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2 *Evidence for odour-mediated assortative mating in humans: The*

3 *impact of hormonal contraception and artificial fragrances*

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5 **Caroline Allen[1,2,3], Jan Havlíček[4], Kate Williams[5], & S. Craig Roberts[3]**

6

7 1 School of Psychology, Newcastle University, Newcastle upon Tyne, UK

8 2 Centre for Behaviour and Evolution, Newcastle University, UK

9 3 Division of Psychology, University of Stirling, Stirling, UK

10 4 Department of Zoology, Charles University, Prague, Czech Republic

11 5 Unilever Research Port Sunlight Laboratory, Merseyside, UK

12

13 *Correspondence:*

14 Caroline Allen, School of Psychology, Newcastle University, Newcastle upon Tyne,

15 NE1 7RU, United Kingdom.

16 Email: caroline.allen@newcastle.ac.uk

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24 **Abstract**

25 There is substantial evidence for assortative partner preferences in humans based on
26 physical characteristics. In contrast, evidence suggests that olfactory preferences tend
27 to be disassortative, with people preferring body odour of potential partners who are
28 dissimilar at key genetic loci, perhaps to gain fitness advantage through offspring
29 heterozygosity. We compared ratings of perceived body odour similarity of real
30 couples with those of randomly paired 'fake' couples. Contrary to prediction, we find
31 that odours of real partners are perceived more, rather than less, similar to each other
32 than fake couples. However, this applied only to natural odour samples: there were no
33 differences in similarity levels of real and fake couples' samples which were collected
34 while wearing artificial fragrances. Furthermore, in light of suggestions that hormonal
35 contraception (HC) disrupts disassortative odour preferences in women, we compared
36 odour similarity among real couples in which the female partner was using or not using
37 HC at the time when the relationship began. We find that odours of HC-using couples
38 are of intermediate similarity between non-using and fake couples, suggesting that HC
39 use during partner choice could affect odour-influenced assortment. We also
40 examined the association between relationship satisfaction and perceived similarity of
41 unfragranced odours of real couples. We found that these are positively correlated in
42 male partners but negatively correlated in the female partners, indicative of a sex
43 difference in the relative favourability of odour similarity in partner preference. Finally,
44 by comparing odour similarity ratings with those given by perfumers using a novel
45 olfactory lexicon we found evidence that similarity judgements were based on the
46 Spicy/Animalic aspects of individual odour profiles. Taken together, our results
47 challenge the conventional view that odour-mediated partner preferences in humans
48 are typically disassortative.
49
50 **Key words:** Homogamy, Fragrance, Hormonal contraception, Assortative mating,

51 Body odour, Olfaction.

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1. Introduction

If there is a 'golden rule' of human mating patterns, it would be the concept of homogamy, or assortative mating [1, 2]. A substantial body of research demonstrates that individuals tend to prefer partners who share socially or culturally relevant attributes, including age, social background, level of education, religion, cultural group and ethnicity [3, 4, for a review see 5]. Furthermore, similarity in personality traits among couples is associated with marital quality [6-8], although other studies have disputed the strength of this effect [9]. There is also evidence for assortative preferences based on evolutionarily relevant traits such as wealth and status, commitment to family, sexual fidelity, life history strategy and sensational interests [10, 11], according to a 'likes-attract' decision rule [10].

This rule applies just as much to physical appearance; individuals express preferences for those who bear a physical self-resemblance. For example, there is some evidence for modest assortment based on height [12, 13] and body-mass index or adiposity [14, 15]. There is especially convincing evidence for assortative partner preferences based on facial appearance. Individuals express moderate preferences for faces that have been digitally manipulated to become more self-resembling [16-19]. Furthermore, the faces of actual couples are perceived to be more similar than by chance. Hinsz [20] compared the perceived resemblance, by unfamiliar judges, of the faces of actual couples and compared these with judgments of randomly-paired individuals (or 'fake couples'), finding that similarity ratings were higher for judgments of real couples [see also 21, 22]. Such preferences may likely arise through imprinting-like effects on parental traits [23]. Consistent with the latter, several studies suggest that preferences for facial shape and eye colour in potential partners is strongly influenced by the traits of the opposite-sex parent [24, 25].

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85   Against this background, it is thought that olfactory preferences may be an

86   exception to the "like-prefers-like" decision rule in human mating. It has been

87   suggested that disassortative odour preferences, as observed in many other

88   vertebrates [26, 27], is likely to be a critical evolutionary mechanism serving to achieve

89   an optimal level of genetic dissimilarity at key genetic loci, and thereby influencing

90   health and survival of potential offspring via heterozygote advantage. The particular

91   focus of this idea is the relationship between odour preference and relative dissimilarity

92   at genes in the major histocompatibility complex (MHC, formally referred to as HLA,

93   human leukocyte antigen, in humans). The MHC is a family of co-dominantly

94   expressed genes that underpins adaptive immunity functioning in vertebrates (28,29).

95   Selection of mates who share relatively few MHC genes will thus increase offspring

96   MHC heterozygosity, conferring an immune advantage in form of higher repertoire of

97   recognizing molecules.

98   Evidence for MHC-disassortative odour preferences in humans is admittedly

99   mixed [30, 31, 68]. Several experimental studies have suggested that men or women

100   prefer odours of MHC-dissimilar individuals [e.g. 32, 33], although other studies report

101   no clear effect [34-36], and one study provides evidence for preference for an

102   intermediate rather than extreme level of dissimilarity [37]. Similarly, evidence for lower

103   than chance levels of MHC allele-sharing in real couples is sparse; for example, one

104   study provides such evidence within a closed-mating population [38], but several

105   others do not [39, 40]. On the other hand, other studies suggest that relatively high

106   MHC dissimilarity within couples is associated with higher sexual attraction to partner

107   and relationship satisfaction [41, 42]. In summary, while some researchers [31] have

108   argued that MHC-mediated mate preferences may not be evident in humans, the

109   evidence remains mixed. Nonetheless it is still true that most researchers expect, if

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110 odour preferences do play a role in mate selection, that they will most likely be

111 underpinned by negative rather than positive assortment.

112   In this study, we aimed to test this idea directly by adapting a methodology used

113 previously for investigating assortative facial preferences [20]. We collected odour

114 samples from both male and female partners in established romantic relationships,

115 while refraining from use of artificial fragrance. We then examined the perceived

116 similarity of these odours according to a panel of independent judges, and compared

117 the similarity ratings of these odour pairs against a sample of 'fake couples', created

118 by randomly pairing a male and female odour from the population of samples. On the

119 basis of the literature described above, we predicted that odours of the real couples

120 would be rated as more dissimilar to each other than the randomly paired odours.

121   We know of only one paper to date which has examined the similarity of odours

122 within romantic couples. Porter and colleagues [43] recruited 12 spouses and had their

123 odours matched to one another by thirty participants, finding that participants were not

124 successful at this matching task. However, this study had a different aim from our own,

125 and these findings do not speak to the level of similarity between these spousal

126 odours, which is of direct interest to us. In this study we have odours rated rather than

127 matched, and we compare the odour ratings with random pairings of fake couples.

128 Finally, we explicitly test the effects of environmental influences (discussed further

129 below) by comparing fragrance and non-fragrance sample ratings – as Porter and

130 colleagues were interested in similarity *resulting* from shared environments of spouses

131 they did not control for this.

132   In addition, we set out to investigate the extent to which within-couple odour

133 dissimilarity would be affected by two potential confounding influences. First, among

134 our real couples, we recruited half in which the female partner was using hormonal

135   contraception (HC) when the relationship began, and half in which she was not. This

136   decision was based on pre-existing evidence that HC may disrupt women's

137   disassortative odour preference. This possible effect was first reported by Wedekind

138   et al. [33], who found that women using oral contraception preferred odours of

139   relatively MHC-similar men. Consistent with this, Roberts et al. [34] subsequently

140   found a preference shift towards MHC-similarity in women after initiating oral

141   contraceptive use, a change which was not evident in a control group of non-users.

142   Based on this evidence, we predicted that levels of within-couple odour similarity

143   would be higher in those couples in which the woman used HC at the time of pair

144   formation.

145   Second, we also investigated the effects of fragrance use on relative odour

146   similarity. Fragrance use could influence the communication of socially relevant

147   olfactory information in one of two main ways [44]. The most obvious effect is that

148   artificial fragrances mask the underlying body odour, obscuring any meaningful social

149   cues. Alternatively, fragrance use might not interfere with, or may even enhance, the

150   communication of underlying social information, if individuals choose between

151   fragranced products in a way that complements their own body odour and produces a

152   distinctive and congruent fragrance-body odour blend. Although the second possibility

153   may seem unlikely, Lenochová et al. [45] found that such blends were rated as more

154   pleasant when they involved an individual's preferred fragrance compared with blends

155   involving a fragrance assigned to them experimentally, even when there was no

156   difference in pleasantness of the alternative fragrances in isolation. In addition to this,

157   Allen and colleagues [46] found that participants discriminated between odours of

158   individuals more successfully when they were wearing a chosen rather than an

159   assigned deodorant, suggesting that the fragrances people choose to wear do in some

160   way maintain useful information contained in their odours. Furthermore, there is some

161   evidence for associations between liking for fragrance ingredients and individual MHC

162   type. Milinski and Wedekind [47] reported a significant association between MHC

163   alleles and certain ingredients preferred for perfumes to be used by individuals

164   themselves, but not for their partners. They suggested that this supports the

165   hypothesis that fragrances are chosen to enhance the availability of MHC-related cues

166   in mate choice (for supporting evidence, see also 48). To examine these alternatives,

167   we also collected, from the same couples, samples of their own odour together with

168   their own preferred fragrance. We expected that within-couple odour dissimilarity

169   judged using these body odour-fragrance blends would be at the same level as 'fake

170   couples' if fragrances mask cues of body odour dissimilarity. Alternatively, if

171   fragrances complement or enhance odour individuality, we expected that levels of

172   perceived dissimilarity would be at the same level, or even higher, than would be

173   observed for judgments of unfragranced samples of real couples.

174   Finally, previous studies have raised the issue that rating scales used in studies

175   investigating the perceptual qualities of body odours are often quite simple and may

176   potentially fail to capture some of the olfactory nuances present [49]. In this study, we

177   employ a simple rating scale of similarity (from 1 -not at all similar, to 9 - completely

178   similar) and directly test the utility of this by comparing these ratings to those given by

179   olfactory experts who used a novel lexicon to describe the odour samples.

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2. Methods

2.1 Odour Donors

Thirty heterosexual couples who had been in a romantic relationship for at least 6 months, and in which the female partner had not yet reached menopause, were recruited to provide odour samples. We deliberately recruited fifteen couples who reported they had begun their relationship whilst the woman was using some form of hormonal contraception (HC), and fifteen whilst the woman was not using any form of HC (mean age of women = 28, SD = 8.59, range 20-51 years; mean age of male partners = 29.47, SD = 9.21, range 20-51 years). All individuals were of European origin and recruited in Scotland, UK. Our participants used a range of HC - 12 using oral contraception, 2 using an implant, and 1 using contraceptive injections.

Each individual underwent two 24 hour odour collection periods on consecutive days, the first of which was without any fragranced products and the second whilst wearing the individuals' usual deodorant or antiperspirant. In line with previous research, we instructed our body odour donors to avoid drinking alcohol, being in smoky places, exercising and eating certain strong-smelling foods (e.g. garlic, asparagus, curry) one day prior to, and during, odour collection periods [34]. They were additionally asked to refrain from sexual activity and to avoid sharing their bed with anyone during the odour collection phases [45]. Donors were also provided with fragrance free soap (Simple PureTM) and asked to use only this in place of any fragranced hygiene products for 24 hours prior to the first day, and during the first day of odour collection.

Each donor was provided informed consent and was given an odour collection pack containing instructions, including a reminder to avoid the aforementioned behaviour/foods, as well as experimenter contact details. The pack also included

207   100% cotton oval shaped make-up pads (approximately 9.5cm x 6.5cm, 3mm thick,

208   Cosmetic Oval Pads, The Boots Company PLC) and surgical tape (FineporeTM,

209   2.5cm wide). Donors were instructed to apply the cotton pad onto their armpit, using

210   the tape to hold this in place, and to remove it after 24 hours had passed. There is

211   variation in sampling time across studies, though numerous studies to date have

212   adopted 24 hour sampling periods for odour collection [50-52]. Furthermore, Havlíček

213   et al. [50] found that 12 hour sampling yielded samples which were less intense, and

214   less likely to be perceived, compared with a 24 hour sampling period. Donors were

215   instructed to remove the pads after 24h, and seal them in small, pre-labelled, plastic

216   zip lock bags which we provided. The donors returned the samples, labelled and in

217   sealed plastic bags, to the lab within 2 hours of removal, where they were stored in a

218   freezer at -20˚C until use. Samples were thawed at room temperature for 2 hours prior

219   to test sessions. Previous research suggests freezing and thawing of samples has

220   minimal impact on the perceptual quality of the odour [34, 53].

221   Donors also completed an online questionnaire to collect basic demographic

222   information, as well as information on length of their relationship, cohabitation status

223   and current and past contraceptive use. Of those who met whilst using hormonal

224   contraception, 10 were cohabiting and 5 were not. Of those who were not using

225   hormonal contraception when they met, 12 were cohabiting and 3 were not. Couples

226   also completed the Relationship Assessment Scale [54], consisting of 7 items (e.g. "In

227   general, how satisfied are you with your relationship?"), which participants completed

228   using a 5-point scale, where high scores indicated relative satisfaction.

229

2.2 Raters

231   Recruitment of the raters including the subsequent odour rating sessions took

232   place at the Centre for Life in Newcastle upon Tyne, where 437 visitors participated

233   (280 women, 157 men). After excluding those individuals who did not complete the

234   task, there was a total sample size of 261 female (mean age = 40.89, SD = 10.35,

235   range: 17-76) and 152 male raters (M = 42.67, SD = 12.26, range = 17-78). All but 30

236   of these also completed the Sniffin' SticksTM 12-item odour identification test. In order

237   to avoid olfactory fatigue, each rater only rated a sub-sample of the odour stimuli, and

238   so on average, each sample was rated by 27.5 participants (range = 23-34, SD =

239   3.42).

240   After these ratings had taken place, the samples (plus one additional couple)

241   were employed in a further study [49] where they were used to develop a novel lexicon

242   for describing human body odours. They were subsequently rated using this lexicon

243   by two perfumers and two perfume evaluators (see [49] for details). The ratings given

244   by these four trained individuals and using this novel lexicon are incorporated into the

245   results of the current paper (allowing us to compare ratings given by novices from this

246   study with assessments made using our novel lexicon by olfactory experts in the

247   previous study).

248

2.3 Procedure

250   Each participant took part in one test session only. After providing informed consent,

251   they were presented with 6 pairs of 500ml conical flasks containing body odours (12

252   individual samples in total). Participants were not presented with a greater number of

253   odours in order to reduce any potential effects of sensory overload or olfactory fatigue.

254   Participants did not know the sex of the samples or that the samples came from

255   individuals in romantic relationships. Participants were instructed to remove the tin foil

256   caps from each pair of flasks, to sniff both samples, and then to rate them simply on

257   how similar the two smelled to each other (using a scale from 1 -not at all similar, to 9

258   - completely similar). Pair 1 contained the unfragranced odour samples from one donor

259   couple who began their relationship whilst using HC (male and female odours in

260   separate flasks) and pair 2 were the same couples' fragranced samples. Pairs 3 and

261   4 were the odour samples of a couple who began their relationship whilst not using

262   HC (unfragranced and fragranced samples, respectively). The final two pairs were

263   from a single 'fake' couple: a man and a woman from separate couples were assigned

264   as a pair by the experimenter (again, using the unfragranced and fragranced samples

265   from the same two individuals). Presentation order of the odour pairs was randomised.

266   The individuals chosen for the 'fake' couples were those whose samples had been, or

267   were about to be, used in one of the other two test sessions from the same day; in this

268   way, we were able to reduce the amount of time that samples were unfrozen. Each

269   sample was thawed and used for one day (6-8 hours, before being re-frozen). Samples

270   were stored in a cool box with ice packs when not in use during the day. In all, 15 test

271   sessions were carried out over 5 days (3 sessions each day). Each session lasted

272   between 1.5 and 3 hours depending on recruitment rate, and contained samples from

273   different couples. Finally, each participant also completed the Sniffin' Sticks olfactory

274   identification test to ascertain their olfactory identification abilities, one measure of

275   general olfactory competence [55].

276

277   **_2.4 Analysis_**

278   The data were analysed in two ways. We first used individual raters as the unit of

279   analysis, using repeated measures ANOVA, with both Couple Type (No HC, HC,

280   Fake) and Sample Type (Fragranced, Unfragranced) as within-subjects factors. This

281   approach follows directly from the experimental design and maximises available

282   statistical power. A further benefit of this approach is that we can additionally control

283   for individual variability in ratings by including each individual rater's score on the

284   Sniffin' Sticks test as a covariate and rater sex as a between-subjects fixed factor

285   (women are often thought to have higher average olfactory acuity; indeed, women in

286   our sample had significantly higher odour identification scores, $t_{381} = 2.17$, $p = .030$).

287   We then go on to examine average similarity ratings among the odours of real

288   and fake couples (i.e. couple as the unit of analysis). This analysis comes at the cost

289   of lower statistical power, but benefits from generalisability and the potential to explore

290   further associations between odour similarity and variables related to relationship

291   functioning among the real couples. In both approaches, where appropriate, we used

292   planned orthogonal contrasts to investigate differences between real and 'fake'

293   couples, and then to compare between HC and non-HC using couples.

294   Finally, we compare our simple ratings scale in this study with ratings given to

295   the same samples by perfumers using a novel lexicon [49]. Allen and colleagues had

296   olfactory experts individually rate odours samples using a novel lexicon – they were

297   unaware that samples belonged to couples. They then calculated mean z scores for

298   each of the descriptors used across ratings given by the four olfactory experts.

299   Following this they conducted an exploratory factor analysis of these verbal

300   descriptors which revealed two main factors: Spicy/Animalic (containing the

301   descriptors Onion, Spicy, Animalic, and Heavy), and Sweet/Milky (containing the

302   descriptors Sweet, and Milky). We used these two factors and calculated differences

303   scores (from the mean Z scores) for each of the couples (real and fake) to use in the

304   analyses below.

305

306   **3. Results**

307   *3.1 Raters as the unit of analysis*

308   We first conducted a simple repeated measures ANOVA including all completed

309   ratings, with Sample Type (fragranced, unfragranced) and Couple type (No HC, HC,

310   Fake) as within-subject factors. This revealed significant main effects of both Couple

311   Type ($F_{2, 824}$ = 6.76, p = .001) and Sample Type ($F_{1, 412}$ = 4.00, p = .046), but more

312   importantly, a significant Couple Type x Sample Type interaction ($F_{2, 824}$ = 3.65, p =

313   .027). As shown in Figure 1, however, the direction of this result was opposite to our

314   prediction: real couples were judged more, not less, similar than fake couples. Indeed,

315   planned contrasts revealed that, for this interaction, similarity ratings were significantly

316   higher for real than fake couples ($F_{1, 412}$ = 6.34, p = .012), but there was no significant

317   difference among the two groupings of real couples (NHC v HC: $F_{1, 412}$ = 1.18, p =

318   .279). As can be seen in Figure 1, the interaction indicates that differences between

319   couple types were only evident in the unfragranced, but not the fragranced, samples.

320   Indeed, post hoc paired samples t-tests to further probe these differences revealed

321   significant differences, in the unfragranced samples, between NHC and HC couples

322   (t_{412} = 2.02, p = .044), between NHC and fake couples (t_{412} = 4.52, p < .001), and

323   between HC and fake couples (t_{412} = 2.51, p = .012). There were no significant

324   between-group differences in the fragranced samples. In addition, across sample type,

325   unfragranced samples from NHC couples were judged more similar compared with

326   fragranced samples from both NHC (t_{412} = 2.91, p = .004) and HC couples (t_{412} = 3.30,

327   p = .001).

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328   We checked that these results were not unduly influenced by variation in rater's

329   olfactory functioning, by re-running the ANOVA while including rater sex as a fixed

330   factor and their Sniffin' Stick odour identification score as a covariate. Again, planned

331   contrasts showed that similarity ratings were higher for real than fake couples ($F_{1, 380}$

332    $= 9.26$, p $= .003$), but there was no significant difference between couples who met

333   while the woman was using or not using HC ($F_{1, 380} = 1.65$, p $= .199$). Furthermore, in

334   this model, the Couple Type x Sample Type interaction remained significant ($F_{2, 760} =$

335   5.24, $p = .006$).

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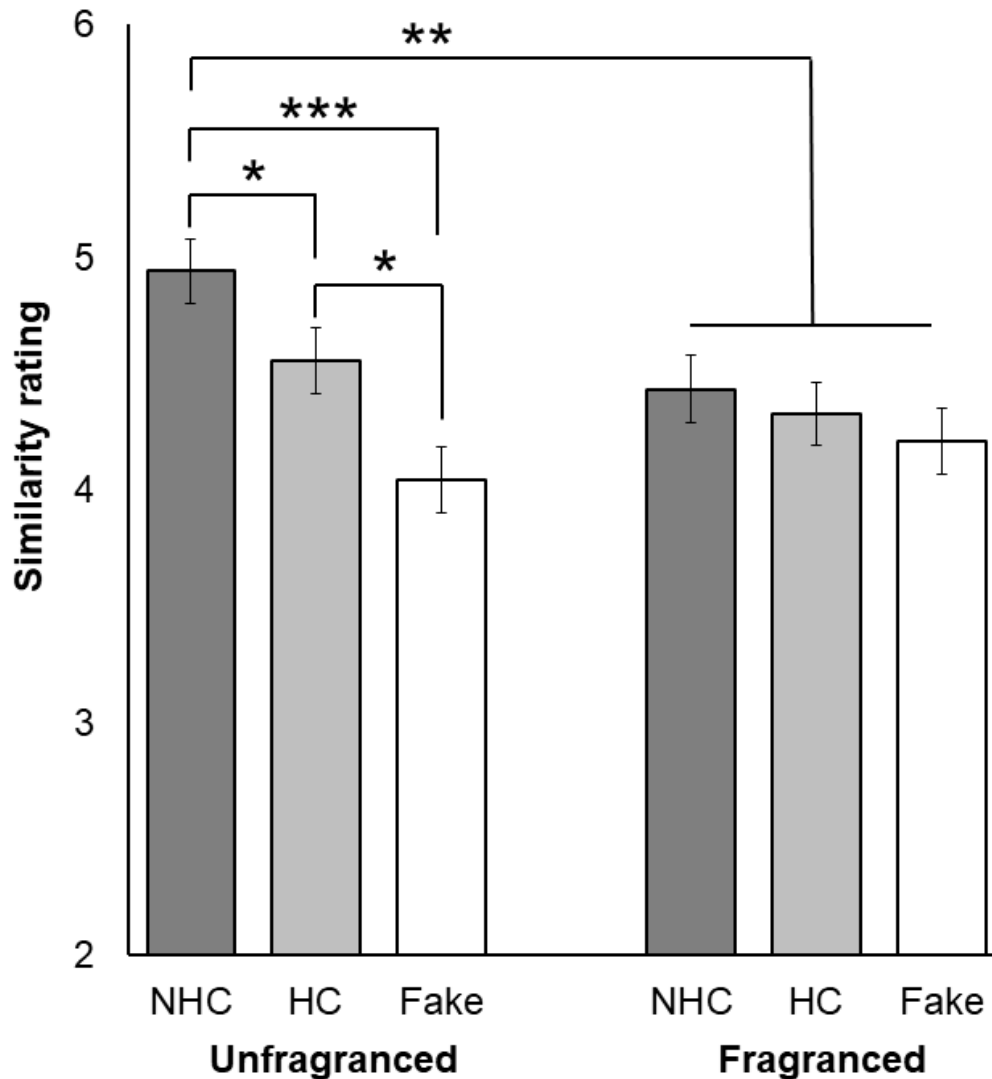
Figure 1 Mean ratings (±SEM) given to unfragranced and fragranced samples from two groups of real couples (NHC, woman was not using hormonal contraception when the relationship began; HC, woman used hormonal contraception when the relationship began) and Fake couples (arbitrarily paired male and female odours). The interaction between condition and fragrance was significant (see text). Ratings were given on a 9-point scale (1 = not at all similar, 9 = completely similar). Lines indicate post hoc paired samples t tests, *p < .05, **p <.01, ***p < .001.

3.2 Demographic and relationship data among couples

In view of the unexpected findings that (i) odours of real couples were more, rather than less, similar than fake couples, and (ii) unfragranced odours of couples who met while the woman was using HC were less, rather than more, similar than NHC couples,

351   we examined whether these differences might be explained by demographic

352   differences among our sampled couples.

353   We reasoned that the creation of fake couples may have introduced an age

354   difference confound. Indeed, we discovered that the mean age difference in the fake

355   couples (9 years, s.d. = 8.97) was larger than the mean difference in the real couples

356   (2 years, s.d. = 2.21; independent samples t-test, t = 2.98, adjusted df = 14.9, p =

357   .009). However, this does not appear to be responsible for the observed differences

358   in odour similarity, for two reasons. First, mean odour similarity ratings (calculated for

359   each couple across all raters) were not predicted by age difference, neither across all

360   45 couples (i.e. real and fake combined: Pearson r = .058 and .031 for unfragranced

361   and fragranced samples respectively, p = .71 and .84) nor across only the 30 real

362   couples (r = .168 and .037, p = .37 and .85). Second, a comparison of age differences

363   among the real couples showed that NHC couples were slightly less matched for age

364   (mean = 2.73, s.d. = 2.76) than the HC couples (mean = 1.27, s.d. = 1.16; t = 1.89,

365   adjusted df = 18.8, p = .074), and yet were judged to have more similar odours.

366   We then checked for other differences among the two groups of real couples.

367   A key possible confound that might influence odour similarity between groups is

368   whether couples in one group were more likely to be cohabiting. However, most

369   couples were cohabiting in both groups (12 NHC and 10 HC, Chi-square = .68, p =

370   .41). To check this further, we compared odour similarity ratings between cohabiting

371   and non-cohabiting couples, finding no difference for unfragranced samples (t_{28} = .10,

372   p = .92). For fragranced samples, there was a significant difference (t_{28} = 2.50, p =

373   .018), but similarity ratings were higher for the non-cohabiting couples (mean = 5.14)

374   rather than those who cohabited (mean = 4.06). There was also no significant

375   correlation between odour similarity and duration of cohabitation (scoring non-

376   cohabiting couples as zero on this measure; Spearman *r* = .07 and -.22, p = .73 and

377   .24 for unfragranced and fragranced samples, respectively). These analyses indicate

378   that it is unlikely that the unexpected similarity between odours within couples is

379   entirely explained by shared environmental influences on odour.

380   Independent samples t-tests also indicated that there were no significant

381   differences between relationship length, cohabitation length, age difference, RAS

382   scores, or RAS difference scores (women's scores subtracted from the corresponding

383   male partner's score) between the HC and NHC couples (Table 1).

384

385   **Table 1** Demographic and relationship data from couples who met whilst using HC and those who met

386   when not using HC. Data are means ± SEM; differences were tested using independent-samples t tests

Variable	Mean NHC	Mean HC	t	df	p
Relationship Length (months)	85.07 ± 19.52	66.40 ± 20.26	.66	28	.513
Cohabitation length (months)	59.87 ± 20.59	36.40 ± 18.11	0.86	28	.399
Male partner age	32.47 ± 2.78	26.47 ± 1.64	1.86	28	.074
Female partner age	29.87 ± 2.3	26.13 ± 1.80	1.20	28	.240
RAS Female	4.69 ± .09	4.46 ± .23	.93	27	.359
RAS Male	4.64 ± .35	4.58 ± .14	.35	26	.732
RAS difference score	.28 ± .07	.44 ± .13	0.79	26	.435

387

388   ### 3.3 Odour donors as the unit of analysis

389   Here, we used repeated measures ANOVA to compare mean within-couple odour

390   similarity scores, now with Sample Type (fragranced, unfragranced) and Rater Sex

391   (male, female) as within-subjects factors, and a between-subjects factor of Couple

392   Type (NHC, HC, Fake couples). Mean scores are shown in Figure 2, which indicates

393   that the overall pattern of effect is qualitatively similar to those in Figure 1. However,

394   in contrast to when we used raters as the units of analysis, there was no main effect

395   of Sample Type ($F_{1,42}$ = .91, p = .346), no main effect of Couple Type ($F_{2,42}$ = .64, p

396   = .530) nor significant Sample Type x Couple Type interaction ($F_{2,42}$ = .85, p = .435).

397   Planned contrasts revealed no significant difference in this analysis between the

398   ratings of similarity given to real and fake couples (p = .380), or between NHC and HC

399   couples (p = .483), although an *ad hoc* t-test showed significantly higher scores for

400   NHC than Fake couples among female raters (t_{28} = 2.35, p = .026; see Figure 2). The

401   only significant effect in the ANOVA was for Rater Sex ($F_{1,42}$ = 7.79, p = .008), with

402   men on average giving higher similarity scores to odour pairs (mean = 4.65) than

403   women did (mean = 4.27).
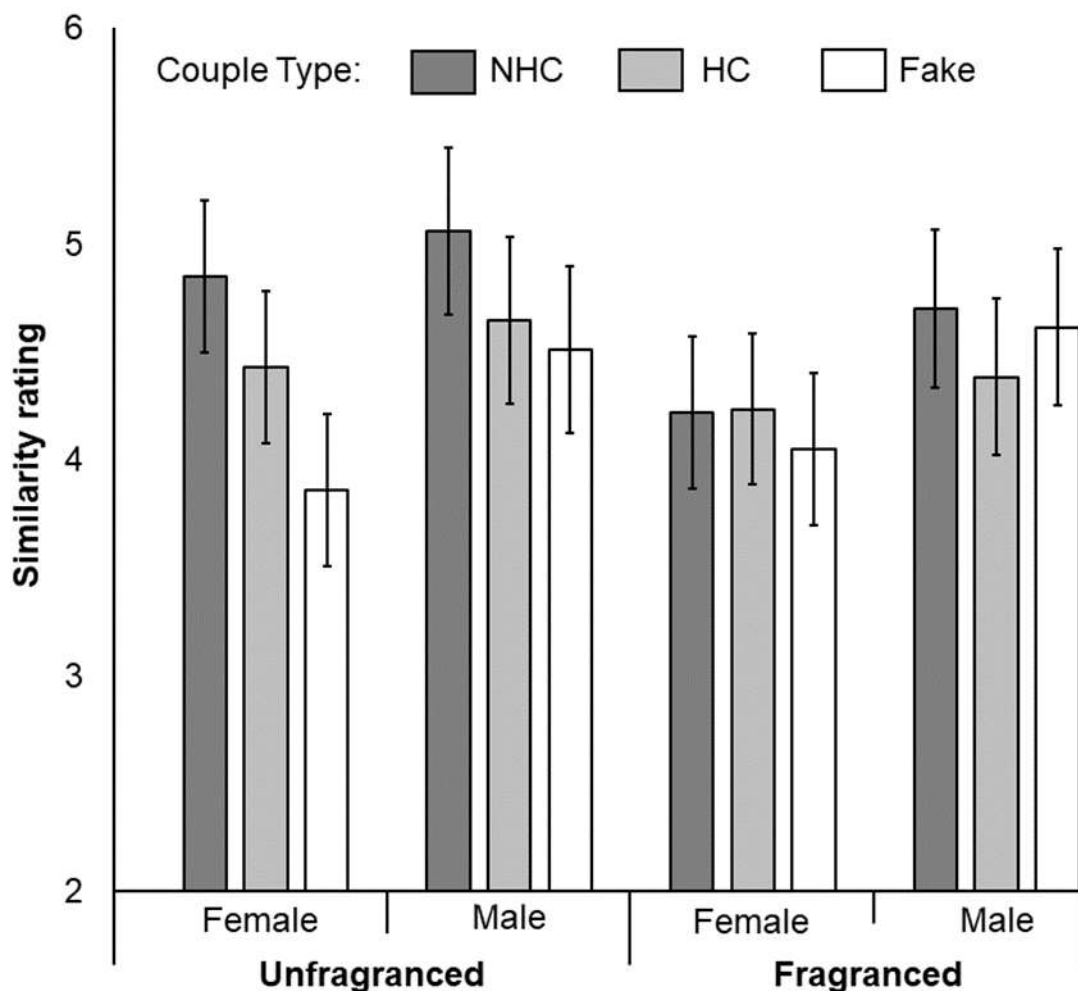
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405   **Figure 2** Mean (± SEM) ratings of similarity for odours donated by couples. Mean scores are shown for

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406   both female and male raters to fragranced and unfragranced samples of each couple type. Ratings

407   were given on a 9-point scale (1 = not at all similar, 9 = completely similar).

408

409   Subsequently, we examined potential correlates of odour similarity within the

410   real couples, in view of previous findings on odour preferences for genetically

411   dissimilar partners. Noting that between-group differences were most evident in

412   unfragranced samples, we therefore conducted exploratory analyses of within-couple

413   similarity scores among these unfragranced samples only. Using univariate ANOVA,

414   we tested the predictive effects on within-couple odour similarity of Couple Type as a

415   fixed factor (NHC, HC), and we included as covariates in the model the couples'

416   relationship duration (in months) and male and female RAS scores. (Note that this

417   analysis includes 15 NHC couples and 13 HC couples, because members of 2 couples

418   chose not to complete the RAS scale). We found a significant main effect of Couple

419   Type ($F_{1, 23}$ = 5.19, p = .032), with odour similarity scores being higher in NHC than

420   HC couples. The effect of relationship duration was not significant ($F_{1, 23}$ = 1.46, p =

421   .240), but there were also significant and independent effects of both the female ($F_{1,}$

422   $_{23}$ = 10.33, p = .004) and male ($F_{1, 23}$ = 11.45, p = .003) partners' RAS scores.

423   We explored these using partial correlations between odour similarity and RAS scores,

424   controlling for RAS score of respective partners. This showed that men's RAS scores

425   were positively correlated with odour similarity (r_p = .499, df = 25, p = .008) but

426   women's RAS scores were negatively correlated with odour similarity (r_p = -.462, df =

427   25, p = .015), even though RAS scores within couples were strongly correlated (r =

428   .618, p < .001). This is illustrated further in Figure 3, which shows the significant

429   negative correlation (r = -.449, p = .017) between RAS difference score within couples

430   (subtracting men's RAS score from their female partner's score) and their odour

431   similarity. In summary, these analyses indicate that, independent of the effect of

19

432   Couple Type, men's satisfaction is predicted by how similar their partner's odour is to

433   their own, while women tend to be more satisfied when their partner's odour is

434   somewhat dissimilar.

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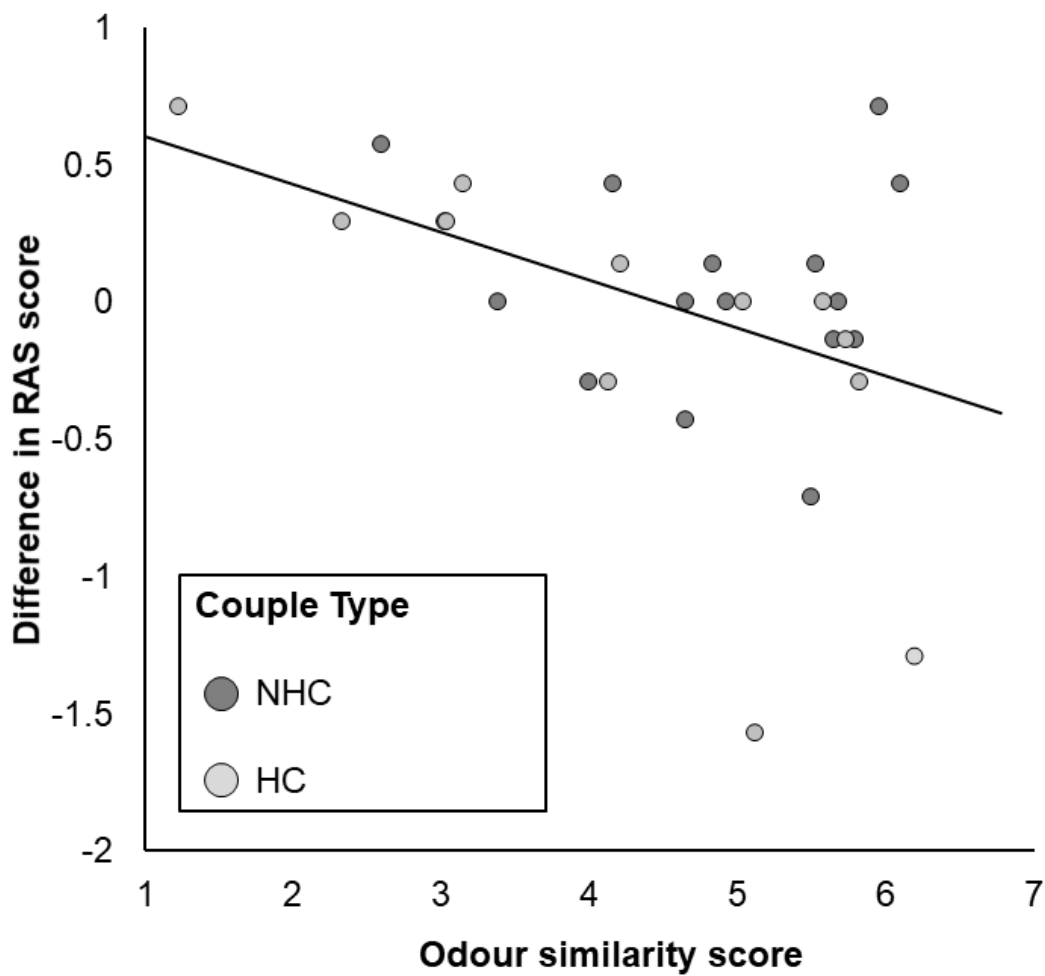
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446 **Figure 3** Relationship between odour similarity within-couples and difference in relationship satisfaction
447 between couple members. Odour similarity scores are means from all raters for the unfragranced
448 samples of each couple. The difference in Relationship Assessment Scale scores for male and female
449 partners in each couple is calculated by subtracting male from female scores; higher scores indicate
450 that women are more satisfied than their partner and lower scores indicate that women are relatively
451 dissatisfied, compared with the rated satisfaction of their male partner.

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458 ### *3.4 Comparison of rating scales*

459 Finally, we aimed to investigate whether the simple rating scale of similarity utilised in

460 this study mapped onto a novel lexicon which has recently been developed for

461 assessing human body odours. We correlated similarity ratings from the current study

462 (all raters, female raters only, and male raters only) with the difference scores each

463 couple received for the Milky/Sweet and Spicy/Animalic factors extracted from the

464 olfactory lexicon [49]. We did this for the unfragranced samples only, as the fragranced

465 samples were not scored by the perfumers. We found significant negative correlations

466 between the similarity ratings for the 30 couples and the difference between scores of

467 Spicy/Animalic which the couples received from the perfumer scoring [49]. In other

468 words, the more similar a couple's odour was rated, the less they differed in how

469 perfumers scored their respective odours for the Spicy/Animalic descriptor.

470 **Table 2 Correlations between ratings of similarity which couples (real and fake) received in the**
471 **current study and difference scores which the same couples received for two verbal descriptors**
472 **given by olfactory experts (see Allen et al., 2018 [49]). * p > .05**

Measure:	Spicy/Animalic difference scores	Milky/Sweet difference scores
Similarity rating (whole sample)	**-.340***	.167
Similarity rating (male raters only)	-.253	.257
Similarity rating (female raters only)	**-.351***	.111

473

474 Given this positive association between the two methods of rating, we then

475 investigated whether difference scores of the Spicy/Animalic factor differed based on

476 couple type (HC, NHC, Fake). We ran a Univariate ANOVA with Spicy/Animalic

477 difference scores as the dependent variable, and couple type as a fixed factor, finding

478 no main effect of couple type ($F_{2, 42} = .032$, $p = .969$) Planned contrasts revealed no

479 difference between difference scores of Spicy/Animalic received by NHC and HC

480 couples (p=.812), or between real couples and fake couples (p=.936).

481

482 **4. Discussion**

483 Previous research suggests positive assortment in actual couples in various social,

484 psychological, and physical characteristics, with body odour being an exception from

485 this general pattern. We investigated the perceived similarity of body odours between

486 romantic partners comparing observed similarity ratings with those for 'fake' couples,

487 and additionally comparing real couples who met whilst using or not using hormonal

488 contraception, in order to detect evidence for alteration of odour preferences. We did

489 this using both their unfragranced body odour, and samples in which individuals used

490 their own fragrances, to investigate the potential for artificial fragrance use to disrupt

491 odour-mediated assortative mating. Finally, we further assessed which perceptual

492 qualities of our odour samples were being used to make these similarity judgements

493 by comparing these with assessments made using a novel verbal lexicon for

494 describing odours.

495 *4.1. Assortative odour preferences*

496   Our first analysis was conducted with raters as the unit of analysis, comparing

497 each individual's assessment of the fragranced and unfragranced samples for each of

498 the three couple types (real couples who met while the woman was using or not using

499 HC, and a fake couple). This approach uses maximal statistical power and takes into

500 account individual variability in raters' olfactory capability. This revealed a significant

501 interaction between odour similarity ratings across the three couple types and between

502 fragranced and unfragranced samples. There were significant differences in similarity

503 ratings between real and fake couples, and between the two real couple types, but

504 only in the unfragranced samples.

505   We had predicted a difference between real and fake couples, but intriguingly,

506 the direction of the result was in the opposite direction. Based on studies of odour-

507 mediated MHC-disassortative mating preferences in several vertebrate species [27]

508 and laboratory-measured preferences in humans (e.g. 30, 33), we had expected that

509 real couples would be judged to have more dissimilar odours compared with fake

510 couples. Furthermore, regarding the two groups of real couples, we had expected that

511 NHC couples would be more dissimilar than couples who met while the female partner

512 was using HC, again based on the same literature on women's MHC-correlated odour

513 preferences and specifically on findings that HC shifts these preferences towards

514 MHC-similar partners [34]. Our data did indicate a difference in the level of similarity

515 between NHC and HC couples, but in the opposite direction to our prediction; HC

23

516 couples had a level of odour similarity that was intermediate to the NHC couples and

517 the fake couples. This is indeed suggestive of HC influencing odour-mediated partner

518 preference, but we do not have a clear explanation for the direction of effect, and it

519 may be that the result does not turn out to be robust if further tested with a larger

520 number of HC and NHC couples.

521 We did not find a corresponding, statistically significant interaction in the

522 subsequent analysis in which each couple was used as the unit of analysis (neither

523 using similarity ratings nor differences scores for couples of Spicy/Animalic). Although

524 this analysis has more limited statistical power, this result warrants some caution

525 regarding generalizability across couples. However, it should be noted that more

526 focused analysis based only on the unfragranced ratings provided some consistent

527 evidence: mean odour similarity of NHC couples (but not HC couples) was higher than

528 fake couples, and odour similarity was found to be predicted by couple type, with NHC

529 couples being more similar than HC couples.

530 Taken together, these findings provide evidence for assortative mating based

531 on odour in humans. In comparing real and fake couples, our study is the first to

532 examine within-couple odour similarity following the analogous experimental design

533 that has been used for facial preferences (though as we note in the introduction there

534 is one previous study which employed a matching paradigm to investigate this).

535 Consistency in the direction of effect between our study and the previous face-based

536 studies suggest that similar processes may underpin mate choices made in either

537 modality.

538 It remains possible that some aspect of shared experience within couples is

539 responsible for couples having more similar odours than expected by chance (as

540 represented by the test against 'fake' couples). For example, age [56] and diet [57-59]

541   may influence body odours, and similarities in these could be responsible for the

542   observed results. However, as described above, it seems unlikely that the results were

543   due to smaller age differences between couple members in real couples than fake

544   couples, because there was no correlation between couple similarity and age

545   differences and age differences were in fact slightly larger for NHC couples, despite

546   having more similar odours than HC couples. Similarly, among the real couples, there

547   was no difference in the frequency of cohabitation between NHC and HC groups,

548   cohabitation length was uncorrelated with odour similarity, and where there was a

549   difference between cohabiting and non-cohabiting couples (for fragranced samples

550   only), it was the non-cohabiting couples who were rated more similar. These

551   considerations lead to the conclusion that our finding of high within-couple similarity is

552   more likely to reflect an outcome of mate preferences than to be produced by shared

553   environmental experience.

554   If this is true, our results raise interesting questions regarding our current

555   understanding of how odour influences mate preferences. As discussed above, odours

556   appear to mediate mate choices in many vertebrate taxa, and the dominant view in

557   the literature is that odour preferences are generally disassortative, rather than

558   assortative as we report here. How can we reconcile these results?

559   One answer may be that the literature reporting disassortative mating is

560   focused exclusively on the MHC. While MHC-mediated preferences may well be

561   functionally important, MHC genes are an undeniably small fraction of the genetic

562   contribution to the chemical signature that underlies an individual's perceived odour.

563   We must also not forget that chemical signatures are additionally influenced by a

564   variety of environmental effects, including diet [57-59]. The contribution of MHC is

565   therefore only a small fraction of the entire odour profile of any individual. Recognition

25

566 of the broader influences on odour profiles reveals possibilities for complex and

567 perhaps hierarchical mate choice decision-making influenced by sub-components of

568 the odour profile. In other words, it is possible that in the real-world milieu of mate

569 choice, a first-level preference for a potential partner's odour might be determined by

570 overall similarity: we prefer the smell of those with similar odour to our own, as we do

571 with faces and indeed many other traits. It is then conceivable that a second-level

572 preference for odour is shaped by chemical markers of MHC genes. According to such

573 a hierarchical flow structure, ultimately preferred partners would be those who are

574 generally similar, but who lie at the dissimilar end of the MHC-similarity continuum.

575 Nested preferences and trade-offs between different qualities should not be

576 unexpected within complex decision-making processes such as choosing a mate.

577 Indeed, there is experimental evidence from mice for exactly this kind of trade-off even

578 within a single olfactory signal, such that expression of preference for relatively MHC-

579 dissimilar mates is dependent on other markers of absolute quality and the co-variance

580 in these different traits among available mates [60]. However, it should be noted that

581 our expectations of similarity were based on literature which directly genotyped MHC,

582 which was something that we did not do in the current study. Consequently, while our

583 findings seem counterintuitive, they do not necessarily rule out MHC-disassortative

584 odour based mating preferences.

585 Further studies to test and confirm our conclusion are now called for, since ours

586 is the first to test for odour similarity across real and fake couples. However, we note

587 that our results regarding relationship satisfaction in the real couples are consistent

588 with our suggestion for MHC-linked preferences being nested within a priority level

589 preference for overall odour similarity. Even though odours of real couples were

590 judged more similar than fake couples, and even though relationship satisfaction

591   scores of each partner were highly correlated within couples, the reported relationship

592   satisfaction of the female partner was relatively low in those couples with the most

593   similar odour. This is exactly what we might expect based on previous research on

594   both sex differences in olfactory functioning, in which women out-perform men, and

595   sex differences in choosiness and the costs of mate choice. Our results are thus

596   consistent with previous literature which has found that women whose partners are

597   relatively MHC-similar are less satisfied and more likely to seek extra-pair affairs

598   compared with other women who have less MHC-similar partners [41, 42]. Similar

599   effects are also observed in other socially monogamous species [61,62].

600   As this work represents a preliminary investigation, future work is needed to

601   assess the robustness of our findings. Studies should focus on increasing the number

602   of odour donors recruited in the HC and no HC groups, and consider current as well

603   as previous use of hormonal contraception by female donors in the study design. We

604   note that, in our sample, two of the HC group were no longer using HC at the time of

605   sample collection, and five women in the NHC group had begun to use HC by the time

606   of sample collection. Changes in HC use during a relationship might present an

607   interesting opportunity to further investigate levels of olfactory similarity and

608   relationship satisfaction, as we know both that hormone levels have an influence on

609   body odour (65, 66, 67) and that changes in HC use during the course of a relationship

610   may alter attraction to, and satisfaction with, a partner (70). However, as this was not

611   something we set out to test, we do not have sufficient variation in the current sample

612   to investigate this, and future researchers should take this into consideration.

613   Furthermore, it would be interesting to run a longitudinal study assessing whether body

614   odour similarity is predictive of long term relationship quality and potential dissolution,

615   and to directly incorporate MHC genotyping where possible.

616

617 *4.2 Effects of fragrance use*

618 Interestingly, there was no difference in similarity ratings in the fragranced samples,

619 with ratings of the three couple conditions not differing significantly from one another.

620 Our findings therefore suggest that fragrance use disrupts the ability of human

621 smellers to detect the similarity of underlying body odour. This lends support to the

622 idea that fragrance use has the effect of masking odours, rather than the alternative

623 suggestion that individual fragrance choices may serve to complement one's MHC

624 genotype or even enhance the distinctiveness and attractiveness of one's underlying

625 odour [45, 47].

626 However, it is worth noting the nature of fragrance use in our sample. Previous

627 studies linking fragrance preferences to MHC types have tended to use perfumes or

628 perfume ingredients, whereas odour donors in our study used their day-to-day

629 fragranced deodorants. Deodorants contain fragrances, but also contain specific anti-

630 microbial compounds that target bacteria responsible for odour production. It is

631 possible that these anti-microbial effects (and potentially compounds which reduce the

632 overall production of sweat if antiperspirants were used) are responsible for the

633 reported results, rather than a masking effect of fragrance components *per se*. Further

634 studies could test between these possible mechanisms. To date, there are only two

635 studies investigating the ways in which deodorants and antiperspirants might influence

636 the detection of socially relevant cues from body odour. Allen and colleagues [63]

637 found evidence that use of deodorants can enhance or mimic certain information

638 available in body odour, potentially making it harder to differentiate between

639 individuals. A second study also found that deodorant may somewhat suppress

640 identifying characteristics of an odour, compared to no fragrance at all, but importantly

641 maintaining a level of idiosyncrasy in odour samples when using a chosen deodorant

642 over an experimenter assigned one [46].

643 At first sight this result suggests that fragrance (or deodorant) use has the

644 potential to interfere and disrupt important mate choice processes. Certainly, it may

645 have some effect in real life, but it is important to remember that both the unfragranced

646 and fragranced samples came from the same couples and were rated by the same

647 raters, and that odour similarity in the unfragranced samples was significantly different

648 from the fake couples. In other words, if we assume that people do indeed seek and

649 prefer partners with similar odours to themselves, then our results suggest that they

650 are able to achieve this *despite* using fragrances in their daily lives. Although we did

651 not ask our odour donors about their frequency of fragrance use at the time they met

652 their partner, all of them were using artificial fragrances of some kind when they took

653 part. Thus, while judgments of underlying odour similarity by our raters were altered

654 by the addition of fragrances, there appears to still be opportunity for long-term and

655 intimate partners to exercise their odour preferences during relationship formation.

656 The importance of incorporating fragrances into investigations of human olfactory

657 communication has recently been highlighted in a review by Allen and colleagues (69),

658 and the current findings further support this.

659 4.3 *Comparison of rating scales*

660 Finally, we investigated our similarity rating scale, with the aim of establishing

661 which components of an odour profile were being used to assess this. Previous

662 literature has worked to enhance the complexity of odour assessments used in human

663 olfaction studies [see 49], the argument being that an individuals' odour profile is very

664 complex unlike the rating scales we often employ. We found that more complex lexicon

665 based assessments of our couples' odour samples which had been completed by

666   olfactory experts were actually positively associated with the simple similarity rating

667   scale utilised by our non-expert raters in the current study. Our findings tell us that

668   when we ask non-experts to assess odour samples for similarity, it is the

669   Spicy/Animalic perceptual qualities on which these similarity judgements are being

670   made, and not the Milky/Sweet aspects (which we know are detectable in the current

671   samples from the expert ratings). Additional work is needed to further validate the

672   olfactory lexicon and establish whether it is feasible to use this more complex odour

673   assessment with participants who have little or no olfactory expertise.

674   *4.3 Conclusion*

675   Our results lend further support to the emerging literature that odour may play a role

676   in both human mate choice and the subsequent dynamics of within-couple relationship

677   satisfaction. Contrary to prediction, however, our results suggest an affinity for

678   partners with similar rather than dissimilar odours. Our study indicates that odour

679   preferences follow the same assortative rule as has been demonstrated for many other

680   partner attributes, including physical traits such as face shape. At the same time, the

681   level of within-couple odour similarity is associated with relative relationship

682   satisfaction between the male and female partners, with women being more satisfied

683   in couples with relatively dissimilar odour. Taken together, these findings suggest that

684   the much-discussed role of odour-mediated MHC-disassortative preferences, perhaps

685   more salient in women's preferences than in men's, may represent a secondary

686   process which is subsumed within a more prioritised assortative mating decision rule.

687   This is consistent with a similar two-tiered decision process previously suggested to

688   explain the conundrum of women's MHC-assortative preferences for male faces [64].

689   Thus, while our results were surprising, such a nested decision-making process could

690   be one mechanism by which individuals select not extreme MHC-dissimilarity but

691   rather an intermediate level of MHC-sharing with eventual partners. This could then

692   serve to achieve an optimal, rather than extreme, level of heterozygosity in resulting

693   offspring, exactly as predicted by optimal immunological diversity theory [65].

694

695   **Ethical approval**

696   All procedures performed in studies involving human participants were in accordance with

697   the ethical standards of the institutional and/or national research committee and with the

698   1964 Helsinki declaration and its later amendments or comparable ethical standards.

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