. Conclusions

Our study highlights the relevance of olfaction in the study of bodily self-consciousness. Despite the relative neglect of this sensory modality in the field, we here show its importance for modulating an often used implicit measure of embodiment. This modulation follows unique characteristics of the sense of smell in human cognition. Future research is needed to understand the dynamics underlying our findings more thoroughly.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationshipsthat could have appeared to influence the work reported in this paper.

Data availability

data is shared on osf: https://osf.io/3k86r/.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.biopsycho.2022.108477.

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