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Evidence for odour-mediated assortative mating in humans: The impact of hormonal contraception and artificial fragrances

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Abstract

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

Key words: Homogamy, Fragrance, Hormonal contraception, Assortative mating, Body odour, Olfaction.

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].

Against this background, it is thought that olfactory preferences may be an exception to the “like-prefers-like” decision rule in human mating. It has been suggested that disassortative odour preferences, as observed in many other vertebrates [26, 27], is likely to be a critical evolutionary mechanism serving to achieve an optimal level of genetic dissimilarity at key genetic loci, and thereby influencing health and survival of potential offspring via heterozygote advantage. The particular focus of this idea is the relationship between odour preference and relative dissimilarity at genes in the major histocompatibility complex (MHC, formally referred to as HLA, human leukocyte antigen, in humans). The MHC is a family of co-dominantly expressed genes that underpins adaptive immunity functioning in vertebrates (28,29). Selection of mates who share relatively few MHC genes will thus increase offspring MHC heterozygosity, conferring an immune advantage in form of higher repertoire of recognizing molecules.

Evidence for MHC-disassortative odour preferences in humans is admittedly mixed [30, 31, 68]. Several experimental studies have suggested that men or women prefer odours of MHC-dissimilar individuals [e.g. 32, 33], although other studies report no clear effect [34-36], and one study provides evidence for preference for an intermediate rather than extreme level of dissimilarity [37]. Similarly, evidence for lower than chance levels of MHC allele-sharing in real couples is sparse; for example, one study provides such evidence within a closed-mating population [38], but several others do not [39, 40]. On the other hand, other studies suggest that relatively high MHC dissimilarity within couples is associated with higher sexual attraction to partner and relationship satisfaction [41, 42]. In summary, while some researchers [31] have argued that MHC-mediated mate preferences may not be evident in humans, the evidence remains mixed. Nonetheless it is still true that most researchers expect, if odour preferences do play a role in mate selection, that they will most likely be underpinned by negative rather than positive assortment.

In this study, we aimed to test this idea directly by adapting a methodology used previously for investigating assortative facial preferences [20]. We collected odour samples from both male and female partners in established romantic relationships, while refraining from use of artificial fragrance. We then examined the perceived similarity of these odours according to a panel of independent judges, and compared the similarity ratings of these odour pairs against a sample of ‘fake couples’, created by randomly pairing a male and female odour from the population of samples. On the basis of the literature described above, we predicted that odours of the real couples would be rated as more dissimilar to each other than the randomly paired odours.

We know of only one paper to date which has examined the similarity of odours within romantic couples. Porter and colleagues [43] recruited 12 spouses and had their odours matched to one another by thirty participants, finding that participants were not successful at this matching task. However, this study had a different aim from our own, and these findings do not speak to the level of similarity between these spousal odours, which is of direct interest to us. In this study we have odours rated rather than matched, and we compare the odour ratings with random pairings of fake couples. Finally, we explicitly test the effects of environmental influences (discussed further below) by comparing fragrance and non-fragrance sample ratings – as Porter and colleagues were interested in similarity *resulting* from shared environments of spouses they did not control for this.

In addition, we set out to investigate the extent to which within-couple odour dissimilarity would be affected by two potential confounding influences. First, among our real couples, we recruited half in which the female partner was using hormonal contraception (HC) when the relationship began, and half in which she was not. This decision was based on pre-existing evidence that HC may disrupt women's disassortative odour preference. This possible effect was first reported by Wedekind et al. [33], who found that women using oral contraception preferred odours of relatively MHC-similar men. Consistent with this, Roberts et al. [34] subsequently found a preference shift towards MHC-similarity in women after initiating oral contraceptive use, a change which was not evident in a control group of non-users. Based on this evidence, we predicted that levels of within-couple odour similarity would be higher in those couples in which the woman used HC at the time of pair formation.

Second, we also investigated the effects of fragrance use on relative odour similarity. Fragrance use could influence the communication of socially relevant olfactory information in one of two main ways [44]. The most obvious effect is that artificial fragrances mask the underlying body odour, obscuring any meaningful social cues. Alternatively, fragrance use might not interfere with, or may even enhance, the communication of underlying social information, if individuals choose between fragranced products in a way that complements their own body odour and produces a distinctive and congruent fragrance-body odour blend. Although the second possibility may seem unlikely, Lenochová et al. [45] found that such blends were rated as more pleasant when they involved an individual's preferred fragrance compared with blends involving a fragrance assigned to them experimentally, even when there was no difference in pleasantness of the alternative fragrances in isolation. In addition to this, Allen and colleagues [46] found that participants discriminated between odours of individuals more successfully when they were wearing a chosen rather than an assigned deodorant, suggesting that the fragrances people choose to wear do in some way maintain useful information contained in their odours. Furthermore, there is some evidence for associations between liking for fragrance ingredients and individual MHC type. Milinski and Wedekind [47] reported a significant association between MHC alleles and certain ingredients preferred for perfumes to be used by individuals themselves, but not for their partners. They suggested that this supports the hypothesis that fragrances are chosen to enhance the availability of MHC-related cues in mate choice (for supporting evidence, see also 48). To examine these alternatives, we also collected, from the same couples, samples of their own odour together with their own preferred fragrance. We expected that within-couple odour dissimilarity judged using these body odour-fragrance blends would be at the same level as 'fake couples' if fragrances mask cues of body odour dissimilarity. Alternatively, if fragrances complement or enhance odour individuality, we expected that levels of perceived dissimilarity would be at the same level, or even higher, than would be observed for judgments of unfragranced samples of real couples.

Finally, previous studies have raised the issue that rating scales used in studies investigating the perceptual qualities of body odours are often quite simple and may potentially fail to capture some of the olfactory nuances present [49]. In this study, we employ a simple rating scale of similarity (from 1 -not at all similar, to 9 - completely similar) and directly test the utility of this by comparing these ratings to those given by olfactory experts who used a novel lexicon to describe the odour samples.

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

100% cotton oval shaped make-up pads (approximately 9.5cm x 6.5cm, 3mm thick, Cosmetic Oval Pads, The Boots Company PLC) and surgical tape (FineporeTM, 2.5cm wide). Donors were instructed to apply the cotton pad onto their armpit, using the tape to hold this in place, and to remove it after 24 hours had passed. There is variation in sampling time across studies, though numerous studies to date have adopted 24 hour sampling periods for odour collection [50-52]. Furthermore, Havlíček et al. [50] found that 12 hour sampling yielded samples which were less intense, and less likely to be perceived, compared with a 24 hour sampling period. Donors were instructed to remove the pads after 24h, and seal them in small, pre-labelled, plastic zip lock bags which we provided. The donors returned the samples, labelled and in sealed plastic bags, to the lab within 2 hours of removal, where they were stored in a freezer at -20˚C until use. Samples were thawed at room temperature for 2 hours prior to test sessions. Previous research suggests freezing and thawing of samples has minimal impact on the perceptual quality of the odour [34, 53].

Donors also completed an online questionnaire to collect basic demographic information, as well as information on length of their relationship, cohabitation status and current and past contraceptive use. Of those who met whilst using hormonal contraception, 10 were cohabiting and 5 were not. Of those who were not using hormonal contraception when they met, 12 were cohabiting and 3 were not. Couples also completed the Relationship Assessment Scale [54], consisting of 7 items (e.g. “In general, how satisfied are you with your relationship?”), which participants completed using a 5-point scale, where high scores indicated relative satisfaction.

2.2 Raters

Recruitment of the raters including the subsequent odour rating sessions took place at the Centre for Life in Newcastle upon Tyne, where 437 visitors participated (280 women, 157 men). After excluding those individuals who did not complete the task, there was a total sample size of 261 female (mean age = 40.89, SD = 10.35, range: 17-76) and 152 male raters (M = 42.67, SD = 12.26, range = 17-78). All but 30 of these also completed the Sniffin' SticksTM 12-item odour identification test. In order to avoid olfactory fatigue, each rater only rated a sub-sample of the odour stimuli, and so on average, each sample was rated by 27.5 participants (range = 23-34, SD = 3.42).

After these ratings had taken place, the samples (plus one additional couple) were employed in a further study [49] where they were used to develop a novel lexicon for describing human body odours. They were subsequently rated using this lexicon by two perfumers and two perfume evaluators (see [49] for details). The ratings given by these four trained individuals and using this novel lexicon are incorporated into the results of the current paper (allowing us to compare ratings given by novices from this study with assessments made using our novel lexicon by olfactory experts in the previous study).

2.3 Procedure

Each participant took part in one test session only. After providing informed consent, they were presented with 6 pairs of 500ml conical flasks containing body odours (12 individual samples in total). Participants were not presented with a greater number of odours in order to reduce any potential effects of sensory overload or olfactory fatigue.

Participants did not know the sex of the samples or that the samples came from individuals in romantic relationships. Participants were instructed to remove the tin foil caps from each pair of flasks, to sniff both samples, and then to rate them simply on how similar the two smelled to each other (using a scale from 1 -not at all similar, to 9 - completely similar). Pair 1 contained the unfragranced odour samples from one donor couple who began their relationship whilst using HC (male and female odours in separate flasks) and pair 2 were the same couples' fragranced samples. Pairs 3 and 4 were the odour samples of a couple who began their relationship whilst not using HC (unfragranced and fragranced samples, respectively). The final two pairs were from a single 'fake' couple: a man and a woman from separate couples were assigned as a pair by the experimenter (again, using the unfragranced and fragranced samples from the same two individuals). Presentation order of the odour pairs was randomised. The individuals chosen for the 'fake' couples were those whose samples had been, or were about to be, used in one of the other two test sessions from the same day; in this way, we were able to reduce the amount of time that samples were unfrozen. Each sample was thawed and used for one day (6-8 hours, before being re-frozen). Samples were stored in a cool box with ice packs when not in use during the day. In all, 15 test sessions were carried out over 5 days (3 sessions each day). Each session lasted between 1.5 and 3 hours depending on recruitment rate, and contained samples from different couples. Finally, each participant also completed the Sniffin' Sticks olfactory identification test to ascertain their olfactory identification abilities, one measure of general olfactory competence [55].

2.4 Analysis

The data were analysed in two ways. We first used individual raters as the unit of analysis, using repeated measures ANOVA, with both Couple Type (No HC, HC, Fake) and Sample Type (Fragranced, Unfragranced) as within-subjects factors. This approach follows directly from the experimental design and maximises available statistical power. A further benefit of this approach is that we can additionally control for individual variability in ratings by including each individual rater's score on the Sniffin' Sticks test as a covariate and rater sex as a between-subjects fixed factor (women are often thought to have higher average olfactory acuity; indeed, women in our sample had significantly higher odour identification scores, $t_{381} = 2.17$, $p = .030$).

We then go on to examine average similarity ratings among the odours of real and fake couples (i.e. couple as the unit of analysis). This analysis comes at the cost of lower statistical power, but benefits from generalisability and the potential to explore further associations between odour similarity and variables related to relationship functioning among the real couples. In both approaches, where appropriate, we used planned orthogonal contrasts to investigate differences between real and 'fake' couples, and then to compare between HC and non-HC using couples.

Finally, we compare our simple ratings scale in this study with ratings given to the same samples by perfumers using a novel lexicon [49]. Allen and colleagues had olfactory experts individually rate odours samples using a novel lexicon – they were unaware that samples belonged to couples. They then calculated mean z scores for each of the descriptors used across ratings given by the four olfactory experts. Following this they conducted an exploratory factor analysis of these verbal descriptors which revealed two main factors: Spicy/Animalic (containing the descriptors Onion, Spicy, Animalic, and Heavy), and Sweet/Milky (containing the descriptors Sweet, and Milky). We used these two factors and calculated differences scores (from the mean Z scores) for each of the couples (real and fake) to use in the analyses below.

3. Results

3.1 Raters as the unit of analysis

We first conducted a simple repeated measures ANOVA including all completed ratings, with Sample Type (fragranced, unfragranced) and Couple type (No HC, HC, Fake) as within-subject factors. This revealed significant main effects of both Couple Type ($F_{2, 824}$ = 6.76, *p* = .001) and Sample Type ($F_{1, 412}$ = 4.00, *p* = .046), but more importantly, a significant Couple Type x Sample Type interaction ($F_{2, 824}$ = 3.65, *p* = .027). As shown in Figure 1, however, the direction of this result was opposite to our prediction: real couples were judged more, not less, similar than fake couples. Indeed, planned contrasts revealed that, for this interaction, similarity ratings were significantly higher for real than fake couples ($F_{1, 412}$ = 6.34, *p* = .012), but there was no significant difference among the two groupings of real couples (NHC v HC: $F_{1, 412}$ = 1.18, *p* = .279). As can be seen in Figure 1, the interaction indicates that differences between couple types were only evident in the unfragranced, but not the fragranced, samples. Indeed, post hoc paired samples t-tests to further probe these differences revealed significant differences, in the unfragranced samples, between NHC and HC couples (t_{412} = 2.02, p = .044), between NHC and fake couples (t_{412} = 4.52, p < .001), and between HC and fake couples (t_{412} = 2.51, p = .012). There were no significant between-group differences in the fragranced samples. In addition, across sample type, unfragranced samples from NHC couples were judged more similar compared with fragranced samples from both NHC (t_{412} = 2.91, p = .004) and HC couples (t_{412} = 3.30, p = .001).

We checked that these results were not unduly influenced by variation in rater's olfactory functioning, by re-running the ANOVA while including rater sex as a fixed factor and their Sniffin' Stick odour identification score as a covariate. Again, planned contrasts showed that similarity ratings were higher for real than fake couples ($F_{1,\ 380}$ = 9.26, p = .003), but there was no significant difference between couples who met while the woman was using or not using HC ($F_{1,\ 380}$ = 1.65, p = .199). Furthermore, in this model, the Couple Type x Sample Type interaction remained significant ($F_{2,\ 760}$ = 5.24, *p* = .006).

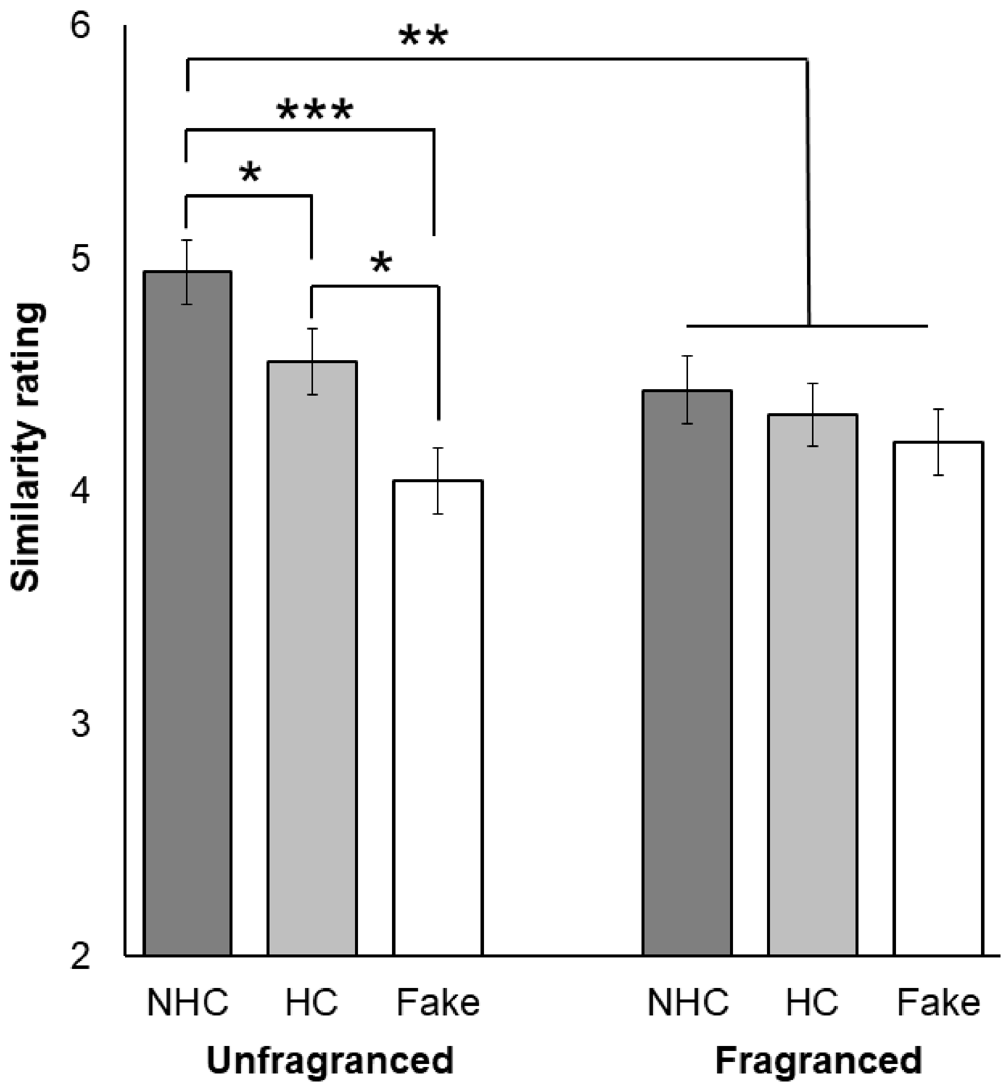

Figure 1 Mean ratings (±SEM) given to unfragranced and fragranced samples from two groups of real couples (NHC, woman was not using hormonal contraception when the relationship began; HC, woman used hormonal contraception when the relationship began) and Fake couples (arbitrarily paired male and female 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, we examined whether these differences might be explained by demographic differences among our sampled couples.

We reasoned that the creation of fake couples may have introduced an age difference confound. Indeed, we discovered that the mean age difference in the fake couples (9 years, s.d. = 8.97) was larger than the mean difference in the real couples (2 years, s.d. = 2.21; independent samples *t*-test, $t = 2.98$, adjusted df = 14.9, $p = .009$). However, this does not appear to be responsible for the observed differences in odour similarity, for two reasons. First, mean odour similarity ratings (calculated for each couple across all raters) were not predicted by age difference, neither across all 45 couples (i.e. real and fake combined: Pearson $r = .058$ and .031 for unfragranced and fragranced samples respectively, $p = .71$ and .84) nor across only the 30 real couples ($r = .168$ and .037, $p = .37$ and .85). Second, a comparison of age differences among the real couples showed that NHC couples were slightly less matched for age (mean = 2.73, s.d. = 2.76) than the HC couples (mean = 1.27, s.d. = 1.16; $t = 1.89$, adjusted df = 18.8, $p = .074$), and yet were judged to have more similar odours.

We then checked for other differences among the two groups of real couples. A key possible confound that might influence odour similarity between groups is whether couples in one group were more likely to be cohabiting. However, most couples were cohabiting in both groups (12 NHC and 10 HC, Chi-square = .68, p = .41). To check this further, we compared odour similarity ratings between cohabiting and non-cohabiting couples, finding no difference for unfragranced samples ($t_{28} = .10$, p = .92). For fragranced samples, there was a significant difference ($t_{28} = 2.50$, p = .018), but similarity ratings were higher for the non-cohabiting couples (mean = 5.14) rather than those who cohabited (mean = 4.06). There was also no significant correlation between odour similarity and duration of cohabitation (scoring non-cohabiting couples as zero on this measure; Spearman *r* = .07 and -.22, p = .73 and .24 for unfragranced and fragranced samples, respectively). These analyses indicate that it is unlikely that the unexpected similarity between odours within couples is entirely explained by shared environmental influences on odour.

Independent samples t-tests also indicated that there were no significant differences between relationship length, cohabitation length, age difference, RAS scores, or RAS difference scores (women’s scores subtracted from the corresponding male partner’s score) between the HC and NHC couples (Table 1).

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

3.3 Odour donors as the unit of analysis

Here, we used repeated measures ANOVA to compare mean within-couple odour similarity scores, now with Sample Type (fragranced, unfragranced) and Rater Sex (male, female) as within-subjects factors, and a between-subjects factor of Couple Type (NHC, HC, Fake couples). Mean scores are shown in Figure 2, which indicates that the overall pattern of effect is qualitatively similar to those in Figure 1. However, in contrast to when we used raters as the units of analysis, there was no main effect of Sample Type ($F_{1, 42} = .91$, $p = .346$), no main effect of Couple Type ($F_{2, 42} = .64$, $p = .530$) nor significant Sample Type x Couple Type interaction ($F_{2, 42} = .85$, $p = .435$). Planned contrasts revealed no significant difference in this analysis between the ratings of similarity given to real and fake couples ($p = .380$), or between NHC and HC couples ($p = .483$), although an *ad hoc* t-test showed significantly higher scores for NHC than Fake couples among female raters ($t_{28} = 2.35$, $p = .026$; see Figure 2). The only significant effect in the ANOVA was for Rater Sex ($F_{1, 42} = 7.79$, $p = .008$), with men on average giving higher similarity scores to odour pairs (mean = 4.65) than women did (mean = 4.27).

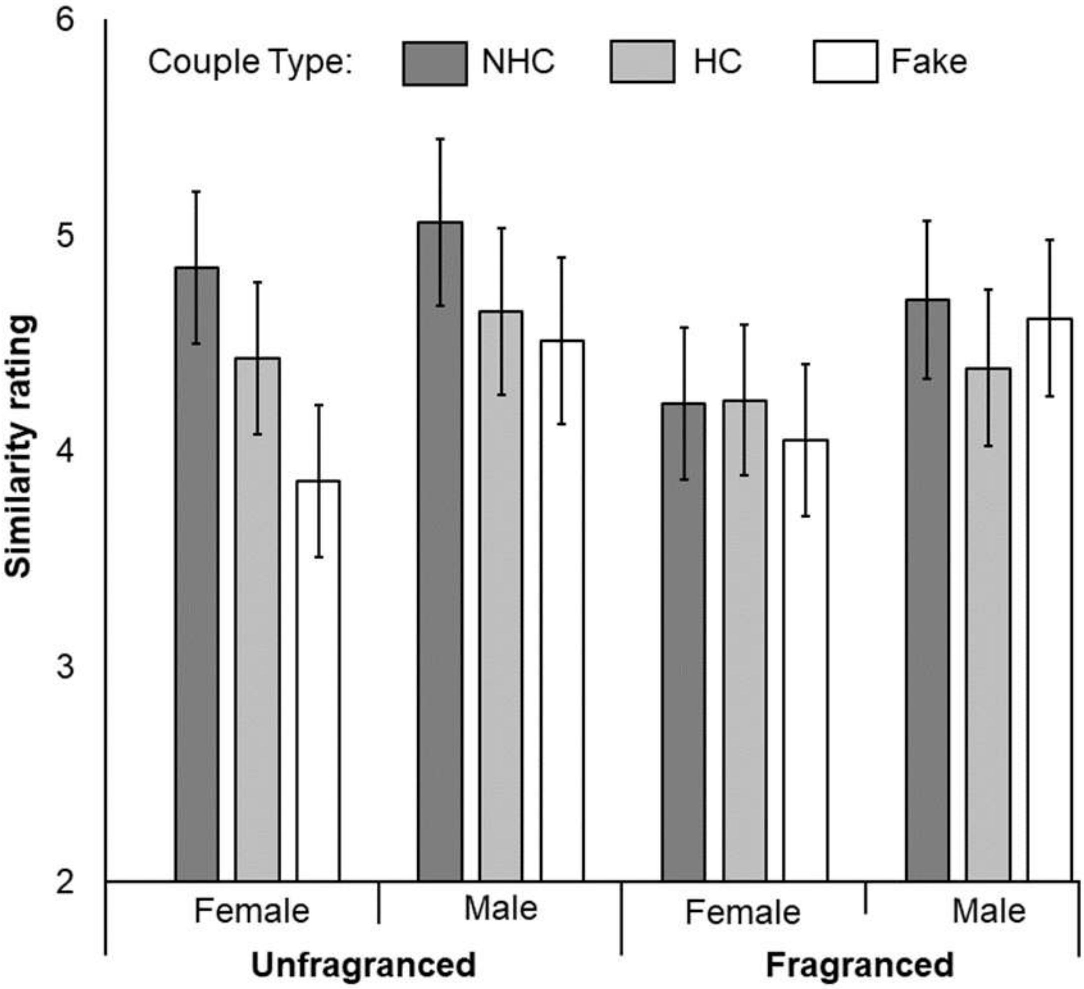

Figure 2 Mean (± SEM) ratings of similarity for odours donated by couples. Mean scores are shown for

both female and male raters to fragranced and unfragranced samples of each couple type. Ratings were given on a 9-point scale (1 = not at all similar, 9 = completely similar).

Subsequently, we examined potential correlates of odour similarity within the real couples, in view of previous findings on odour preferences for genetically dissimilar partners. Noting that between-group differences were most evident in unfragranced samples, we therefore conducted exploratory analyses of within-couple similarity scores among these unfragranced samples only. Using univariate ANOVA, we tested the predictive effects on within-couple odour similarity of Couple Type as a fixed factor (NHC, HC), and we included as covariates in the model the couples' relationship duration (in months) and male and female RAS scores. (Note that this analysis includes 15 NHC couples and 13 HC couples, because members of 2 couples chose not to complete the RAS scale). We found a significant main effect of Couple Type ($F_{1, 23} = 5.19$, $p = .032$), with odour similarity scores being higher in NHC than HC couples. The effect of relationship duration was not significant ($F_{1, 23} = 1.46$, $p = .240$), but there were also significant and independent effects of both the female ($F_{1, 23} = 10.33$, $p = .004$) and male ($F_{1, 23} = 11.45$, $p = .003$) partners' RAS scores.

We explored these using partial correlations between odour similarity and RAS scores, controlling for RAS score of respective partners. This showed that men's RAS scores were positively correlated with odour similarity ($r_p = .499$, df = 25, $p = .008$) but women's RAS scores were negatively correlated with odour similarity ($r_p = -.462$, df = 25, $p = .015$), even though RAS scores within couples were strongly correlated ($r = .618$, $p < .001$). This is illustrated further in Figure 3, which shows the significant negative correlation ($r = -.449$, $p = .017$) between RAS difference score within couples (subtracting men's RAS score from their female partner's score) and their odour similarity. In summary, these analyses indicate that, independent of the effect of

Couple Type, men's satisfaction is predicted by how similar their partner's odour is to their own, while women tend to be more satisfied when their partner's odour is somewhat dissimilar.

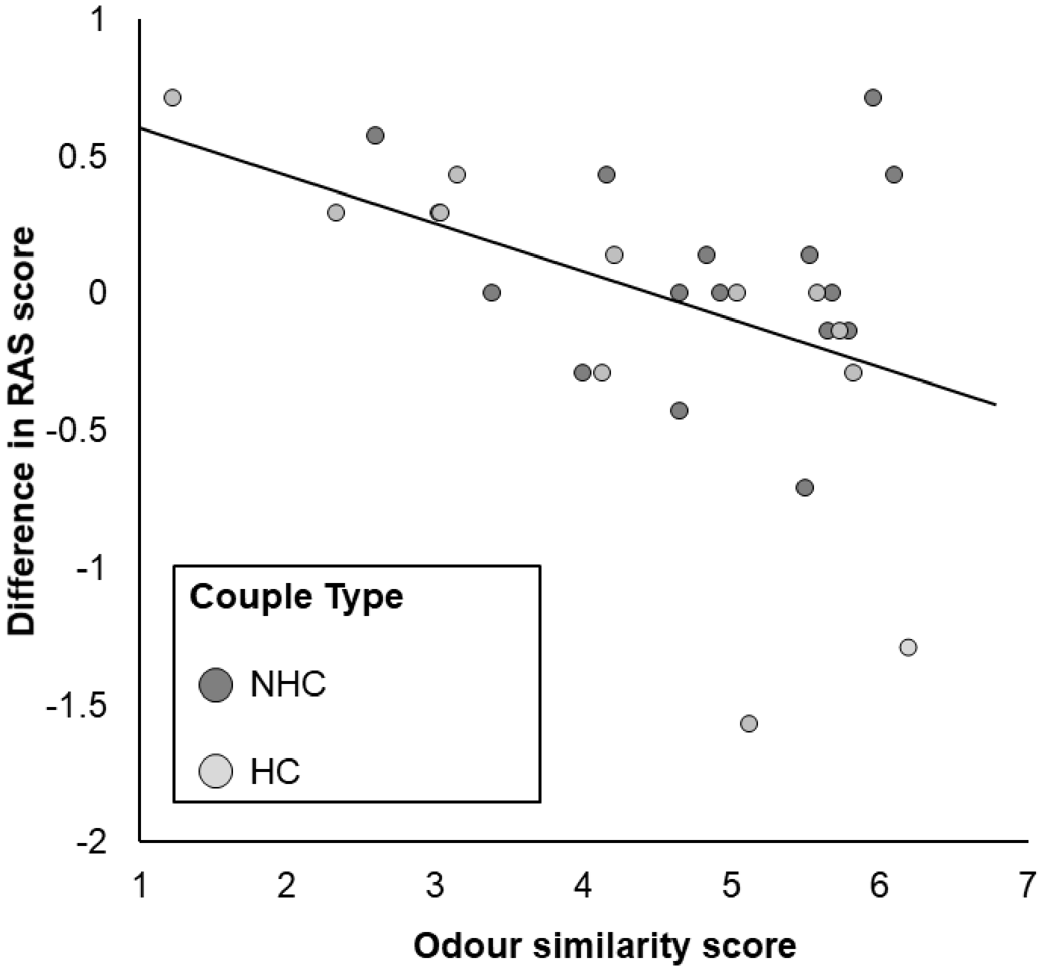

Figure 3 Relationship between odour similarity within-couples and difference in relationship satisfaction between couple members. Odour similarity scores are means from all raters for the unfragranced samples of each couple. The difference in Relationship Assessment Scale scores for male and female partners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

3.4 Comparison of rating scales

Finally, we aimed to investigate whether the simple rating scale of similarity utilised in this study mapped onto a novel lexicon which has recently been developed for assessing human body odours. We correlated similarity ratings from the current study (all raters, female raters only, and male raters only) with the difference scores each couple received for the Milky/Sweet and Spicy/Animalic factors extracted from the olfactory lexicon [49]. We did this for the unfragranced samples only, as the fragranced samples were not scored by the perfumers. We found significant negative correlations between the similarity ratings for the 30 couples and the difference between scores of Spicy/Animalic which the couples received from the perfumer scoring [49]. In other words, the more similar a couple's odour was rated, the less they differed in how perfumers scored their respective odours for the Spicy/Animalic descriptor.

Table 2 Correlations between ratings of similarity which couples (real and fake) received in the current study and difference scores which the same couples received for two verbal descriptors 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

Given this positive association between the two methods of rating, we then investigated whether difference scores of the Spicy/Animalic factor differed based on couple type (HC, NHC, Fake). We ran a Univariate ANOVA with Spicy/Animalic difference scores as the dependent variable, and couple type as a fixed factor, finding no main effect of couple type ($F_{2, 42} = .032$, $p = .969$) Planned contrasts revealed no difference between difference scores of Spicy/Animalic received by NHC and HC couples (p=.812), or between real couples and fake couples (p=.936).

4. Discussion

Previous research suggests positive assortment in actual couples in various social, psychological, and physical characteristics, with body odour being an exception from this general pattern. We investigated the perceived similarity of body odours between romantic partners comparing observed similarity ratings with those for ‘fake’ couples, and additionally comparing real couples who met whilst using or not using hormonal contraception, in order to detect evidence for alteration of odour preferences. We did this using both their unfragranced body odour, and samples in which individuals used their own fragrances, to investigate the potential for artificial fragrance use to disrupt odour-mediated assortative mating. Finally, we further assessed which perceptual qualities of our odour samples were being used to make these similarity judgements by comparing these with assessments made using a novel verbal lexicon for describing odours.

4.1. Assortative odour preferences

Our first analysis was conducted with raters as the unit of analysis, comparing each individual's assessment of the fragranced and unfragranced samples for each of the three couple types (real couples who met while the woman was using or not using HC, and a fake couple). This approach uses maximal statistical power and takes into account individual variability in raters' olfactory capability. This revealed a significant interaction between odour similarity ratings across the three couple types and between fragranced and unfragranced samples. There were significant differences in similarity ratings between real and fake couples, and between the two real couple types, but only in the unfragranced samples.

We had predicted a difference between real and fake couples, but intriguingly, the direction of the result was in the opposite direction. Based on studies of odour-mediated MHC-disassortative mating preferences in several vertebrate species [27] and laboratory-measured preferences in humans (e.g. 30, 33), we had expected that real couples would be judged to have more dissimilar odours compared with fake couples. Furthermore, regarding the two groups of real couples, we had expected that NHC couples would be more dissimilar than couples who met while the female partner was using HC, again based on the same literature on women's MHC-correlated odour preferences and specifically on findings that HC shifts these preferences towards MHC-similar partners [34]. Our data did indicate a difference in the level of similarity between NHC and HC couples, but in the opposite direction to our prediction; HC couples had a level of odour similarity that was intermediate to the NHC couples and the fake couples. This is indeed suggestive of HC influencing odour-mediated partner preference, but we do not have a clear explanation for the direction of effect, and it may be that the result does not turn out to be robust if further tested with a larger number of HC and NHC couples.

We did not find a corresponding, statistically significant interaction in the subsequent analysis in which each couple was used as the unit of analysis (neither using similarity ratings nor differences scores for couples of Spicy/Animalic). Although this analysis has more limited statistical power, this result warrants some caution regarding generalizability across couples. However, it should be noted that more focused analysis based only on the unfragranced ratings provided some consistent evidence: mean odour similarity of NHC couples (but not HC couples) was higher than fake couples, and odour similarity was found to be predicted by couple type, with NHC couples being more similar than HC couples.

Taken together, these findings provide evidence for assortative mating based on odour in humans. In comparing real and fake couples, our study is the first to examine within-couple odour similarity following the analogous experimental design that has been used for facial preferences (though as we note in the introduction there is one previous study which employed a matching paradigm to investigate this). Consistency in the direction of effect between our study and the previous face-based studies suggest that similar processes may underpin mate choices made in either modality.

It remains possible that some aspect of shared experience within couples is responsible for couples having more similar odours than expected by chance (as represented by the test against ‘fake’ couples). For example, age [56] and diet [57-59] may influence body odours, and similarities in these could be responsible for the observed results. However, as described above, it seems unlikely that the results were due to smaller age differences between couple members in real couples than fake couples, because there was no correlation between couple similarity and age differences and age differences were in fact slightly larger for NHC couples, despite having more similar odours than HC couples. Similarly, among the real couples, there was no difference in the frequency of cohabitation between NHC and HC groups, cohabitation length was uncorrelated with odour similarity, and where there was a difference between cohabiting and non-cohabiting couples (for fragranced samples only), it was the non-cohabiting couples who were rated more similar. These considerations lead to the conclusion that our finding of high within-couple similarity is more likely to reflect an outcome of mate preferences than to be produced by shared environmental experience.

If this is true, our results raise interesting questions regarding our current understanding of how odour influences mate preferences. As discussed above, odours appear to mediate mate choices in many vertebrate taxa, and the dominant view in the literature is that odour preferences are generally disassortative, rather than assortative as we report here. How can we reconcile these results?

One answer may be that the literature reporting disassortative mating is focused exclusively on the MHC. While MHC-mediated preferences may well be functionally important, MHC genes are an undeniably small fraction of the genetic contribution to the chemical signature that underlies an individual’s perceived odour. We must also not forget that chemical signatures are additionally influenced by a variety of environmental effects, including diet [57-59]. The contribution of MHC is therefore only a small fraction of the entire odour profile of any individual. Recognition of the broader influences on odour profiles reveals possibilities for complex and perhaps hierarchical mate choice decision-making influenced by sub-components of the odour profile. In other words, it is possible that in the real-world milieu of mate choice, a first-level preference for a potential partner’s odour might be determined by overall similarity: we prefer the smell of those with similar odour to our own, as we do with faces and indeed many other traits. It is then conceivable that a second-level preference for odour is shaped by chemical markers of MHC genes. According to such a hierarchical flow structure, ultimately preferred partners would be those who are generally similar, but who lie at the dissimilar end of the MHC-similarity continuum. Nested preferences and trade-offs between different qualities should not be unexpected within complex decision-making processes such as choosing a mate. Indeed, there is experimental evidence from mice for exactly this kind of trade-off even within a single olfactory signal, such that expression of preference for relatively MHC-dissimilar mates is dependent on other markers of absolute quality and the co-variance in these different traits among available mates [60]. However, it should be noted that our expectations of similarity were based on literature which directly genotyped MHC, which was something that we did not do in the current study. Consequently, while our findings seem counterintuitive, they do not necessarily rule out MHC-disassortative odour based mating preferences.

Further studies to test and confirm our conclusion are now called for, since ours is the first to test for odour similarity across real and fake couples. However, we note that our results regarding relationship satisfaction in the real couples are consistent with our suggestion for MHC-linked preferences being nested within a priority level preference for overall odour similarity. Even though odours of real couples were judged more similar than fake couples, and even though relationship satisfaction scores of each partner were highly correlated within couples, the reported relationship satisfaction of the female partner was relatively low in those couples with the most similar odour. This is exactly what we might expect based on previous research on both sex differences in olfactory functioning, in which women out-perform men, and sex differences in choosiness and the costs of mate choice. Our results are thus consistent with previous literature which has found that women whose partners are relatively MHC-similar are less satisfied and more likely to seek extra-pair affairs compared with other women who have less MHC-similar partners [41, 42]. Similar effects are also observed in other socially monogamous species [61,62].

As this work represents a preliminary investigation, future work is needed to assess the robustness of our findings. Studies should focus on increasing the number of odour donors recruited in the HC and no HC groups, and consider current as well as previous use of hormonal contraception by female donors in the study design. We note that, in our sample, two of the HC group were no longer using HC at the time of sample collection, and five women in the NHC group had begun to use HC by the time of sample collection. Changes in HC use during a relationship might present an interesting opportunity to further investigate levels of olfactory similarity and relationship satisfaction, as we know both that hormone levels have an influence on body odour (65, 66, 67) and that changes in HC use during the course of a relationship may alter attraction to, and satisfaction with, a partner (70). However, as this was not something we set out to test, we do not have sufficient variation in the current sample to investigate this, and future researchers should take this into consideration. Furthermore, it would be interesting to run a longitudinal study assessing whether body odour similarity is predictive of long term relationship quality and potential dissolution, and to directly incorporate MHC genotyping where possible.

4.2 Effects of fragrance use

Interestingly, there was no difference in similarity ratings in the fragranced samples, with ratings of the three couple conditions not differing significantly from one another. Our findings therefore suggest that fragrance use disrupts the ability of human smellers to detect the similarity of underlying body odour. This lends support to the idea that fragrance use has the effect of masking odours, rather than the alternative suggestion that individual fragrance choices may serve to complement one's MHC genotype or even enhance the distinctiveness and attractiveness of one's underlying odour [45, 47].

However, it is worth noting the nature of fragrance use in our sample. Previous studies linking fragrance preferences to MHC types have tended to use perfumes or perfume ingredients, whereas odour donors in our study used their day-to-day fragranced deodorants. Deodorants contain fragrances, but also contain specific anti-microbial compounds that target bacteria responsible for odour production. It is possible that these anti-microbial effects (and potentially compounds which reduce the overall production of sweat if antiperspirants were used) are responsible for the reported results, rather than a masking effect of fragrance components *per se*. Further studies could test between these possible mechanisms. To date, there are only two studies investigating the ways in which deodorants and antiperspirants might influence the detection of socially relevant cues from body odour. Allen and colleagues [63] found evidence that use of deodorants can enhance or mimic certain information available in body odour, potentially making it harder to differentiate between individuals. A second study also found that deodorant may somewhat suppress identifying characteristics of an odour, compared to no fragrance at all, but importantly maintaining a level of idiosyncrasy in odour samples when using a chosen deodorant over an experimenter assigned one [46].

At first sight this result suggests that fragrance (or deodorant) use has the potential to interfere and disrupt important mate choice processes. Certainly, it may have some effect in real life, but it is important to remember that both the unfragranced and fragranced samples came from the same couples and were rated by the same raters, and that odour similarity in the unfragranced samples was significantly different from the fake couples. In other words, if we assume that people do indeed seek and prefer partners with similar odours to themselves, then our results suggest that they are able to achieve this *despite* using fragrances in their daily lives. Although we did not ask our odour donors about their frequency of fragrance use at the time they met their partner, all of them were using artificial fragrances of some kind when they took part. Thus, while judgments of underlying odour similarity by our raters were altered by the addition of fragrances, there appears to still be opportunity for long-term and intimate partners to exercise their odour preferences during relationship formation. The importance of incorporating fragrances into investigations of human olfactory communication has recently been highlighted in a review by Allen and colleagues (69), and the current findings further support this.

4.3 *Comparison of rating scales*

Finally, we investigated our similarity rating scale, with the aim of establishing which components of an odour profile were being used to assess this. Previous literature has worked to enhance the complexity of odour assessments used in human olfaction studies [see 49], the argument being that an individuals' odour profile is very complex unlike the rating scales we often employ. We found that more complex lexicon based assessments of our couples' odour samples which had been completed by olfactory experts were actually positively associated with the simple similarity rating scale utilised by our non-expert raters in the current study. Our findings tell us that when we ask non-experts to assess odour samples for similarity, it is the Spicy/Animalic perceptual qualities on which these similarity judgements are being made, and not the Milky/Sweet aspects (which we know are detectable in the current samples from the expert ratings). Additional work is needed to further validate the olfactory lexicon and establish whether it is feasible to use this more complex odour assessment with participants who have little or no olfactory expertise.

4.3 Conclusion

Our results lend further support to the emerging literature that odour may play a role in both human mate choice and the subsequent dynamics of within-couple relationship satisfaction. Contrary to prediction, however, our results suggest an affinity for partners with similar rather than dissimilar odours. Our study indicates that odour preferences follow the same assortative rule as has been demonstrated for many other partner attributes, including physical traits such as face shape. At the same time, the level of within-couple odour similarity is associated with relative relationship satisfaction between the male and female partners, with women being more satisfied in couples with relatively dissimilar odour. Taken together, these findings suggest that the much-discussed role of odour-mediated MHC-disassortative preferences, perhaps more salient in women's preferences than in men's, may represent a secondary process which is subsumed within a more prioritised assortative mating decision rule. This is consistent with a similar two-tiered decision process previously suggested to explain the conundrum of women's MHC-assortative preferences for male faces [64]. Thus, while our results were surprising, such a nested decision-making process could be one mechanism by which individuals select not extreme MHC-dissimilarity but rather an intermediate level of MHC-sharing with eventual partners. This could then serve to achieve an optimal, rather than extreme, level of heterozygosity in resulting offspring, exactly as predicted by optimal immunological diversity theory [65].

Ethical approval

All procedures performed in studies involving human participants were in accordance with the ethical standards of the institutional and/or national research committee and with the 1964 Helsinki declaration and its later amendments or comparable ethical standards.

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