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The impact of artificial fragrances on the assessment of mate quality cues in body odor.

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Abstract

We investigated the impact of artificial fragrances on the accurate detection of biologically relevant information in human body odor. To do this, we examined cross-sensory consistency (across faces and odors) in the perception of masculinity and femininity in men and women, and how consistency is influenced by the use of artificial fragrance. Independent sets of same and opposite-sex participants rated odor samples (with and without a fragrance, N = 239 raters), and photographs (N = 130) of 20 men and 20 women. In female, but not male raters, judgments of masculinity/femininity of non-fragranced odor and faces were correlated. However, the correlation between female ratings of male facial and odor masculinity was not evident when assessing a body odor and fragrance blend. Further analysis also indicated that differences in ratings of male odor masculinity between men with very masculine or high and low levels of facial masculinity were removed by the addition of fragrance. This effect was absent in ratings of female odors by both female and male raters, suggesting sex-specificity in the effects of fragrance on odor perception. The widespread use of artificial fragrance in many modern populations raises questions about how this cultural practice influences ability to detect and utilize mate-choice relevant cues. Our findings suggest that women may be more sensitive to these cues, and therefore also to disruption of this information through fragrance use. We discuss our results using the framework of culture-gene coevolution.

Key words: fragrance; olfactory communication; body odor; mate choice; cosmetics; perfume.

Introduction

It is well-established that many non-human species use olfactory information to assess potential mates on attributes such as reproductive status (Clarke, Barrett, & Henzi, 2009; Miranda, Almeida, Hubbard, Barata, & Canário, 2005), competitive ability (Rich & Hurst, 1998; Huck, Banks, & Wang, 1981) and genetic compatibility (Ilmonen, Stundner, Thoss, & Penn, 2009; Ruther, Matschke, Garbe, & Steiner, 2009). Additionally, olfactory signals not only reveal characteristics of the individual, but have also been found to induce physiological and behavioral changes in the perceiver, such as accelerating or delaying the onset of puberty, inducing ovulation, inducing abortion, increasing and decreasing sperm allocation as well as affecting the performance of copulatory behaviours in many non-human animals (for a review see Petrulis, 2013). Humans however, have a reduced number of olfactory receptor cells and functional olfactory receptor genes compared to other mammals, such as dogs and mice (Schaal & Porter, 1991; Young, 2002). This has previously led to the conclusion that humans are chiefly visual creatures. However, while we may be inferior to other species regarding our ability to detect odors, we are in fact quite well endowed with sebaceous and apocrine glands (Kippenberger et al., 2012); this led Stoddart (1990) to label humans as ‘the scented ape’. These glands become active during puberty (Montagna & Parakkal, 1974), suggesting a role in sexual selection. Based on such information, it has been hypothesized that humans retain the ability to assess olfactory cues in mate choice scenarios, with body odor being posited as serving an analogous signaling function in humans to urinary and glandular odor cues in other animals (Comfort, 1971; Penn et al., 2007; Schleidt, Hold, & Attili, 1981; Stoddart, 1990).

In support of this, research suggests that humans indeed use olfactory cues present in odor to assess a range of qualities. For example, humans can assess an individual's sex (Schleidt, Hold, & Attili, 1981), personality (Sorokowska, 2013), diet (Fialová, Roberts, & Havlíček, 2013), genetic compatibility (Havlíček & Roberts, 2009, 2013) or health status (Moshkin et al., 2012). Humans also have the capacity to recognize kin via body odor (Ferdenzi, Schaal, & Roberts, 2010; Roberts et al., 2005; Weisfeld, Czilli, Phillips, Gall, & Lichtman, 2003), which is important in sexual selection in order to avoid inbreeding. Individuals can detect olfactory cues of a woman's ovulatory stage with studies finding that men perceive female odors collected during the follicular phase of the menstrual cycle to be more attractive than those from the luteal phase, the latter being associated with a low conception risk (Singh & Bronstad, 2001;Gildersleeve, Haselton, Larson, & Pillsworth, 2012; Kuukasjärvi, Eriksson, Koskela, Mappers, Nissinen, Rantala, 2004). Furthermore, findings to date demonstrate that information which is available in body odor is often correlated with mate-choice relevant information present in cues from other modalities. For example, individuals prefer the smell of others who exhibit attractive nonverbal behavior (Roberts et al., 2011) or low fluctuating asymmetry, believed to reflect genetic and developmental stability, who are also often rated as being more attractive facially (Rikowski & Grammer, 1999; Thornhill & Gangestad, 1999). Additionally, findings suggest that these olfactory cues may not only provide information, but, as found with non-human animals, potentially alter the physiological state of the perceiver. For example, Bensafi and colleagues found that presentation of a human sex steroid derived compound lead to increased physiological arousal in women and decreased arousal in men (Bensafi et al., 2003).

In spite of the apparent value of olfactory cues in evaluating others, there are a number of cultures where conscious detection of body odor is perceived negatively (e.g. Schleidt et al., 1981). This is echoed in the early development and use of fragrances and perfumes worldwide, which dates back to at least the ancient Egyptian and Greek civilisations (Stoddart, 1990). Indeed, the fragrance industry in western societies is worth billions of dollars, and personal fragrance use is widespread, with one study finding that 79% of women and 60% of men sampled in the UK reported using a deodorant every day (Roberts, Miner, & Shackelford, 2010). The use of such products raises the question of what effect they might have on the cues present in body odor, and in turn how this influences social and sexual interactions with others.

One model which has been employed to help explain the apparent contradiction between the communicatory significance of body odor and our apparent desire to repress it is the culture-gene coevolution paradigm. According to this paradigm, the cultural attitudes, beliefs, practices and perceptions of others can be selected in a similar fashion to that of genetic material and as such these cultural norms and behaviors are subject to a process analogous to natural selection (Feldman & Laland, 1996; Richerson & Boyd, 2006). Consequently, it has been posited that this contradiction regarding olfaction and fragrance may represent an interaction between culturally evolved practices and biologically evolved olfactory signals. Indeed it has been proposed that biologically evolved preferences might even shape cultural practices. Havlíček and Roberts (2013) discuss the use of cosmetics in this regard, an example of this being that individuals may wear foundation in order to improve the appearance of skin health – a biologically evolved preference being enhanced via a cultural practice. In support of this one study found there to be greater contrast in the luminance of females' faces than males', and that gender assumptions of androgynous faces could be manipulated by increasing or decreasing the luminosity contrast of images (Russell, 2009). Furthermore the authors found that the same face had higher levels of contrast when makeup was applied compared to having no makeup applied, lending support to the concept that facial cosmetics are used to enhance sexually dimorphic attributes, in this case femininity, which may play a role in human mate choice scenarios.

Based on this framework, recent research suggests that rather than completely masking cues present in body odor, fragrances may instead be chosen (perhaps unintentionally) to enhance the unique qualities of an individual's body odor. Preference for common perfume ingredients is correlated with genotype at the major histocompatibility complex (MHC), a set of genes involved in immune function (Hämmerli, Schweisgut, & Kaegi, 2012; Milinski & Wedekind, 2001). MHC is potentially an important cue of genetic compatibility in humans, as in other species, and MHC-disassortative odor and mating preferences have been recorded (Havlíček & Roberts, 2013). MHC-correlated perfume choice may thus enhance idiosyncratic immunogenetic cues available in body odor and used in mate choice, as predicted by the culture-gene coevolution paradigm. In further support of this, Lenochová and colleagues (2012) found that mixtures of participants' body odor with their perfume of choice were perceived to be more pleasant than mixtures of body odor and an experimenter-assigned perfume, suggesting choice for fragrances that complement underlying body odor. However, how fragrance use may interfere with odor-based discrimination of other mate qualities has not been explored.

In order to clarify this issue, we investigated the effects of fragrance use on the perception of masculinity and femininity in men and women. These traits have been previously linked to mate choice and sexual selection in humans, with masculinity potentially reflecting good genetic quality in males (Thornhill & Gangestad, 1999) and femininity being identified as a trait representing good reproductive quality in human females (e.g. Fraccaro et al., 2010). Both traits are detectable across multiple modalities (Fraccaro et al., 2010; Little, Connely, Feinberg, Jones, & Roberts, 2011), with perceptions of facial masculinity having recently been found to correlate with morphological sexually dimorphic traits such as height and weight (Holzleitner et al., 2014). Additionally, both traits are central constructs used in the commercial development of fragrances, with most perfumes and deodorants being classified as either masculine or feminine (so-called unisex fragrances are in the minority; Lindqvist, 2012). This further cements the cultural relevance of these sexually dimorphic traits for males and females, making them prime candidates for cultural practices which may have emerged as a result of a biologically evolved preference. Fragrances, as with other cosmetics, may be designed and used to enhance the perception of these traits, thus making an individual more appealing to the opposite sex.

The current study aimed to investigate whether commercially available fragranced products lead to improvements in ratings of masculinity/femininity. This would be predicted by a culture-gene co-evolution framework where cultural norms are shaped by evolved, sexually dimorphic, preferences. In order to assess this, we aimed to first replicate previous findings that these mate-choice relevant, sexually dimorphic traits assessed using one modality are correlated with the assessments of the same trait in another modality. This was accomplished by specifically examining the relationship between odor rated and facially rated masculinity/femininity. By comparison of these cross-modal relationships between faces and axillary odor, with and without the presence of a fragrance, we were able to investigate the impact that fragrance had on the assessment of individuals' odor, here taken as representing one aspect of their attractiveness to a potential mate. We hypothesized that fragranced odor samples would be rated as more masculine or feminine than unfragranced samples (in keeping with a culture-gene coevolution paradigm). Furthermore, we predicted that the ratings of masculinity and femininity given to male and female *unfragranced* axillary odors would be correlated with the ratings given to the same individuals' faces. Finally, we hypothesized that the addition of an artificial fragrance would prevent the accurate assessment of an individual's masculinity/femininity through body odor, thus resulting in no correlation being found between fragranced odor ratings and face ratings of masculinity/femininity, asfragrances are specifically designed to enhance these traits reducing the individual variation in these underlying body odor cues (Lindqvist, 2012).

Method

The study received ethical approval from the University of Stirling's Psychology Ethics Committee.

Odor Donors

Odor samples were collected from 20 men (mean age ± SD = 23.25 ± 4.23; range: 19-33) and 20 women (21.2 ± 2.50; range: 18-27) recruited from the University of Stirling, all of whom were heterosexual non-smokers who regularly wore deodorant. We restricted our recruitment of female odor donors to women who were using hormonal contraception, in order to control for cyclical hormonal changes which are known to influence women's body odor (Gildersleeve et al., 2012; Havlíček, Dvorakova, Bartos, & Flegr, 2006).

We collected two axillary odor samples from each donor: one while donors were wearing no underarm fragrance (hereafter termed the 'unfragranced sample') and one while donors were wearing their usual underarm fragrance (hereafter termed 'fragranced sample'). The two odor collection periods were on consecutive days (unfragranced followed by fragranced), and donors were instructed to shower in between the two periods. Odor was collected on cotton pads which participants attached to their armpits, using surgical tape, and left in place for 24 hours. There is variation in sampling time across studies, though numerous studies to date have adopted 24 hour sampling periods for odor collection (e.g.

Kohoutová, Rubešová, & Havlíček, 2011; Martins et al., 2005; Santos, Schinemann, Gabardo, & Bicalho, 2005; Sorokowska, Butovskaya, & Veselovskaya, 2015). Furthermore Havlíček et al. (2011) found that 12 hour sampling yielded samples which were less intense, and less likely to be perceived, compared with a 24 hour sampling period. Each donor was provided with fragrance free soap (Simple Pure^{TM}) and asked to use only this in place of any fragranced hygiene products for 24 hours prior to odor collection, and in between the two odor collection periods. For the fragrance free sample participants simply showered, dried, and then applied the cotton pads to their armpits. For the fragranced samples participants showered and then once dry applied their usual deodorant to each armpit before applying the cotton pads provided.They were also asked to avoid wearing any other fragranced products or perfumes. In line with previous research, we instructed our donors to avoid drinking alcohol, being in smoky places, exercising and eating certain strong-smelling foods (e.g. garlic, asparagus, curry). They were asked to refrain from sexual activity and to avoid sharing their bed with anyone during the odor collection phase (Kohoutová et al., 2011; Lenochová et al., 2012; Roberts et al., 2011). The donors returned the samples, in sealed plastic bags, to the lab within 2 hours of removal, where they were stored in a freezer at -30˚C until use. Samples were thawed at room temperature for 2 hours prior to test sessions and re-frozen between test sessions. Previous research suggests freezing has minimal impact on the perceptual quality of odor samples (Lenochova, Roberts, & Havlicek, 2009; Roberts, Gosling, Carter, & Petrie, 2008).

Finally, digital color facial photographs were taken of each donor (head and shoulders) in standardized lighting conditions, at a standard 1.5m distance against a neutral grey background, using a Canon PowerShot G6 digital camera (7.1 megapixel, focal length range of 7.2 to 28.8mm). For the purpose of the photo, participants were instructed to adopt a neutral expression. All participants were requested to remove make-up beforehand, and to remove glasses, jewelry and facial piercings.

Odor Raters

Odor samples were rated by 275 same and opposite-sex raters. We excluded scores if raters did not complete all of the ratings (N = 23), indicated they were homosexual (N = 12) or answered ‘prefer not to say’ with regard to their sexual orientation (N = 1), leaving a total of 239 raters used in analyses.

Male odor samples were rated by a total of 75 women (mean age ± SD = 20.12 ± 2.39; range: 17-30), and by 45 men (21.26 ± 4.16; range: 18-40). Female odor samples were rated by an independent set of 75 women (21.67 ± 4.05; range: 18-49) and 44 men (21.25 ± 2.01; range: 19-26).

Face Raters

Participants were an independent set of 204 individuals recruited via online social networking sites, and were not familiar with the individuals they were rating. As with odor ratings, incomplete responses (N = 65) and those from raters who were homosexual (N = 6) or who chose ‘prefer not to say’ (N =3) when completing the sexual orientation question were excluded, leaving a total of 130 raters used in the analysis. For the male face rating task, the final sample of raters included 42 women (mean age ± SD = 28.26 ± 9.61; range: 21-62) and 16 men (30.81 ± 11.37; range: 23-62). Female faces were rated by an independent set of 54 women (24.99 ± 8.28; range: 18-54) and 18 men (30.17 ± 10.39; range: 19-49).

Odor Rating Procedure

After providing informed consent, participants were asked for some basic demographic information. Each participant then rated odor samples presented in clear glass

500ml conical flasks with aluminum foil coverings. Participants were asked to rate the perceived masculinity or femininity of each odor on a 7-point scale (1 = below average, 4 = average, 7 = above average). Female samples were rated for femininity and male samples for masculinity. In order to avoid sensory overload, each rater judged samples from 5 donors (all male or all female), rating both the unfragranced and fragranced samples from these 5 donors (10 samples in total). In this way, the 20 male and 20 female donor samples were each divided into four groups of 5. The four groups of male odor samples were judged by similar numbers of female raters (N = 19, 18, 18, 20 for groups 1-4, respectively) and male raters (N = 10, 11, 13, 11). This was also true of female raters (N = 20, 18, 20, 18) and male raters (N = 9, 13, 10, 12) assessing female odor samples. Mean values were computed for each donor separately from ratings given by same- or opposite-sex participants, for both face and odor.

The order in which participants rated the unfragranced and fragranced samples was counterbalanced, but within these conditions, raters assessed the samples from the 5 donors in the same order. Raters were given no information about the donors.

Face rating procedure

Two online photograph rating tasks were created, one for male donors and one for female donors. Images appeared individually and participants rated faces for masculinity/femininity (depending on sex of the stimuli) odor. The order in which each image appeared was randomized between participants. Participants who completed the face ratings also provided basic demographic information (age, sex, sexual orientation).

Results

Effects of fragrance on odour ratings

In order to investigate the effect of fragrance on sample ratings, we ran a repeated-measures ANOVA with two within-subjects factors, each with two levels (fragrance condition:

fragranced, unfragranced; rater sex: same, opposite). As the male and female donor samples were assessed on an analogous but different scale (i.e. masculinity, femininity) we ran the analysis for each donor's sex separately.

For ratings given to male donors, there was a significant main effect of rater sex, with female raters giving higher ratings of masculinity to odor samples ($M = 3.51$, $SD = .62$) than male raters ($M = 3.31$, $SD = .68$), $F (1,19) = 5.657$, $p = .028$, $d = .31$. However, there was overall no significant difference between unfragranced and fragranced samples, $F (1,19) = .219$, $p = .645$. There was also a significant interaction between the sex of the rater, and the ratings given to the two fragrance conditions, $F (1,19) = 6.103$, $p = .023$ (Fig. 1). Post hoc paired sample t-tests revealed that there was no significant difference between the ratings given by females to fragranced and unfragranced samples, $t(19) = -.857$, $p =.402$, or between ratings given by males to fragranced and unfragranced samples, $t(19) = 1.321$, $p = .202$. However further analysis did reveal a significant difference between ratings given by males ($M = 3.13$, $SD = .81$) and females ($M = 3.59$, $SD = .69$) to fragranced samples, $t(19) = 3.782$, $p = .001$, $d = .61$, but not between the ratings of unfragranced samples by males and females, $t(19) = -.337$, $p = .740$ (Fig. 1a).

The same analysis was then completed for the responses obtained for female donors' odour samples. Here there was no significant main effect of rater sex, $F(1,19) = 1.556$, $p = .227$, but there was a significant main effect of fragrance, with the fragranced samples being rated as more feminine ($M = 3.76$, $SD = .93$) than the unfragranced samples ($M = 3.06$, $SD = .64$), $F(1,19) = 17.450$, $p = .001$, $d = .88$ (Fig. 1b). Unlike with the male donors, there was no significant interaction between rater sex and ratings given to the two fragrance conditions, $F (1,19) = .029$, $p = .866$. In exploratory post hoc analyses, we found that there were significant differences between ratings of fragranced and unfragranced samples given by both male and female raters, $t (19) = -3.12$, $p = .006$, $d = .82$; $t (19) = -4.96$, $p < .001$, $d = .78$.

Relationship between face and odor ratings

Next, we investigated whether perception of femininity/masculinity was concordant across modalities by running correlational analyses using the mean ratings given to the odors and facial photographs of the donors.

For female raters, there was a significant and positive correlation between their ratings of unfragranced odors and face ratings of female donors, r (20) = .53, p = .02 (Figure 2a), as well as the fragranced odors and face ratings of female donors, r (20) = .50, p = .03 (Figure 2b). Furthermore, we found a significant and positive correlation between ratings given by females to unfragranced odors and male donors faces, r (20) = .45, p = .046 (Figure 2c), but the correlation between ratings of fragranced odor and male donors faces was not significant, r (20) = .005, p = .98 (Figure 2d).

For ratings given by male participants, there were found to be no significant correlations between unfragranced odor ratings and face ratings, r (20) = .34, p = .15 (Figure 3a), or fragranced odor ratings and face ratings given to female donors, r (20) = .17, p = .46 (Figure 3b.). Additionally there were no significant correlations found between unfragranced ratings of odor and face ratings, r (20) = .08, p = .74 (Figure 3c), or fragranced ratings and face ratings given to male donors samples, r (20) = .07, p = .77 (Figure 3d).

In order to further understand the differential effect that fragrance appeared to be having on ratings of masculinity and femininity given by same- and opposite-sex raters, we used a median split to divide the male and female donors into two groups; those who had received relatively high face ratings of masculinity/femininity and those who had received relatively low ratings. We then ran a repeated measures ANOVA, including fragrance as a within-subjects factor (fragranced, unfragranced), and high/low masculinity/femininity face ratings (split by the median) as a between-subjects factor. This analysis was run separately for male and female donors' ratings, as well as for same and opposite sex raters.

There was no significant main effect of fragrance condition for women rating men, $F (1,18) = .88$, $p = .36$. However, there was a significant interaction between ratings given by women to the male fragranced and unfragranced samples and the high/low score for facial masculinity, $F (1,18) = 4.84$, $p = .04$ (Figure 4a). Post-hoc independent samples t-tests revealed that there was a significant difference between mean ratings given to the unfragranced samples of individuals in the high ($M = 3.83$, $SD = .65$) and low ($M = 3.03$, $SD = .74$) face masculinity groups, $t (18) = -2.55$, $p = .02$, $d = 1.13$, but not between the fragranced samples, $t (18) = -.17$, $p = .87$ (Figure 4a). Paired samples t-tests further indicated that while there was a significant difference between the ratings for fragranced ($M = 3.56$, $SD = .66$) and unfragranced ($M = 3.04$, $SD = .74$) samples given to men grouped with 'low' facial masculinity, $t (9) = 3.36$, $p < .01$, $d = .74$, the same difference was not significant for the men grouped as having 'high' facial masculinity, $t (9) = -.71$, $p = .49$ (Figure 4a). This model was re-run using ratings given by males, and as before, there was no significant main effect of fragrance, $F (1,18) = 1.66$, $p = .21$, and there was no longer found to be a significant interaction between the ratings given to fragranced and unfragranced samples, and donors high/low face masculinity, $F (1,18) = .08$, $p = .79$ (Figure 4c).

The same analysis was conducted for female donors' ratings. For ratings of femininity from males we found that, unlike with male donors ratings by females, there was a significant main effect of fragrance, $F (1,18) = 10.61$, $p = .004$, $d = .82$ with fragranced samples receiving higher ratings of femininity than unfragranced. However there was no significant analogous interaction between face ratings and odor ratings, $F (1,18) = .08$, $p = .79$, as had been found with the male donors (Figure 4b). When analyzing responses from female raters there remained a main effect of fragrance, $F (1,18) = 23.33$, $p < .001$, with fragranced samples receiving on average higher ratings of femininity than unfragranced samples, and, as with male raters, there was no significant interaction between face and odor ratings, F (1,18) = .04, p = .84 (Figure 4d).

Discussion

In this study we set out to investigate the effects of artificial fragrance use on the detection of masculinity/femininity from body odor. In order to assess the impact of fragrance use, the relationships between face and odor ratings was investigated, both with and without fragrance.

Initially we were interested in the general effect of the addition of a fragrance on the perception of body odor, and the current analysis suggests that this effect differs depending on the sex of the odor donor and of the rater. When looking at male odors, female raters tended to give higher ratings of masculinity than male raters, especially in the fragranced samples, suggesting that women are perhaps more sensitive to perceptual changes in these traits. Despite this, fragranced samples were not rated as significantly more masculine than unfragranced samples by either men or women, and ratings of femininity for female samples did not differ between male and female raters. However, female samples were still found to be significantly more feminine with the addition of a fragrance, when rated by men and women, supporting the idea that fragrance may be used, as other cosmetics may be (e.g. Russell, 2009), to enhance potentially biologically evolved preferences.

This pattern of results potentially reflects some difference between fragrances designed for males and females –female fragrances may be designed to be more feminine than male fragrances are masculine. This explanation is still consistent with a culture-gene coevolution framework. For example, there are negative associations with being perceived as extremely masculine, with one study finding that masculine faces had decreased perceptions of warmth, emotionality, honesty, cooperativeness and parental quality (Perrett et al., 1998). Females have also been found to prefer a moderate level of masculinity over an extreme level (Rhodes, Hickford, & Jeffery, 2000). We know of no such studies that find analogous consequences of women being 'too feminine', with research suggesting that extreme feminization may not elicit these same negative responses (Rhodes et al., 2000), thus giving no reason to avoid over-feminizing a fragrance. This difference in opposite sex preferences for these two traits may be a reflection of the different mating strategies adopted by men and women. Research has found that women seek partners with different qualities depending on their intentions – long term vs. short term mating. Due to the sex differences in biological costs related to reproduction, traits linked to genetic quality such as dominance and physical attractiveness are valued more for short term mating, whereas loyalty, access to resources and the potential to be an invested father are more important for women choosing long term partners (see Gangestad & Simpson, 2000). It is likely that masculinity presents a trait which will be differentially favored by women in these two mating scenarios, as it has been linked to perceptions of warmth, honesty, cooperativeness and parental care, as previously mentioned. Men however do not show such varied strategies for short term and long term mating which is likely why there is no difference for preferences in levels of femininity found in the literature. Consequently, fragrance developers may avoid high levels of masculinity in male fragrances but not of femininity in female fragrances.

Our second prediction, that ratings of traits would be correlated across modalities, was partially supported, but this again appeared to be sex-dependent. There were significant correlations between ratings of masculinity and femininity given to unfragranced samples and faces which were rated by females (for both male and female samples), but this was not the case for ratings given by males (for both male and female samples). This finding builds on the one discussed above, further suggesting a sex-dependent sensitivity in perception of traits relating to masculinity/femininity. One potential explanation for this is that, due to sex differences in the physical/biological costs of reproduction, it is more important for women to accurately assess these cues of potential mate quality, and so women show an increased sensitivity to the detection of this information. This is supported by previous work indicating that women are more sensitive in general than men are to odors (Brand & Millot, 2001). This sex difference may be exacerbated at certain times of a woman's menstrual cycle, as women's olfactory ability has been found to be heightened during the ovulatory phase of the cycle when conception risk is relatively high (Doty, 1981; Navarrete-Palacios, Hudson, Reyes-Guerrero, & Guevara-Guzmán, 2003). It could also be argued that women use more fragranced products than men do (Roberts et al., 2010) and that this additional experience may lead to an increased sensitivity. Though this argument could be reversed; women are more sensitive to odors, which leads them to use more fragranced products. Finally, while women may use more fragranced products, it is likely that the average man is exposed to a large number of fragranced products through daily interactions with women. In order to investigate this further future studies may benefit from measuring hygiene habits and fragranced product use in raters.

The final hypothesis, that the addition of an artificial fragrance would prevent the accurate assessment of an individuals' masculinity/femininity through body odor, again partially supported by the current findings, also appeared to be dependent upon the sex of the rater. A significant correlation between facial masculinity ratings and odor masculinity ratings by women for unfragranced samples was no longer statistically significant when fragranced samples were assessed. Further analysis using a median split on men's facial masculinity also supported this: men with highly rated facial masculinity had significantly higher masculinity ratings of their unfragranced samples than those men with low face ratings. Importantly, this discrepancy between odor ratings in men with high and low facial masculinity disappeared with the addition of a fragrance. From an individual strategy perspective, and in support of the use of cultural practices to improve upon traits for which we show evolved preferences, this finding may suggest that those who already have desirable levels of masculinity achieve little benefit from wearing a fragrance. However, individuals low in these traits can potentially improve how others' perceive them through the application of a fragrance.

The story is less clear concerning the relationship between females' odors and face ratings. Unlike male raters, the significant correlation ratings of femininity of odors and faces by female raters, when assessing the unfragranced samples, also remained in the fragranced samples. Further analysis indicated that women rating female odors did not discriminate between donors who had received high or low scores for facial femininity. This pattern was also noted in male ratings of female odors, in keeping with the lack of concordance between face and odor ratings given by men as discussed above. This finding provides further evidence of a sex-specific sensitivity in detecting these olfactory cues, with heterosexual women appearing to have more accurate perception of these traits than males. This increased olfactory sensitivity may be useful in a mate choice scenario, both for inter- and intrasexual selection, aiding the choice of a mate but also perhaps allowing accurate assessment of potential female competitors. However, it must be noted that fragrance use only appeared to *interfere* with accurate rating of mens' odours. Consequently future research should investigate whether factors including current relationship status and relationship intent also play a role in an individuals' sensitivity/perception of these cues. Indeed, previous research has shown these factors are important contributors to mate preference. For instance, female preference for dominance in male body odor varies with relationship status (Havlicek, Roberts, & Flegr, 2005).

The current study provides evidence which further supports the cross-modality of mate quality cues in humans and their availability for use in a mate choice context, though it appears, at least with masculinity/femininity, to be specific to female perceivers. Additionally, as predicted using a culture-gene coevolution model, the findings suggest that current widespread fragrance use might potentially interfere with the accuracy of information which women can perceive from male body odor, with fragrances potentially being used in an analogous fashion to other cosmetic products such as makeup (Havlíček & Roberts, 2013). At least for men, fragrance use appears to be enhancing levels of masculinity detected in body odor, and this in turn appears to make it harder for females to discriminate between individual males based on this trait.

The current study sampled quite a narrow age range of both donors and participants, so future research may benefit from establishing whether the findings are robust across a larger range of ages. Additionally, it is unclear how our findings can be extended to regularly cycling women, as all female donors were using hormonal contraceptives. This afforded us good control of the samples, however it prevents us from generalizing our findings across all women. There was also potentially some noise introduced into the data since our female raters included women both on and off hormonal contraception and did not account for cycle stage. Furthermore, participants used fragranced deodorants rather than simple fragrances, so there may be a confounding factor of body odor suppression coupled with fragrance addition. Future research should address these issues and carefully control the commercial products used. Finally, it is difficult to predict from the current study whether use of fragrance would interfere with the assessment of other mate choice relevant traits (e.g., health, personality), which may be influenced differently by the addition of artificial fragrances. Future research will be important to determine the wider impact of fragrance use on these important social variables.

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References

Bensafi, M., Brown, W. M., Tsutsui, T., Mainland, J. D., Johnson, B. N., Bremner, E. A., … Sobel, N. (2003). Sex-steroid derived compounds induce sex-specific effects on autonomic nervous system function in humans. *Behavioral Neuroscience*, *117*, 1125–34. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/14674833

Brand, G., & Millot, J. L. (2001). Sex differences in human olfaction: Between evidence and enigma. *The Quarterly Journal of Experimental Psychology. B, Comparative and Physiological Psychology*, *54*, 259–70.

Clarke, P. M. R., Barrett, L., & Henzi, S. P. (2009). What role do olfactory cues play in chacma baboon mating? *American Journal of Primatology*, *71*, 493–502.

Doty, R. L. (1981). Olfactory communication in humans. *Chemical Senses*, *6*, 351–376.

Feldman, M. W., & Laland, K. N. (1996). Gene culture coevolutionary theory. *Trends in Ecology and Evolution*, *11*, 453–457.

Ferdenzi, C., Schaal, B., & Roberts, S. C. (2010). Family scents: developmental changes in the perception of kin body odor? *Journal of Chemical Ecology*, *36*, 847–54.

Fialová, J., Roberts, S. C., & Havlíček, J. (2013). Is the perception of dietary odour cues linked to sexual selection in humans? In M. L. East & M. Denhard (Eds.), *Chemical Signals in Vertebrates XII* (pp. 161–170). Springer New York.

Fraccaro, P. J., Feinberg, D. R., DeBruine, L. M., Little, A. C., Watkins, C. D., & Jones, B. C. (2010). Correlated male preferences for femininity in female faces and voices. *Evolutionary Psychology*, *8*, 447–61.

Gangestad, S. W., & Simpson, J. A. (2000). The evolution of human mating : Trade-offs and strategic pluralism. *Behavioral and Brain Sciences*, *23*, 573–644.

Gildersleeve, K. A., Haselton, M. G., Larson, C. M., & Pillsworth, E. G. (2012). Body odor attractiveness as a cue of impending ovulation in women: Evidence from a study using hormone-confirmed ovulation. *Hormones and Behavior*, *61*, 157–66.

Hämmerli, A., Schweisgut, C., & Kaegi, M. (2012). Population genetic segmentation of MHC-correlated perfume preferences. *International Journal of Cosmetic Science*, *34*, 161–168.

Havlíček, J., Dvorakova, R., Bartos, L., & Flegr, J. (2006). Non-advertized does not mean concealed: Body odour changes across the human menstrual cycle. *Ethology*, *112*, 81–90.

Havlíček, J., Lenochová, P., Oberzaucher, E., Grammer, K., & Roberts, S. C. (2011). Does Length of Sampling Affect Quality of Body Odor Samples? *Chemosensory Perception*, *4*, 186–194. Retrieved from http://link.springer.com/10.1007/s12078-011-9104-6

Havlíček, J., & Roberts, S. C. (2009). MHC-correlated mate choice in humans: A review. *Psychoneuroendocrinology*, *34*, 497–512.

Havlíček, J., & Roberts, S. C. (2013). The perfume-body odour complex: An insightful model for culture–gene coevolution? In M L East & M. Dehnhard (Eds.), *Chemical Signals in Vertebrates 12* (pp. 1–13). New York: Springer.

Havlicek, J., Roberts, S. C., & Flegr, J. (2005). Women's preference for dominant male odour: effects of menstrual cycle and relationship status. *Biology Letters*, *1*, 256–9.

Holzleitner, I. J., Hunter, D. W., Tiddeman, B. P., Seck, A., Re, D. E., & Perrett, D. I. (2014). Men's facial masculinity: when (body) size matters. *Perception*, *43*, 1191–1202. Retrieved from http://www.perceptionweb.com/abstract.cgi?id=p7673

Huck, W. U., Banks, E. M., & Wang, S. (1981). Olfactory discrimination of social status in the brown lemming. *Behavioral and Neural Biology*, *33*, 364–371. Retrieved from http://linkinghub.elsevier.com/retrieve/pii/S0163104781921233

Ilmonen, P., Stundner, G., Thoss, M., & Penn, D. J. (2009). Females prefer the scent of outbred males: good-genes-as-heterozygosity? *BMC Evolutionary Biology*, *9*, 104.

Kippenberger, S., Havlíček, J., Bernd, A., Thaçi, D., Kaufmann, R., & Meissner, M. (2012). "Nosing Around" the human skin: what information is concealed in skin odour? *Experimental Dermatology*, *21*, 655–9.

Kohoutová, D., Rubešová, A., & Havlíček, J. (2011). Shaving of axillary hair has only a transient effect on perceived body odor pleasantness. *Behavioral Ecology and Sociobiology*, *66*, 569–581.

Kuukasjärvi, S., Eriksson, C. J. P., Koskela, E., Mappers, T., Nissinen, K., & Rantala, M. J. (2004). Attractiveness of women's body odors over the menstrual cycle: the role of oral contraceptives and receiver sex. *Behavioral Ecology*, *15*, 579–584.

Lenochová, P., Roberts, S. C., & Havlicek, J. (2009). Methods of human body odor sampling: the effect of freezing. *Chemical Senses*, *34*, 127–38.

Lenochová, P., Vohnoutová, P., Roberts, S. C., Oberzaucher, E., Grammer, K., & Havlíček, J. (2012). Psychology of fragrance use: perception of individual odor and perfume blends reveals a mechanism for idiosyncratic effects on fragrance choice. *PLoS One*, *7*, e33810.

Lindqvist, A. (2012). Perfume Preferences and How They Are Related to Commercial Gender Classifications of Fragrances. *Chemosensory Perception*, *5*, 197–204. Retrieved from http://link.springer.com/10.1007/s12078-012-9119-7

Little, A. C., Connely, J., Feinberg, D. R., Jones, B. C., & Roberts, S. C. (2011). Human preference for masculinity differs according to context in faces, bodies, voices, and smell. *Behavioral Ecology*, *22*, 862–868.

Martins, Y., Preti, G., Crabtree, C. R., Runyan, T., Vainius, A. A., & Wysocki, C. J. (2005). Preference for human body odors is influenced by gender and sexual orientation. *Psychological Science*, *16*, 694–701.

Milinski, M., & Wedekind, C. (2001). Evidence for MHC-correlated perfume preferences in humans. *Behavioral Ecology*, *12*, 140–149.

Miranda, A., Almeida, O. G., Hubbard, P. C., Barata, E. N., & Canário, A. V. M. (2005). Olfactory discrimination of female reproductive status by male tilapia (Oreochromis mossambicus). *The Journal of Experimental Biology*, *208*, 2037–43.

Moshkin, M., Litvinova, N., Litvinova, E. A., Bedareva, A., Lutsyuk, A., & Gerlinskaya, L. (2012). Scent recognition of infected status in humans. *The Journal of Sexual Medicine*, *9*, 3211–8.

Navarrete-Palacios, E., Hudson, R., Reyes-Guerrero, G., & Guevara-Guzmán, R. (2003). Lower olfactory threshold during the ovulatory phase of the menstrual cycle. *Biological Psychology*, *63*, 269–279.

Perrett, D. I., Lee, K. J., Penton-Voak, I., Rowland, D., Yoshikawa, S., Burt, D. M., … Akamatsu, S. (1998). Effects of sexual dimorphism on facial attractiveness. *Nature*, *394*, 884–7.

Petrulis, A. (2013). Chemosignals, hormones and mammalian reproduction. *Hormonal Behavior*, *63*, 723–741. doi:10.1016/j.yhbeh.2013.03.011.Chemosignals

Rhodes, G., Hickford, C., & Jeffery, L. (2000). Sex-typicality and attractiveness: are supermale and superfemale faces super-attractive? *British Journal of Psychology*, *91*, 125–40.

Rich, T. J., & Hurst, J. L. (1998). Scent marks as reliable signals of the competitive ability of mates. *Animal Behaviour*, *56*, 727–735.

Richerson, P. J., & Boyd, R. (2006). *Not by genes alone: How culture transformed human evolution*. Chicago: University of Chicago press.

Rikowski, A., & Grammer, K. (1999). Human body odour, symmetry and attractiveness. *Proceedings of the Royal Society B: Biological Sciences*, *266*, 869–74.

Roberts, S. C., Gosling, L. M., Carter, V., & Petrie, M. (2008). MHC-correlated odour preferences in humans and the use of oral contraceptives. *Proceedings of the Royal Society B: Biological Sciences*, *275*, 2715–22.

Roberts, S. C., Gosling, L. M., Spector, T. D., Miller, P., Penn, D. J., & Petrie, M. (2005). Body odor similarity in noncohabiting twins. *Chemical Senses*, *30*, 651–6.

Roberts, S. C., Kralevich, A., Ferdenzi, C., Saxton, T. K., Jones, B. C., DeBruine, L. M., … Havlicek, J. (2011). Body odor quality predicts behavioral attractiveness in humans. *Archives of Sexual Behavior*, *40*, 1111–7.

Roberts, S. C., Miner, E. J., & Shackelford, T. K. (2010). The future of an applied evolutionary psychology for human partnerships. *Review of General Psychology*, *14*, 318–329.

Russell, R. (2009). A sex difference in facial contrast and its exaggeration by cosmetics. *Perception*, *38*, 1211–1219.

Ruther, J., Matschke, M., Garbe, L., & Steiner, S. (2009). Quantity matters: male sex pheromone signals mate quality in the parasitic wasp Nasonia vitripennis. *Proceedings of the Royal Society B: Biological Sciences*, *276*, 3303–10.

Santos, P. S. C., Schinemann, J. A., Gabardo, J., & Bicalho, M. D. G. (2005). New evidence that the MHC influences odor perception in humans: a study with 58 Southern Brazilian students. *Hormones and Behavior*, *47*, 384–388. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/15777804

Schaal, B., & Porter, R. H. (1991). “Microsmatic humans” revisited: The generation and perception of chemical signals. In S. PJ, R. JS, B. C, & M. M (Eds.), *Advances in the Study of Behavior. Vol 20* (pp. 135–199). San Diego: Academic Press.

Schleidt, M., Hold, B., & Attili, G. (1981). A cross-cultural study on the attitude towards personal odors. *Journal of Chemical Ecology*, *7*, 19–31.

Sorokowska, A. (2013). Seeing or smelling? Assessing personality on the basis of different stimuli. *Personality and Individual Differences*, *55*, 175–179.

Sorokowska, A., Butovskaya, M., & Veselovskaya, E. (2015). Partner’s body odor vs . relatives’ body odor : a comparison of female associations. *Polish Psychological Bulletin*, *46*, 209–213.

Stoddart, M. (1990). *The Scented Ape*. Cambridge: Cambridge University Press.

Thornhill, R., & Gangestad, S. W. (1999). The scent of symmetry: A human sex pheromone that signals fitness?, *201*, 175–201.

Weisfeld, G. E., Czilli, T., Phillips, K. A., Gall, J. A., & Lichtman, C. M. (2003). Possible olfaction-based mechanisms in human kin recognition and inbreeding avoidance. *Journal of Experimental Child Psychology*, *85*, 279–295.

Young, J. M. (2002). Different evolutionary processes shaped the mouse and human olfactory receptor gene families. *Human Molecular Genetics*, *11*, 535–546.