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**The perception of gender
in two allegedly sex-specific body odor compounds MSH and HMHA**

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21 **Abstract**

22 3-methyl-3-sulfanylhexasan-1-ol (MSH) and 3-hydroxy-3-methylhexanoic acid (HMHA) are two
23 allegedly sexually dimorphic compounds present in human sweat. While MSH is more
24 typically found in women, HMHA is more typically found in men. Here we investigated
25 whether it was possible to identify these two compounds as explicitly masculine or
26 feminine. We also investigated whether gender and age differences would suggest a
27 possible role of these compounds in opposite-sex attractiveness. To this end, we analyzed
28 the perceptual ratings of t-shirts impregnated with these odors by 2,716 individuals (62%
29 female) aged between 6 and 90, collected during a one-year museum exhibition. Analyses
30 with Bayesian mixed-effects models revealed that only women rated MSH as more feminine
31 than HMHA. However, this effect remained very small and Masculinity/Femininity ratings
32 were extremely variable among the population. Women also rated both odors as more
33 intense and less pleasant than men. Age related differences reflected the effect of
34 increasing experience with body odors, such as an increase in odor familiarity. The loss of
35 olfactory function with age, i.e. presbyosmia, was also reflected by decreased perceived
36 intensity and unpleasantness (at least for HMHA). Overall, the results are not in favor of a
37 role of MSH and/or HMHA in male-female attractiveness, however they do agree with the
38 known gender and age differences in odor perception. Future studies on the olfactory
39 determinants of human attractiveness would benefit from the identification of new sexually
40 dimorphic compounds and from using experimental designs where the effect of odors are
41 tested more implicitly.

42 **Keywords**

43 Olfaction, Body Odor, Attractiveness, Gender differences, Development.

44 **1. Introduction**

45 Human body odor is a complex chemical mixture that conveys biological information about
46 individuals [1]. There is increasing evidence that other individuals are able to detect and
47 process this information. For instance, body odor may provide information about genetic
48 proximity [2,3], hormonal levels [4–6], sickness [7], even personality traits [8] and emotional
49 states [9,10], and thus appears to regulate our social interactions [11]. In addition, body
50 odor chemical composition varies with age [12,13], which leads to different perceptual
51 qualities when participants evaluate samples from different age groups [14,15].
52 Nevertheless, research on human ability to discriminate the body odor of men and women
53 remains inconclusive.

54
55 While some studies have found evidence that humans are able to identify body odor
56 donors' gender from breath odor [16] and torso odor [17], the performances in doing so
57 remained rather low. In a study using axillary odors, almost no rater performed above
58 chance in assigning a gender category; Moreover, only 22% to 67% of the samples were
59 correctly assigned to their gender category depending on the trials [18]. In another study
60 only 20% to 32% of European participants (but 64% of Asian participants) were able to
61 correctly categorize t-shirt owners' sex [17]. Also, intensity and pleasantness of the odors
62 were found to influence gender categorization significantly, with stronger and more
63 unpleasant odors being more likely to be categorized as male than female [18].

64
65 Analytical chemistry approaches provide contrasted conclusions as well. Although the
66 chemical composition of human body odor is not fully known partly due to methodological
67 limitations [19,20], a few studies have investigated gender differences. Some studies fail to

68 find any difference between male and female chemical profiles [12]. Other studies however
69 suggest that, in spite of the large interindividual variability, male and female body odors
70 may differ [21,22], although a consensus regarding the chemicals concerned is far from
71 being reached because studies are rare and methods are heterogeneous. In another study
72 investigating gender differences in major constituents of human sweat odor [23], men and
73 women were found to differ in the ratio of two precursors secreted in the armpit. The first
74 one leads to the formation of MSH (3-methyl-3-sulfanylhexan-1-ol), responsible for the
75 sulfurous onion-like odor of women's sweat. The second precursor leads to the formation of
76 the carboxylic acid HMHA (3-hydroxy-3-methylhexanoic acid), causing a cheesy rancid odor
77 in men's sweat. In female samples, MSH precursor was found in larger quantities and HMHA
78 precursor in smaller quantities on average than in male samples. Although interindividual
79 variability was huge with significant overlap between men and women, the ratio HMHA
80 precursor / MSH precursor was stable and 3 times higher in men than in women. In addition
81 to the quantitative differences in both precursors as a function of gender, men have the
82 potential to produce more HMHA than women because they possess a greater amount of
83 *Corynebacteria* [24], which are responsible for the formation of HMHA [25]. Finally, few
84 studies have been conducted on HMHA and MSH to investigate how they are perceived, and
85 whether HMHA is perceived differently by men and women remains inconclusive to date
86 (see [26] and [27] for differing results).

87

88 In this experiment, we tested whether the more typically feminine compound MSH and the
89 more typically masculine compound HMHA, were perceived as such in an explicit task. The
90 task was simple (rating the odors on a scale from very masculine to very feminine), and was
91 implemented on a very large sample of men and women of all ages in a museum, over a

92 period of one year. Interindividual differences in gender evaluation of the body odor
93 compounds were investigated, with a particular attention to the gender and age of the
94 raters.

95

96 Gender differences in odor perception have been shown frequently [28]. Regarding odors in
97 general, women seem to perform better than men in odor identification and memory tasks
98 [29,30], although they do not necessarily have better detection skills [e.g., 27,28], and they
99 also display higher attention to odors [33–35]. For social odors in particular, women seem to
100 be more responsive to body odors than men (self-declared [36]; hedonic responses to
101 biological samples [37]) and to identify family members based on their smell more
102 accurately [38]. The present study investigates body odor compounds that are reported to
103 be sexually dimorphic, a characteristic that may have a particular relevance in mate choice
104 (as in other modalities, such as voices [39] or faces [40]). A few sexually dimorphic body
105 odor compounds have been studied in the past (androstenes), but their supposed role as
106 sex pheromones has never been shown [41,42] and the reasons leading scientists to focus
107 so much on these molecules alone have been criticized [42]. Therefore, our study will
108 contribute to the development of knowledge of other categories of sexually dimorphic body
109 odor compounds. We hypothesize that gender differences may occur, reflecting either a
110 general superiority of women in odor processing and/or specific odor processing related to
111 a role of the compounds in opposite-sex attractiveness (such as men’s higher pleasantness
112 ratings of the female compound MSH and/or women’s higher pleasantness ratings of the
113 male compound HMHA).

114

115 Finally, developmental and ageing effects were also expected in this study. Indeed, it is likely
116 that masculinity/femininity of a sweat odor is acquired through experience, and that such
117 judgments become more accurate after puberty (see [43] for acquired responses to body
118 odors through childhood and adolescence). If MSH and HMHA are relevant for mate choice,
119 it may also be that the information they convey about gender is relevant only during the
120 sexually active period of life, but not during childhood or in the elderly. Last but not least, an
121 age-related decrease in olfactory abilities [30,44] due to the senescence of the olfactory
122 system may occur and impact the participant's olfactory evaluations. Overall, the ability to
123 categorize MSH and HMHA as being respectively female and male in our study is expected
124 to be higher in young adults than in the other age groups.

125

126 **2. Methods**

127 **2.1. Participants**

128 Between February 15, 2019 and February 23, 2020, a total of 23,236 individuals visited a
129 museum exhibition about the human sense of smell at the Fondation Claude Verdan Musée
130 de la main UNIL-CHUV (Lausanne, Switzerland). One of the interactive modules in the
131 exhibition aimed to test whether it was possible to tell whether two different body odors
132 were masculine or feminine. 2,836 visitors (1,744 women, Age $M = 30.7$, $SD = 18.3$; 1,092
133 men, Age $M = 30.0$, $SD = 20.3$) voluntarily and anonymously took part in this module over a
134 period of 10 months¹. In order to avoid the inclusion of inconsistent data in the analyses, we
135 excluded participants who reported being older than 90 years (44 excluded), those not able
136 to smell MSH or HMHA (67 excluded), and those whose answers were the minimum or

¹ The data collected during the first two months were not retained because the order of presentation of the compounds was fixed, introducing an *obvious* experimental bias. The correct collection after modification of the experiment presentation software (randomization of compounds delivery) started on 21 May 2019 and ended on 23 February 2020.

137 maximum scores on all questions (9 excluded). Analyses were performed on a final database
 138 of 2,716 individuals (1,685 females). The distribution of participants by age group and
 139 gender is presented in Table 1.

140 **Table 1.** Characteristics of the participants (number, age in years: Mean \pm
 141 Standard Deviation), by gender and age groups.

Age group	Women		Men	
	N	Mean age \pm SD	N	Mean age \pm SD
6 to 9	123	7.6 \pm 1.1	105	7.5 \pm 1.2
10 to 19	448	14.2 \pm 3.0	293	13.7 \pm 2.9
20 to 29	292	24.7 \pm 2.9	177	24.9 \pm 2.7
30 to 39	333	34.4 \pm 3.0	197	34.5 \pm 3.2
40 to 49	261	43.9 \pm 2.8	142	44.2 \pm 2.9
50 to 59	122	53.9 \pm 2.7	69	53.6 \pm 2.6
60 to 69	80	64.2 \pm 3.2	29	64.0 \pm 2.8
70 to 90	26	73.8 \pm 3.7	19	73.8 \pm 4.9

142
 143 This study has been conducted in compliance with the rules of the University of Geneva and
 144 the Swiss National Science Foundation. Although this project has not been reviewed by an
 145 independent ethics committee, the strict ethical standards set out in The European Code of
 146 Conduct for Research Integrity (<https://allea.org/portfolio-item/european-code-of-conduct-2023/>) and the WMA declaration of Helsinki (<https://www.wma.net/policies-post/wma-declaration-of-helsinki-ethical-principles-for-medical-research-involving-human-subjects/>)
 147 were applied. The scientific relevance of the question was assessed by the authors of the
 148 publication in accordance with the state of the literature at the time. The protocol
 149 implemented enables the authors to answer the question posed while minimizing any
 150 inconvenience. Visitors' participation was voluntary, they were given information about the
 151 purpose of the study, they could end their participation at any time without any
 152 consequences and no personal data was collected.

155

156 **2.2. Odorants**

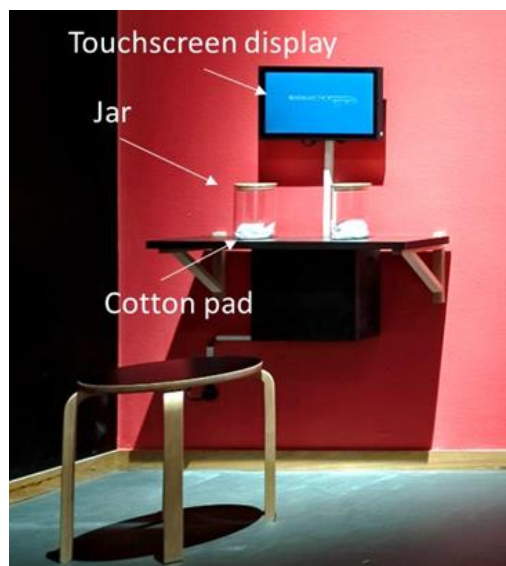
157 One percent solutions of MSH (3-methyl-3-sulfanylhexan-1-ol) and HMHA (3-hydroxy-3-
158 methylhexanoic acid) in triacetin, provided by Firmenich, S.A., were diluted respectively 50
159 times and 5 times in water, leading to a final concentration of 0.02% of MSH and 0.2% of
160 HMHA. Each compound was sprayed (one squeeze, 0.116 ± 0.007 mL) three times a week
161 (Tuesday, Thursday and Saturday), onto a separated piece of cotton cloth (about 10 x 10 cm)
162 cut from a unique plain white T-shirt (renewed between the 10th and 15th of each month).
163 These cloths were then placed at the bottom of two separate glass jars (10 cm diameter, 12
164 cm height, 188.5 cm^3) and hermetically sealed with a cork. This procedure resulted in two
165 well-perceived odors of fairly similar perceived intensity (as evaluated by a small group of 5
166 expert colleagues working at Firmenich, S.A.). These relatively high and supraliminal
167 concentrations (see [27] for HMHA detection threshold), although not corresponding to
168 naturally-occurring concentrations in body odor, were chosen to enable conscious
169 perception.

170

171 **2.3. Procedure**

172 Visitors to the exhibition who wished to participate freely in this experiment sat on the stool
173 positioned in front of the experimental setup (Figure 1). They then began the experiment by
174 touching the touch screen on which was written: "Like the smell of sweat... By participating
175 in the following test, you are taking part in a scientific study. Your responses are anonymous
176 and will only be used in this scientific research conducted by the Swiss Center for Affective
177 Sciences of the University of Geneva". They were invited to provide their gender and age,
178 then to open one of the two jars (random order given by the presentation software), to
179 smell the content, replace the cork and then answer a series of questions using 10-point
180 scales presented on the touch screen. The questions were: [Masculinity/Femininity] How

181 would you describe this smell? (from 0 = very masculine to 10 = very feminine);
182 [Masculinity/Femininity Certainty] Are you sure of your choice? (0 = not at all, 10 = quite
183 sure); [Pleasantness] Do you like this smell? (0 = not at all, 10 = a lot); [Intensity] How
184 intense is this smell? (0 = I cannot smell it, 10 = very strong); [Familiarity] Do you know this
185 smell? (0 = unknown smell, 10 = very familiar smell); [Typicality] For you, does this
186 correspond to typical smell of sweat? (Yes / No). At the very end of the experiment, the
187 participants could read on the screen: “Thank you for your participation. This scientific
188 research will attempt to answer the following question: Is there a typically masculine or
189 feminine smell of sweat?”.



190

191 **Figure 1.** Photograph of the experimental setting in the museum exhibition, including a stool, the two jars and
192 the touch screen to record the participants' answers.

193

194 **2.4. Statistical analyses**

195 Data and analyses scripts (performed in R version 4.3.1 [42]) can be downloaded at

196 <https://osf.io/hdtm7/>.

197 To analyze the gender ratings of the odors MSH and HMHA as well as their modulating

198 factors, we used cumulative link mixed effects models (aka ordinal mixed effects

199 regressions) in the Bayesian framework with the brms R package [46]. The response variable
200 was the Masculinity/Femininity rating of the odor, an ordinal factor (a Likert-scale) that
201 could take one of eleven values between 0 and 10. The fixed part of the model contained
202 the participants' socio-demographic characteristics (Rater Age and Rater Gender), the
203 Compound presented (MSH or HMHA) and its interactions with Rater Age and Rater Gender,
204 and the participant's other odor ratings (Masculinity/Femininity, Pleasantness, Intensity,
205 Familiarity and Typicality). Subject's ID (allowing for individual differences in response to the
206 compound) and compound Presentation Order (first or second) were included in the model
207 as random factors. Additionally, we added a random slope for Compound (MSH or HMHA)
208 to allow for interindividual variation in response to compounds. To facilitate interpretation
209 of the coefficients, all numerical variables (Age, Pleasantness, Intensity and Familiarity) were
210 scaled. As the relationship between Intensity of the odor and its Masculinity/Femininity
211 score was non-linear, we added a quadratic term for Intensity. The binary predictors
212 (Gender, Compound and Typicality of the odor) were treated as factors, with two levels
213 each (Women and Men for Gender, with Women being the reference level; HMHA and MSH
214 for Compound, with HMHA being the reference level; Not typical and Typical for Typicality
215 of the odor, with Not typical being the reference level). As we used a Bayesian framework,
216 we compared models using the Leave-One-Out Information Criterion (looIC), with lower
217 values indicating better fit [47]. The Leave-One-Out Information Criterion (looIC) of the full
218 model with a quadratic term for Intensity (looIC = 24308.8) was much lower than the looIC
219 of the full model with a linear relationship for Intensity (looIC = 24369.5), supporting the
220 choice of the quadratic term. The full model can be read as follows:

221 *Masculinity/Femininity* ~ *Rater Gender* + *Rater Age* + *Compound* + *Rater Gender* ´ *Compound*
222 + *Rater Age* ´ *Compound* + *Pleasantness* + *Intensity* + *Intensity*² + *Familiarity* + *Typicality* +
223 *(1 + Compound|SubjectID)* + *(1|Presentation Order)*.

224 Besides the full model described above, we also ran a reduced model excluding all variables
225 for which the direction of the effect was not highly certain (i.e., the posterior distribution
226 has at least 10% of its distribution going in the opposite direction to the median), a common
227 practice to avoid overfitting [48]. The reduced model can be read as follows:

228 *Masculinity/Femininity* ~ *Rater Gender* + *Rater Age* + *Compound* + *Rater Gender* ´ *Compound*
229 + *Pleasantness* + *Intensity* + *Intensity*² + *Typicality* + *(1 + Compound|SubjectID)* +
230 *(1|Presentation Order)*.

231 We also conducted analyses for the determinants of four other assessments of the odor: its
232 pleasantness, familiarity, intensity, and the certainty of the participant's Masculinity/
233 Femininity judgment. Pleasantness, familiarity and certainty of Masculinity/Femininity rating
234 were each measured on a 11-point Likert scale and were treated as ordinal response
235 variables. Intensity was also originally measured on a 11-point Likert scale, but our inclusion
236 criteria removed the 67 cases in which participants reported an intensity of 0 (i.e., they were
237 not able to smell this odor) and so intensity was treated as a 10-point Likert scale. We ran
238 four separate cumulative link mixed effects models. The same random structure as earlier
239 was applied and we included Rater Gender, Rater Age, Compound, as well as the
240 interactions Rater Gender ´ Compound and Rater Age ´ Compound as fixed effects. Two
241 additional elements were included in the model concerning the certainty of
242 Masculinity/Femininity judgment: Gender-strength and Gender-strength ´ Compound
243 interaction. Gender strength is the result of the transformation of the
244 Masculinity/Femininity scale (ranging from 0 to 10) into a scale ranging from 0 to 5, where 0

245 means gender-neutral odor (i.e., 5 on the original scale) and 5 means highly gendered odor
246 (i.e., either 0/very masculine or 10/very feminine on the original scale). Four reduced
247 models were derived from these four full models by removing all variables for which the
248 direction of the effect was not highly certain (i.e., they had an associated probability $p <$
249 0.90).

250 For all models, we ran 4 Markov chains in parallel, each with 6,000 iterations, of which the
251 first 2,000 were treated as warmup and were therefore not used for inference. Note that,
252 for all models, when factors were involved in significant interactions, main effects of these
253 factors were not interpreted. We report results from the reduced model within the Bayesian
254 framework by presenting the posterior median slope, its associated Median Absolute
255 Deviation (MAD), the 90% Bayesian Credible Interval (90% CI), the proportion of support for
256 positive or negative effects (p_+ or p_- , respectively), as well as derived median and MAD
257 estimates of Cohen's d for the fixed effects [48]. Even though they come from different
258 frameworks, there is typically a linear relationship between the p -values of the frequentist
259 approach and the p_+ or p_- of the Bayesian approach, with thresholds of 0.05, 0.01 and 0.001
260 for p -values corresponding to thresholds of 0.95, 0.99 and 0.999 for p_+ or p_- [49]. Note that
261 when the whole posterior distribution for one parameter is of the same sign, then p_+ or $p_- =$
262 1. General guidelines for interpreting Cohen's d are: very large effect when $d > 1.3$, large
263 when $d > 0.8$, medium when $d > 0.5$ and small effect when $d > 0.2$ [50,51].

264 265 **3. Results**

266 **3.1. Masculinity/Femininity of MSH and HMHA**

267 For our main rating of interest, that is Masculinity/Femininity, we found a significant Rater
268 Gender \times Compound interaction (Est. = -0.22 ± 0.10 , 90% CI [-0.38; -0.04], $p = 0.9826$;

269 Table 2), since women are slightly more likely to rate MSH as more feminine (less masculine)
270 than HMHA while there was no difference between the two compounds in male raters
271 (Fig. 2A). There was also an effect of Rater Age (Est. = 0.05 ± 0.03 , 90% CI [0.01; 0.10],
272 $p_+ = 0.9756$; Table 2), with older participants rating the odors as more feminine (less
273 masculine) than younger ones (Fig. 2B). However, these effects remain very small (absolute
274 value of Cohen's d s < 0.12; Table 2).

275 To further qualify these results with the rating of Certainty, we found that the participants
276 were more confident in their Masculinity/Femininity rating when they perceived the odor as
277 very gendered (very masculine or very feminine) than when they rated it as gender-neutral
278 (Odor Gender-strength: Est. = 1.28 ± 0.04 , 90% CI [1.21; 1.35], $p_+ = 1$; Table 2 and Fig. 3A),
279 and this effect was of medium size (Cohen's $d = 0.71$; Table 2). Also, confidence was higher
280 for MSH than for HMHA (Fig. 3B), higher for men than for women (Fig. 3C), and decreased
281 with age (Fig. 3D), although these effects remained very small (Gender effect:
282 Est. = 0.17 ± 0.10 , 90% CI [0.01; 0.33], $p_+ = 0.9575$; Compound effect: Est. = 0.20 ± 0.05 , 90%
283 CI [0.11; 0.28], $p_+ = 1$; Age effect: Est. = -0.17 ± 0.05 , 90% CI [-0.25; -0.09], $p_- = 0.9996$;
284 Cohen's d s < 0.11; Table 2).

285 As for the other odor ratings, we found that the most prominent predictor of
286 Masculinity/Femininity rating was Pleasantness (Est. = 0.44 ± 0.03 , 90% CI [0.39; 0.49],
287 $p_+ = 1$; Table 2), with a small effect size (Cohen's $d = 0.24$; Table 2): The more pleasant the
288 odor, the more likely it was to be evaluated as feminine (Fig. 2C). Some other effects were
289 found, although they were very small (Cohen's d s < 0.14). First, there was an inverted U-
290 shape relationship between Intensity and Masculinity/Femininity ratings (Est. = -0.17 ± 0.02 ,
291 90% CI [-0.20; -0.13], $p_- = 1$; Table 2): Odors perceived as being of medium intensity (score
292 around 5) were equally likely to be rated feminine or masculine, whereas odors perceived as

293 being of low or high intensity were rated as being more masculine (Fig. 2D). Second, odors
 294 that were perceived as being more typical of sweat were rated as more masculine than
 295 odors perceived as being less typical of sweat (Est. = -0.24 ± 0.06 , 90% CI $[-0.34; -0.15]$,
 296 $p = 0.9999$; Table 2 and Fig. 2E).

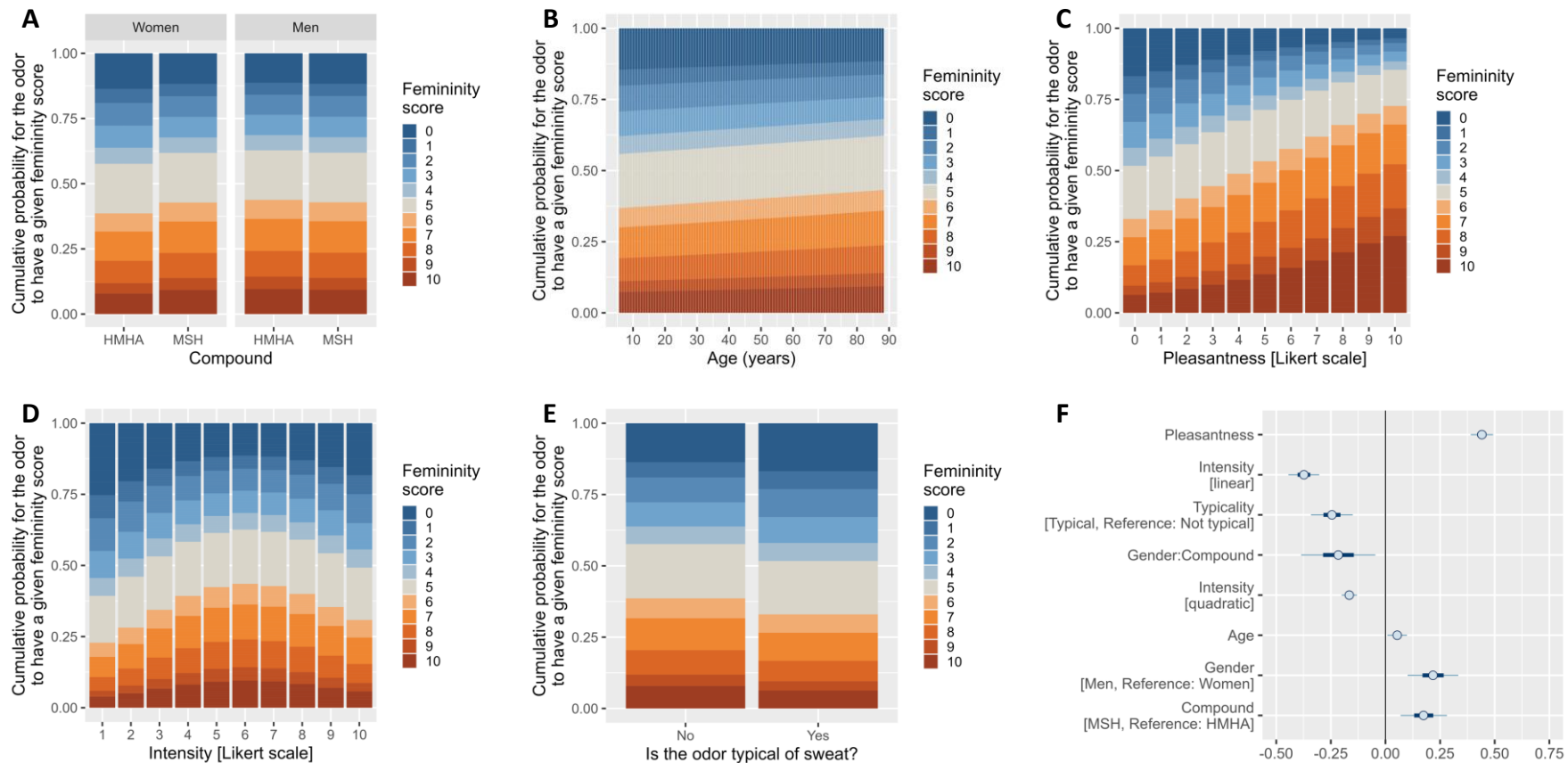
297

298 **Table 2.** Results of the reduced Bayesian linear mixed model on Masculinity/Femininity ratings and on
 299 Certainty of the Masculinity/Femininity rating. The items in the “Variable” column are fixed factors, and
 300 SubjectID (with a random slope for Compound) and Presentation Order were used as random factors. MAD:
 301 Median Absolute Deviation, CI: Bayesian 90% Credible Interval (low and high boundaries), p+ or p-: probability
 302 that the posterior distribution has the same effect direction than the estimate. Variables are sorted according
 303 to the absolute value of their Cohen’s d. Main effects involved in interactions (Int) are presented but not
 304 interpreted. Higher values of the estimates indicate higher probabilities to rate an odor as more feminine.
 305 Lines with minus (-) signs display variables that were removed in the reduced model. For each variable, the
 306 estimate and the limits of the 90% CI correspond respectively to the dot and the limits of the thin line in
 307 Fig. 2F.

Variable	Estimate [median]	Estimate error [MAD]	90% CI [low]	90% CI [high]	p+ or p-	Cohen’s d [median]	Cohen’s d [MAD]
MASCULINITY/FEMININITY							
Pleasantness	0.44	0.03	0.39	0.49	1.0000	0.2433	0.0171
Intensity [linear]	-0.37	0.04	-0.44	-0.30	1.0000	-0.2058	0.0236
Typicality [ref: Not typical]	-0.24	0.06	-0.34	-0.15	0.9999	-0.1351	0.0317
Rater Gender ´ Compound	-0.22	0.10	-0.38	-0.04	0.9826	-0.1191	0.0575
Intensity [quadratic]	-0.17	0.02	-0.20	-0.13	1.0000	-0.0914	0.0115
Rater Age	0.05	0.03	0.01	0.10	0.9756	0.0296	0.0117
Rater Gender [ref: Women]	0.22	0.07	0.10	0.33	Int	Int	Int
Compound [ref: HMHA]	0.17	0.06	0.07	0.28	Int	Int	Int
Rater Age ´ Compound	-	-	-	-	-	-	-
Familiarity	-	-	-	-	-	-	-
CERTAINTY of the masculinity/femininity rating							
Odor Gender-strength	1.28	0.04	1.21	1.35	1.0000	0.7054	0.0232
Compound [Ref: HMHA]	0.20	0.05	0.11	0.28	1.0000	0.1083	0.0281
Rater Gender [Ref: Women]	0.17	0.10	0.01	0.33	0.9575	0.0936	0.0537
Rater Age	-0.17	0.05	-0.25	-0.09	0.9996	-0.0912	0.0266
Rater Gender ´ Compound	-	-	-	-	-	-	-
Rater Age ´ Compound	-	-	-	-	-	-	-
Odor Gender-strength ´ Compound	-	-	-	-	-	-	-

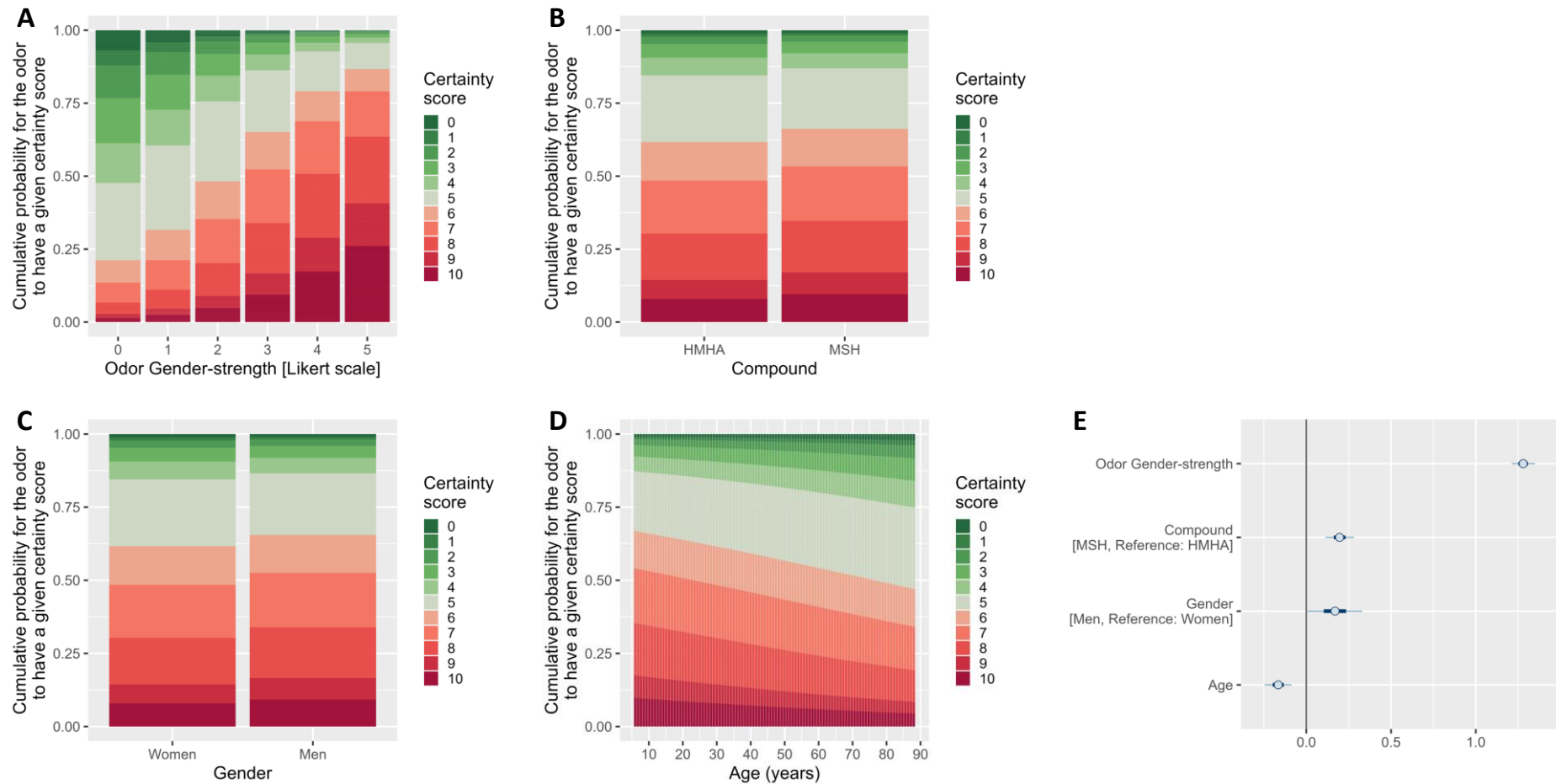
308

Running head: Perception of sex-specific body odor compounds



309
 310 **Figure 2.** Effect of (A) the Rater Gender × Compound interaction, (B) Rater Age, (C) Pleasantness rating, (D) Intensity rating and (E) Typicality on Masculinity/Femininity
 311 ratings (0 = Masculine in blue, 10 = Feminine in orange; expressed in cumulative probability to receive a given score). (F) Log odds-ratio for each variable retained in the
 312 reduced model, with the Masculinity/Femininity rating of the odor as the response variable. Dots, thick lines and thin lines represent the mean, the 50% Credible Interval
 313 [CI] and the 90% CI, respectively. Thin lines not crossing the black vertical line at $x = 0$ indicate that at least 90% of the posterior distribution of that variable has the same
 314 sign (which is equivalent to a significance level of 0.10 in the frequentist framework). For continuous variables (e.g. Pleasantness), positive posterior distributions indicate
 315 that high values on that variable are associated with high ratings of femininity. Conversely, negative posterior distributions indicate that high values on that variable are
 316 associated with low ratings of femininity. For categorical variables (e.g. Gender), positive posterior distributions indicate that the category that is not the reference (e.g.
 317 Men) give higher ratings of femininity than the reference category. Conversely, negative posterior distributions indicate that the category that is not the reference give
 318 lower ratings of femininity than the reference category. Interactions and quadratic terms are easier to interpret by looking at panels A and D. Variables are sorted
 319 according to the absolute value of their Cohen's *d* (highest on top).

Running head: Perception of sex-specific body odor compounds



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Figure 3. Effect of **(A)** Odor Gender-strength, **(B)** Compound, **(C)** Rater Gender, **(D)** Rater Age on the ratings of Certainty of the Masculinity/Femininity response (from 0 = low to 10 = high; expressed in cumulative probability to receive a given score). **(E)** Log odds-ratio for each variable retained in the reduced model, with the Certainty rating as the response variable. Dots, thick lines and thin lines represent the mean, the 50% Credible Interval [CI] and the 90% CI, respectively (see legend of Fig. 2 for more details). Variables are sorted according to the absolute value of their Cohen's d (highest on top).

326 **3.2. Pleasantness, Intensity, Familiarity**

327 In this section focusing on the other odor ratings, only effects with Cohen's $d > 0.2$ are
328 illustrated (Fig. 4; see Supplementary Material for the other effects). No significant Rater
329 Gender \times Compound interactions were found, only main effects of Gender for Intensity
330 (Est. = -0.42 ± 0.09 , 90% CI [-0.56; -0.28], $p = 1$; Table 3), Familiarity (Est. = -0.37 ± 0.12 , 90%
331 CI [-0.56; -0.17], $p = 0.9989$; Table 3), and – with the biggest effect size (Cohen's $d = 0.40$) –
332 Pleasantness (Est. = 0.73 ± 0.10 , 90% CI [0.57; 0.89], $p = 1$; Table 3). More specifically,
333 women provided higher intensity (Fig. 4A) and familiarity ratings (Fig. S1A), as well as lower
334 pleasantness ratings than men (Fig. 4B), independently of the odor compound sampled. We
335 found a significant Rater Age \times Compound interactions for Intensity (Est. = 0.26 ± 0.06 , 90%
336 CI [0.17; 0.36], $p = 1$; Table 3), and for Pleasantness (Est. = -0.31 ± 0.06 , 90% CI [-0.41; -
337 0.21], $p = 1$; Table 3). The perceived intensity tended to increase with age for MSH and to
338 decrease for HMHA (Fig. S1B), and pleasantness tended to decrease with age for MSH while
339 the reverse occurred for HMHA (Fig. S1C). Furthermore, the perceived familiarity of both
340 compounds increased with age (Est. = 0.41 ± 0.06 , 90% CI [0.32; 0.51], $p = 1$; Table 3 and
341 Fig. 4C), and MSH elicited higher familiarity ratings than HMHA (Est. = 0.49 ± 0.06 , 90% CI
342 [0.38; 0.59], $p = 1$; Table 3 and Fig. 4D).

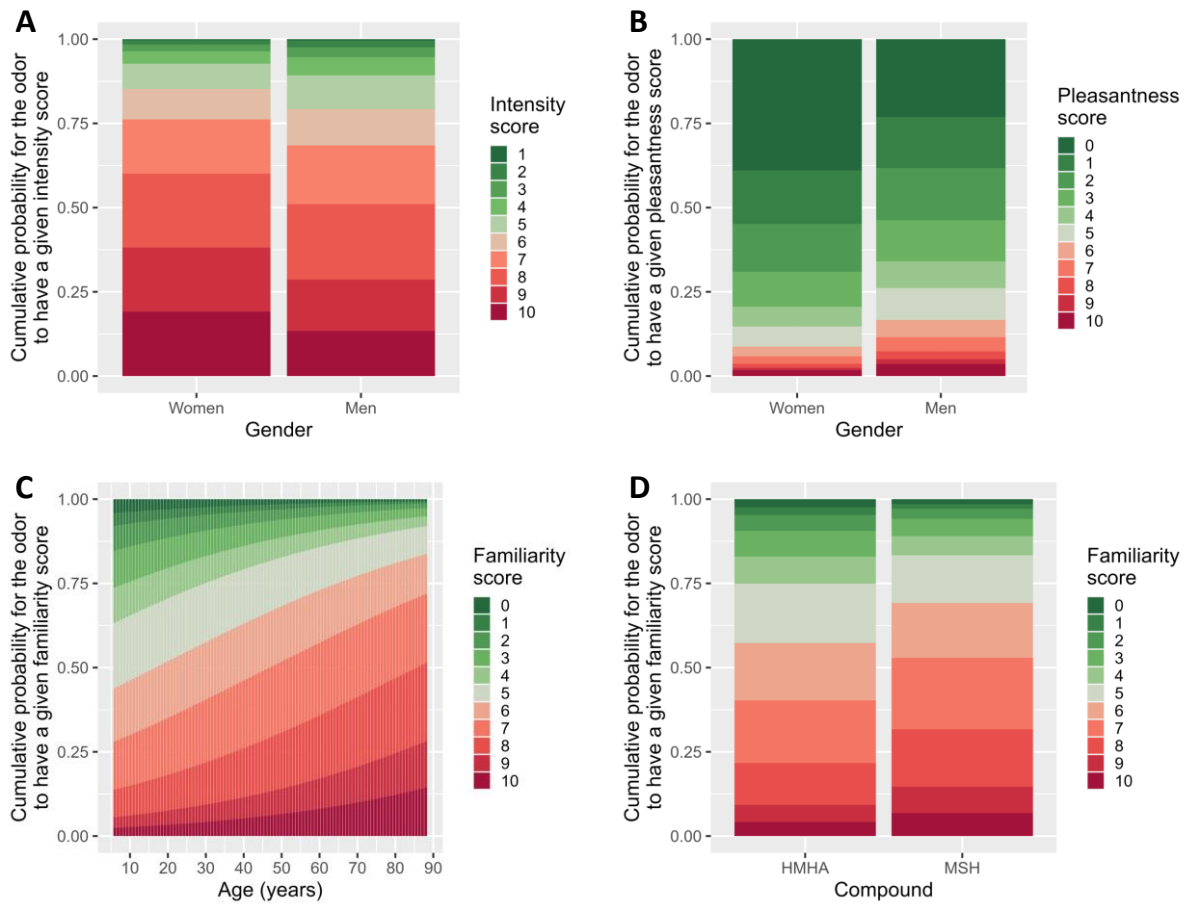
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345 **Table 3.** Results of the three reduced Bayesian linear mixed models on Intensity, Familiarity, and Pleasantness.
 346 The items in the “Variable” column are fixed factors, and SubjectID (with a random slope for Compound) and
 347 Presentation Order were used as random factors. MAD: Median Absolute Deviation, CI: Bayesian 90% Credible
 348 Interval (low and high boundaries), p+ or p-: probability that the posterior distribution has the same effect
 349 direction than the estimate. Variables are sorted according to the absolute value of their Cohen’s d. Main
 350 effects involved in interactions (Int) are presented but not interpreted. Higher values of the estimates indicate
 351 higher probabilities to rate an odor as more intense, familiar, pleasant, or to rate the odor
 352 femininity/masculinity with higher certainty, respectively. Lines with minus (-) signs display variables that were
 353 removed in the reduced model. For each variable, the estimate and the limits of the 90% CI correspond
 354 respectively to the dot and the limits of the thin line in Fig. S2.

Variable	Estimate [median]	Estimate error [MAD]	90% CI [low]	90% CI [high]	p+ or p-	Cohen’s d [median]	Cohen’s d [MAD]
INTENSITY							
Rater Gender [Ref: Women]	-0.42	0.09	-0.56	-0.28	1.0000	-0.2310	0.0476
Rater Age ´ Compound	0.26	0.06	0.17	0.36	1.0000	0.1445	0.0310
Rater Age	-0.05	0.05	-0.13	0.04	Int	Int	Int
Compound [Ref: HMHA]	0.49	0.06	0.40	0.60	Int	Int	Int
Rater Gender ´ Compound	-	-	-	-	-	-	-
FAMILIARITY							
Compound [Ref: HMHA]	0.49	0.06	0.38	0.59	1.0000	0.2840	0.0279
Rater Age	0.41	0.06	0.32	0.51	1.0000	0.2117	0.0288
Rater Gender [Ref: Women]	-0.37	0.12	-0.56	-0.17	0.9989	-0.1794	0.0580
Rater Gender ´ Compound	-	-	-	-	-	-	-
Rater Age ´ Compound	-	-	-	-	-	-	-
PLEASANTNESS							
Rater Gender [Ref: Women]	0.73	0.10	0.57	0.89	1.0000	0.4031	0.0531
Rater Age ´ Compound	-0.31	0.06	-0.41	-0.21	1.0000	-0.1706	0.0330
Rater Age	0.22	0.05	0.13	0.30	Int	Int	Int
Compound [Ref: HMHA]	-0.20	0.08	-0.33	-0.07	Int	Int	Int
Rater Gender ´ Compound	-	-	-	-	-	-	-

355



356

357 **Figure 4.** Effect of Rater Gender on Intensity (A) and Pleasantness ratings (B). Effect of Rater Age on Familiarity
 358 ratings (C). Effect of Compound on Familiarity (D). Ratings (0 = low, 10 = high) are expressed in cumulative
 359 probability to receive a given rating.
 360
 361

362 **Discussion**

363 Using a very large sample of men and women of all ages attending a museum exhibition,
364 this study aimed to investigate how two body odor compounds reported to be emitted in
365 sexually dimorphic amounts (the “feminine” compound MSH and the “masculine”
366 compound HMHA) were perceived.

367

368 The main question tested was whether MSH was perceived as more feminine than HMHA,
369 and conversely HMHA as more masculine than MSH. We found this to be the case only in
370 women, although they were less confident in their ratings than men. However, this result is
371 qualified, because the size of the effect is very small despite the very large sample size
372 (N=2’716) due to very high variability, and because the scores are fairly non-gendered for
373 both compounds (i.e., mean score around 5) (see Supplementary Table S1). If we assume
374 that this effect is of practical interest, it seems likely that it reflects a better ability of women
375 to process body odors, and odors in general. Previous studies have shown that women
376 generally outperform men in all olfactory abilities [28] and in particular are better at
377 performing fine discrimination of body odors (e.g., recognizing the odor of familiar
378 individuals [17,38]). This interpretation of our results is supported by several additional
379 observations in our study. Firstly, we found that women rate the odors (without distinction
380 between the compounds) as more intense and less pleasant than the men. This is consistent
381 with previous recurrent findings on body odors [16,43,52] and unpleasant non-body odors
382 [37]. Secondly, other than for Masculinity/Femininity, no interaction was found between
383 gender and compound in this study, casting doubt on the possible role of HMHA and/or
384 MSH compounds in male-female attractiveness. In particular, one could have expected that
385 MSH would be more pleasant to men and/or that HMHA would be more pleasant to women

386 (pleasantness being usually strongly correlated with attractiveness), which was not
387 observed here. This is in line with our previous studies on HMHA, that was found to be less
388 [26] or equally pleasant [27] to women than to men, and that had no gender-specific effects
389 on the perception of faces in more implicit approaches [26].

390

391 Finally, the small effect size and huge variability observed in gender ratings of MSH and
392 HMHA in our study may also question our choice of these particular compounds. Indeed,
393 the fact that the quantities of these compounds' precursors were described as highly
394 variable from one individual to another (and as largely overlapping between men's and
395 women's sample) [23] may explain why the perceptual outcome was not obvious here.
396 Clearer effects might have been found using more realistic mixtures of HMHA+MSH (instead
397 of single compounds presented separately), each based on male and female ratios that were
398 reported to be stable and 3 times higher in men [23]. Also, it must be kept in mind that
399 HMHA and MSH were not found as 'the most sexually dimorphic molecules *among* a series
400 of body odor compounds (unlike very few other studies did, e.g. [21] who reported a series
401 of 15 'gender markers' found in complex body odor profiles). Rather, sex differences
402 happened to have been found for those compounds while they were investigated to
403 understand body malodor, what is more in a limited number of participants (24 men, 25
404 women). Consequently, it may be that other compounds (possibly not identified yet) may be
405 more sexually dimorphic, and thus more relevant, and would trigger more differentiated
406 gender ratings. A promising future path to identify such compounds could be to use
407 chemical analysis to identify not only the overall changes in body odor composition between
408 pre- and post-puberty [53], but also the compounds for which sexual dimorphism increases
409 after puberty.

410

411 As to the developmental effects of odor perception, in this study we found that, with
412 increasing age, the odors were rated as more feminine (although with lower levels of
413 confidence) and more familiar, probably due to increasing exposure [54]. Also, although
414 difficult to interpret, a different pattern of perceptual changes throughout life was found for
415 MSH, that became more intense and more unpleasant with age, and HMHA, that became
416 less intense and less unpleasant with age. The latter effect is consistent with the
417 presbyosmia and reduced negativity bias phenomena in aging [55,56]. Age related effects in
418 our study may also result from shifts occurring earlier in development, such as during
419 adolescence, as reported by several studies on body odors [57] and body odor compounds
420 [58]. Importantly, however, no interaction between age and compound was found for the
421 variable Masculinity/Femininity, which again does not allow us to argue in favor of a
422 function of these compounds in male-female attractiveness.

423

424 Collecting our data in a museum during an exhibition was a considerable asset in terms of
425 sample size and of representativeness of all age groups. It may also help diluting the effects
426 of factors that we have chosen, for parsimony reasons, not to control (non-binary gender
427 identity, sexual orientation, etc.). Such a methodological choice also has its drawbacks,
428 especially regarding the relative lack of control compared to a laboratory setting. However,
429 we limited as much as possible the bias related to this lack of control, *a priori* by placing the
430 odors in hermetically sealed jars carefully watched over by the museum staff who refreshed
431 the odors every two days, and *a posteriori* by removing the obviously irrelevant responses
432 (see excluded data in Section 2.1.). Moreover, the following findings are highly consistent
433 with the literature, which suggests that we can trust the quality of the collected data: i) the

434 developmental course of HMHA and MSH perception described in the previous paragraph
435 (Fig. S1B,C) is consistent with the well-known positive relationship between intensity and
436 unpleasantness of body and non-body odors [59–61]; ii) the significant increase of
437 familiarity of the odors with age (Fig.4C) is highly consistent with a well-documented effect
438 of exposure [54]; iii) the prominent gender differences found for several perceptual
439 variables are similar to those consistently reported in the literature on olfaction (see [28] for
440 a review).

441

442 The main conclusion of this large-scale study is that, although women perceive HMHA as
443 more masculine than MSH in accordance with the alleged sexual dimorphism of these
444 compounds, this effect is very small and there is little consensus in the cohort (huge
445 variability) on the gender rating of these compounds. The results agree with the existing
446 literature regarding women's advantage in odor (and particularly social odor) processing
447 and age-related perceptual responses reflecting repeated exposure effects, but fail to
448 support the hypothesis that HMHA and/or MSH could be involved in male-female
449 attractiveness. Among the possible perspectives to understand the olfactory determinants
450 of male-female attractiveness [20], a better knowledge of the chemical composition of
451 human body odor (and of its variations as a function of sex and age) would help identifying
452 other possible relevant compounds. Also more ecological approaches where compounds are
453 not presented in an isolated manner but rather as mixtures (e.g. HMHA/MSH in a certain
454 ratio) or embedded in a "baseline body odor" may be helpful, as may experimental designs
455 where the outcome variables are not only explicit but also implicit, such as a behavior or a
456 physiological response.

457

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469

470 **Author contributions**

471 Camille Ferdenzi: Validation; Writing - original draft; Writing - review & editing.
472 Géraldine Coppin: Conceptualization; Data curation; Funding acquisition; Investigation;
473 Methodology; Supervision; Validation; Writing - review & editing.
474 Christophe Bousquet: Formal analysis; Visualization; Writing - original draft; Writing - review
475 & editing.
476 Sylvain Delplanque: Conceptualization; Data curation; Funding acquisition; Investigation;
477 Methodology; Project administration; Supervision; Validation; Writing - review & editing.

478

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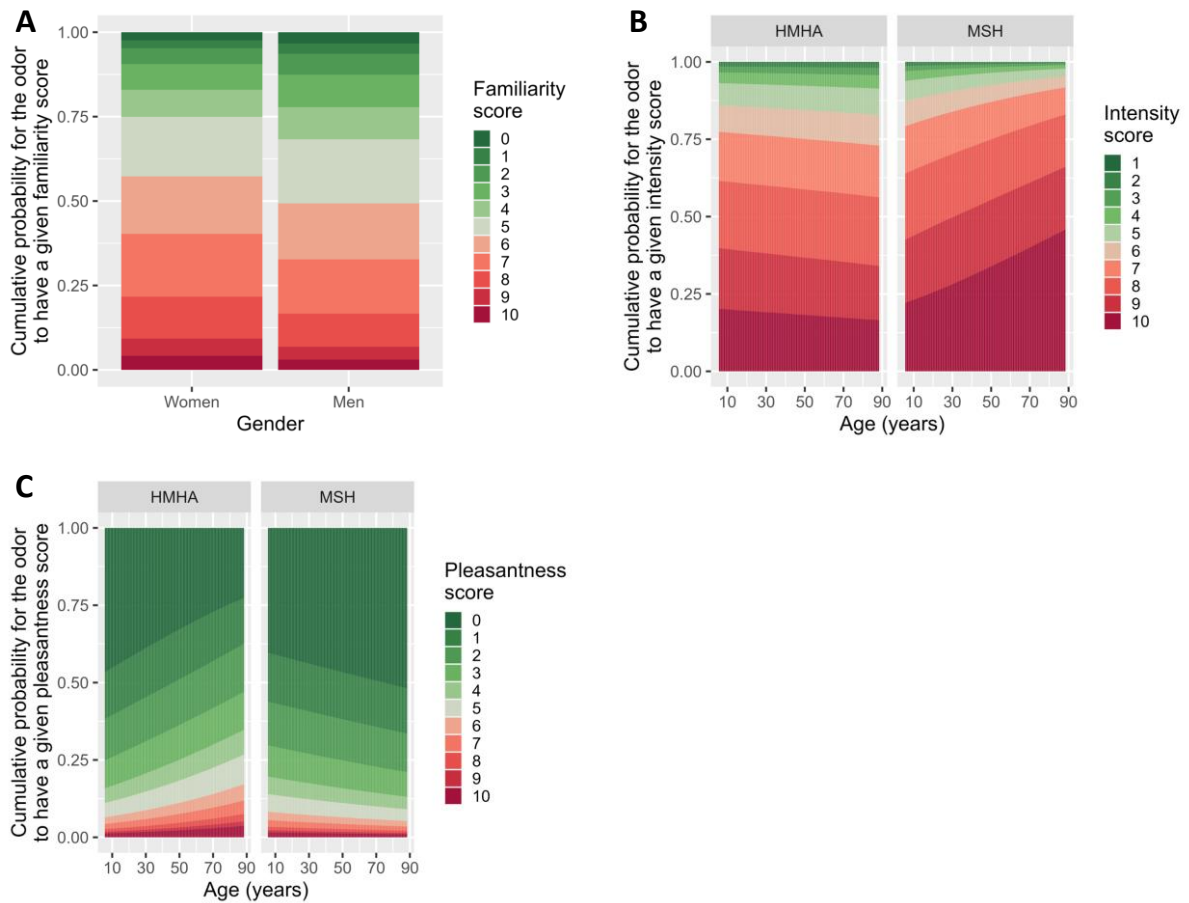
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662 **Supplementary Material**

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666 **Figure S1.** Effect of Rater Gender on Familiarity ratings **(A)**. Effect of the Rater Age × Compound interaction on
 667 Intensity **(B)** and Pleasantness ratings **(C)**. Ratings (0 = low, 10 = high) are expressed in cumulative probability
 668 to receive a given score.

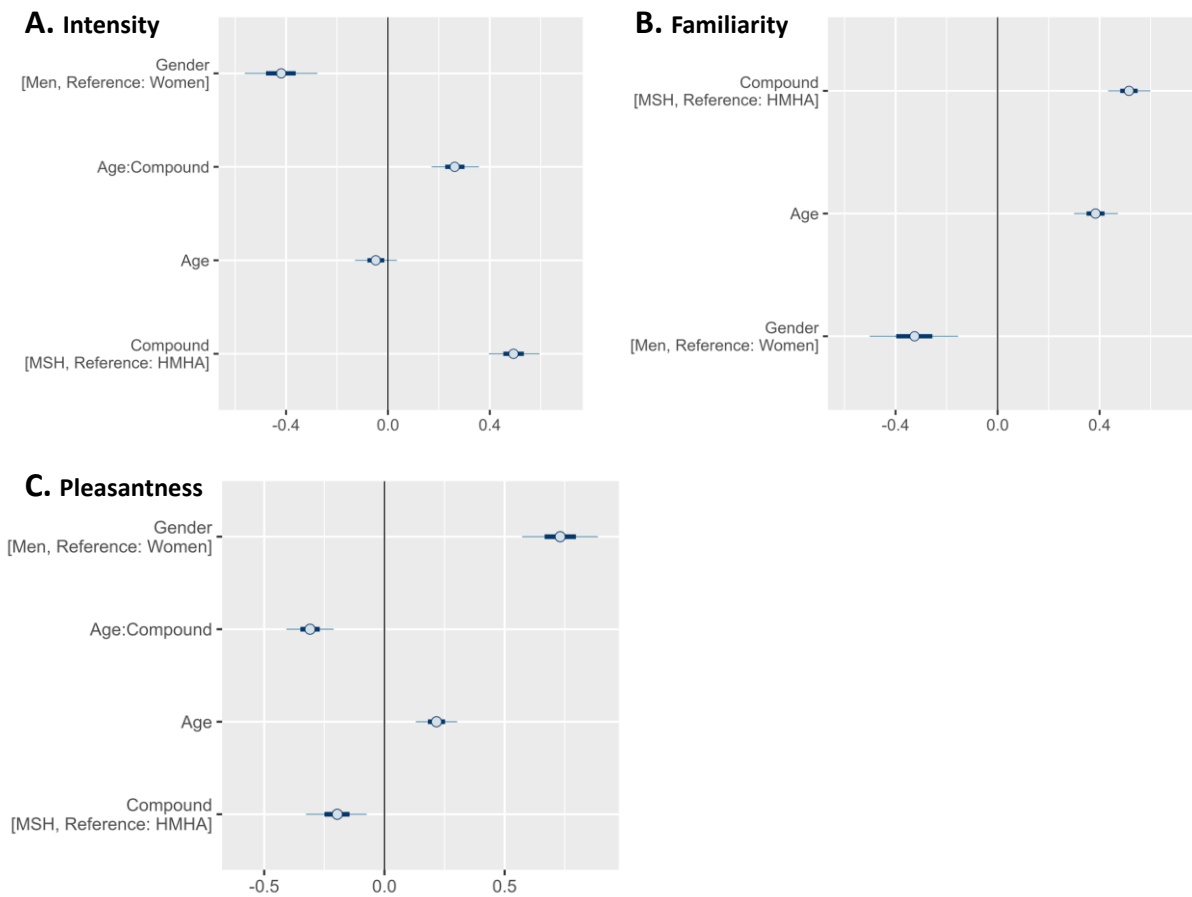
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675 **Figure S2.** Log odds-ratio for each variable retained in the reduced model, with the Intensity **(A)**, Familiarity **(B)**
 676 and Pleasantness of the odor **(C)** as the response variable. Dots, thick lines and thin lines represent the mean,
 677 the 50% Credible Interval [CI] and the 90% CI, respectively. Thin lines not crossing the black vertical line at $x = 0$
 678 indicate that at least 90% of the posterior distribution of that variable has the same sign (which is equivalent to
 679 a significance level of 0.10 in the frequentist framework). Positive posterior distributions indicate that high
 680 values on that variable are associated with high ratings. Conversely, negative posterior distributions indicate
 681 that high values on that variable are associated with low ratings. Variables are sorted according to the absolute
 682 value of their Cohen's d (highest on top).

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Table S1. Mean \pm Standard Deviation of the Masculinity/Femininity ratings and of the Certainty of the Masculinity/Femininity ratings for each compound (MSH, HMHA), by Rater Gender and Rater Age group and for All groups combined.

	Masculinity/Femininity		Certainty of the Masculinity/Femininity rating	
	MSH	HMHA	MSH	HMHA
<i>Women</i>	4.34 \pm 3.38	4.17 \pm 3.15	6.38 \pm 3.11	5.98 \pm 3.21
6 to 9	4.40 \pm 3.83	3.87 \pm 3.67	7.29 \pm 3.17	6.92 \pm 3.32
10 to 19	4.30 \pm 3.27	4.00 \pm 3.08	6.19 \pm 3.09	5.93 \pm 3.18
20 to 29	4.35 \pm 3.25	4.15 \pm 2.99	6.38 \pm 3.12	5.92 \pm 3.19
30 to 39	4.26 \pm 3.36	4.22 \pm 3.11	6.14 \pm 3.05	5.66 \pm 3.09
40 to 49	4.45 \pm 3.38	4.15 \pm 3.13	6.48 \pm 3.11	6.33 \pm 3.21
50 to 59	4.70 \pm 3.72	4.53 \pm 3.34	6.60 \pm 3.19	5.70 \pm 3.24
60 to 69	4.20 \pm 3.44	4.99 \pm 3.33	6.84 \pm 2.83	5.93 \pm 3.25
70 to 90	3.62 \pm 2.59	4.23 \pm 2.55	4.77 \pm 3.39	5.31 \pm 3.64
<i>Men</i>	4.55 \pm 3.36	4.75 \pm 3.15	6.56 \pm 2.97	6.20 \pm 3.03
6 to 9	4.59 \pm 4.04	4.99 \pm 3.74	7.41 \pm 3.21	6.81 \pm 3.46
10 to 19	4.36 \pm 3.30	4.44 \pm 3.26	6.82 \pm 2.91	6.69 \pm 2.96
20 to 29	4.81 \pm 3.31	5.17 \pm 2.98	6.47 \pm 2.87	6.06 \pm 2.83
30 to 39	4.70 \pm 3.20	4.85 \pm 2.86	5.95 \pm 2.96	5.61 \pm 2.92
40 to 49	4.15 \pm 3.15	4.55 \pm 3.01	6.49 \pm 2.83	6.05 \pm 2.97
50 to 59	5.55 \pm 3.42	4.74 \pm 3.17	6.49 \pm 3.06	6.35 \pm 3.03
60 to 69	3.97 \pm 3.31	4.79 \pm 2.91	6.38 \pm 2.87	5.24 \pm 2.95
70 to 90	3.53 \pm 3.06	5.00 \pm 3.30	5.79 \pm 3.28	5.05 \pm 3.47
<i>All</i>	4.42 \pm 3.37	4.39 \pm 3.16	6.44 \pm 3.06	6.07 \pm 3.14

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Running head: Perception of sex-specific body odor compounds

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Table S2. Mean \pm Standard Deviation of the Intensity, Familiarity and Pleasantness ratings, and % “yes” responses to the question “does this correspond to a typical smell of sweat?” for each compound (MSH, HMHA), by Rater Gender and Rater Age group and for All groups combined.

	Intensity		Familiarity		Pleasantness		Typical of sweat	
	MSH	HMHA	MSH	HMHA	MSH	HMHA	MSH	HMHA
<i>Women</i>	8.70 \pm 1.79	8.25 \pm 2.10	6.17 \pm 3.12	5.58 \pm 3.19	1.35 \pm 2.40	1.43 \pm 2.38	78%	68%
6 to 9	7.91 \pm 2.65	7.77 \pm 2.70	4.75 \pm 3.88	3.98 \pm 4.02	2.46 \pm 3.28	1.91 \pm 2.98	67%	61%
10 to 19	8.40 \pm 1.92	8.25 \pm 2.07	5.80 \pm 3.12	5.14 \pm 3.15	1.26 \pm 2.42	1.13 \pm 2.09	74%	66%
20 to 29	8.90 \pm 1.60	8.39 \pm 1.96	6.42 \pm 2.74	5.90 \pm 2.92	1.41 \pm 2.42	1.35 \pm 2.22	81%	69%
30 to 39	8.95 \pm 1.49	8.32 \pm 2.08	6.58 \pm 2.93	5.83 \pm 2.92	1.21 \pm 2.08	1.48 \pm 2.32	79%	68%
40 to 49	9.00 \pm 1.48	8.42 \pm 1.90	6.71 \pm 2.93	6.28 \pm 3.04	1.01 \pm 2.08	1.40 \pm 2.47	84%	76%
50 to 59	8.86 \pm 1.87	8.34 \pm 1.99	6.43 \pm 3.23	6.13 \pm 3.16	1.34 \pm 2.32	1.77 \pm 2.63	79%	71%
60 to 69	8.89 \pm 1.24	7.91 \pm 2.17	6.33 \pm 3.31	5.74 \pm 3.29	1.55 \pm 2.67	1.94 \pm 2.68	84%	68%
70 to 90	7.96 \pm 2.07	6.88 \pm 2.53	4.12 \pm 3.17	3.62 \pm 2.87	1.31 \pm 1.76	1.92 \pm 2.65	73%	54%
<i>Men</i>	8.37 \pm 1.93	7.98 \pm 2.16	5.86 \pm 3.13	5.17 \pm 3.21	1.88 \pm 2.63	1.93 \pm 2.58	74%	64%
6 to 9	8.23 \pm 2.35	8.26 \pm 2.45	3.93 \pm 4.02	3.18 \pm 3.80	2.46 \pm 3.44	1.70 \pm 2.93	70%	62%
10 to 19	8.14 \pm 2.04	7.86 \pm 2.22	5.23 \pm 3.21	4.62 \pm 3.26	2.00 \pm 2.82	1.86 \pm 2.66	66%	63%
20 to 29	8.16 \pm 2.08	7.86 \pm 2.20	6.52 \pm 2.71	5.64 \pm 2.97	1.96 \pm 2.56	2.16 \pm 2.51	77%	66%
30 to 39	8.67 \pm 1.66	8.15 \pm 2.05	6.41 \pm 2.77	5.77 \pm 2.85	1.50 \pm 2.18	1.74 \pm 2.36	77%	61%
40 to 49	8.61 \pm 1.57	7.85 \pm 1.95	6.82 \pm 2.40	5.90 \pm 2.72	1.62 \pm 2.13	2.02 \pm 2.40	83%	65%
50 to 59	8.83 \pm 1.58	8.41 \pm 1.87	6.17 \pm 2.85	6.23 \pm 2.84	1.96 \pm 2.87	2.14 \pm 2.79	84%	71%
60 to 69	8.41 \pm 1.48	7.69 \pm 2.41	6.93 \pm 2.40	5.48 \pm 3.02	2.07 \pm 2.51	2.24 \pm 2.47	86%	76%
70 to 90	8.21 \pm 2.27	7.63 \pm 2.54	4.58 \pm 3.58	4.26 \pm 3.78	1.21 \pm 1.51	2.16 \pm 2.93	63%	58%
<i>All</i>	8.58 \pm 1.85	8.15 \pm 2.13	6.05 \pm 3.13	5.42 \pm 3.20	1.55 \pm 2.50	1.62 \pm 2.47	77%	67%

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