

Menstrual cycle variation in women's preferences for the scent of symmetrical men

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Evidence suggests that female sexual preferences change across the menstrual cycle. Women's extra-pair copulations tend to occur in their most fertile period, whereas their intra-pair copulations tend to be more evenly spread out across the cycle. This pattern is consistent with women preferentially seeking men who evidence phenotypic markers of genetic benefits just before and during ovulation. This study examined whether women's olfactory preferences for men's scent would tend to favour the scent of more symmetrical men, most notably during the women's fertile period. College women sniffed and rated the attractiveness of the scent of 41 T-shirts worn over a period of two nights by different men. Results indicated that normally cycling (non-pill using) women near the peak fertility of their cycle tended to prefer the scent of shirts worn by symmetrical men. Normally ovulating women at low fertility within their cycle, and women using a contraceptive pill, showed no significant preference for either symmetrical or asymmetrical men's scent. A separate analysis revealed that, within the set of normally cycling women, individual women's preference for symmetry correlated with their probability of conception, given the actuarial value associated with the day of the cycle they reported at the time they smelled the shirts. Potential sexual selection processes and proximate mechanisms accounting for these findings are discussed.

Keywords: developmental instability; fluctuating asymmetry; mate choice; menstrual cycle; olfaction; sexual selection

1. INTRODUCTION

A variety of evidence suggests that human female sexual desires change across the menstrual cycle. Peaks in sexual desire appear to occur most commonly during the midfollicular or ovulatory phase (for reviews, see Hill 1988; Regan 1996). Increases in sexual interest prior to and during ovulation may be specific to particular relationships or partner attributes. Baker & Bellis (1995) reported that, whereas the rate of British women's intra-pair copulations (IPCs) tended to remain fairly constant across the menstrual cycle (or even slightly increased during the nonfertile luteal phase), their rate of extra-pair copulations (EPCs) peaked during the last days of the follicular phase, a time at which fertility is maximal, with EPCs occurring at a peak rate about 2.5 times their rate of occurrence during the last week of the cycle (when fertility is low).

These results are consistent with changes across the cycle not only in sexual interest per se, but also in preferences. Women may tend to prefer sexual relations with men who have particular attributes during their period of peak fertility. One possible function of this shift may be a preference for phenotypic markers of genes that increase offspring viability during the fertile phase of the cycle. Although non-reproductive sex can have many functions (e.g. Hrdy 1981), 'good genes' benefits cannot be realized unless conception occurs. Good genes sexual selection is an important form of sexual selection in a variety of animal species (partial reviews in Andersson 1994; Kirkpatrick 1996; Møller & Thornhill 1998b).

For at least two reasons, olfactory perception is an appropriate sensory modality within which to explore changes in preference (see Kohl & Francoeur (1995) for a recent review of the role of scent in human sexuality.) First, whereas men rate visual information about, and odour of, a mate as equally important, women single out olfaction as the sensory modality that most affects their sexual responsivity and mate choice (Herz & Cahill 1997; see also Franzoi & Herzog 1987; Regan & Berscheid 1995). Second, evidence indicates that women's olfaction changes across the menstrual cycle. One sexually dimorphic substance that gives body odour a musky smell is 3α -androstenol (for a review, see Gower & Ruperelia 1993). Women's olfactory sensitivity to 3α -androstenol, and to related synthesized substances, appears to be enhanced before ovulation and during the mid-luteal phase (Vierling & Rock 1967; Doty 1981; but see Amoore et al. 1975; Pause et al. 1996). Perhaps more importantly, normally ovulating women evaluate a related substance in human sweat, androstenone, more favourably near ovulation (Grammer 1993). Although it remains unclear whether androstenol or other androgenderived compounds signal male characteristics that females value in mate choice (see Følstad & Karter 1992; Wedekind 1992), these findings provide a basis for exploring preferences for male scent as a function of changes across the menstrual cycle.

Fluctuating asymmetry (FA) is absolute deviation from perfect symmetry on characters that are, on average, symmetrical on the two sides of the body (Ludwig 1932; Van Valen 1962). It is generally treated as a marker of developmental imprecision, the extent to which a genetic blueprint is imperfectly realized in an organism's phenotypic development due to environmental and genetic perturbations (for a review, see Møller & Swaddle 1997). Meta-analyses and other literature reviews indicate that FA negatively predicts fitness components such as longevity, fecundity, and health status across a wide variety of species (Leung & Forbes 1996; Møller 1997; Thornhill & Møller 1997). Moreover, a meta-analysis reveals that, on average, individuals with low FA experience greater mating success (Møller & Thornhill 1998b). Because FA has a heritable component (Møller & Thornhill 1997a,b), good genes sexual selection may contribute to the greater mating success enjoyed by more symmetrical individuals (although other sexual selection processes may be involved as well). In humans specifically, low FA has been shown to predict men's number of sexual partners (Thornhill & Gangestad 1994), facial attractiveness (Gangestad et al. 1994; Thornhill & Gangestad 1994), number of EPC partners (Gangestad & Thornhill 1997), and number of times chosen as an EPC partner (Gangestad & Thornhill 1997). Moreover, men's symmetry predicts the frequency of their partners' orgasms (Thornhill et al. 1995), which possibly is a means of cryptic female choice in multiple mating contexts (see Baker & Bellis 1995).

In this study, we examined women's responses to men's body odour as a function of men's FA and stages throughout the menstrual cycle. To do so, we asked men to wear T-shirts overnight for two nights. Women then rated the attractiveness of the T-shirts' odour. Using a very similar protocol, Wedekind et al. (1995) showed that women prefer the scent of men whose major histocompatibility genes differ from their own. We were interested in whether women's preferences could also be predicted from men's FA, particularly for women who are in a fertile phase of their ovulatory cycle.

2. METHODS

Forty-two men and 52 women participated in the study. Their ages ranged from 18 to 36 for men (mean = 22.8, s.d. = 4.1) and 18 to 52 for women (mean=22.6, s.d.=3.4). Self-reported ethnicities of men were 67% Caucasian, 21% Hispanic, 7% Asian, and 2% Native American (but one participant did not report his ethnicity); and of women were 52% Caucasian, 37% Hispanic, 4% African American, 4% Native American, 2% Asian, and 2% unspecified other. Neither men's FA nor the odour-attractiveness ratings made by high- or low-fertility women (see below) varied across ethnicities, $F_{4.35} = 0.31 - 1.04$, all p > 0.4, and therefore ethnicity was ignored in further analyses.

(a) Procedures for men

Men reported in groups of up to three for an initial measurement session. After reading and signing an informed consent form, each was given a brief questionnaire on demographic and other information (e.g. height, weight, sexual orientation, socioeconomic status of family of origin). One at a time, they were taken into an adjoining room, where the right and left sides of ten characters were measured using a digital caliper, sensitive to 0.01 mm: ear length, ear width, elbow width, wrist width, ankle width, foot breadth, and lengths of all fingers excluding the thumb. In previous samples (N > 700), these characters have been shown to exhibit very little directional asymmetry and slight leptokurtosis, as expected of FA (Furlow et al. 1997; Gangestad & Thornhill 1998b). To assess, and increase reliability, we measured each character twice.

After the measurements had been taken and the questionnaire completed, each participant was given a clean, never-worn, white T-shirt and provided explicit wearing instructions. Each was told that he should wear the T-shirt for a particular two nights (identical for all participants) while sleeping. Each was also instructed to wash his bedsheets with unscented laundry detergent (provided by us) prior to those two nights and, during the two-day period, refrain from (1) using scented soaps, deodorant, or fragrance such as cologne or aftershave, and instead use only unscented soap (which we provided); (2) eating garlic, onion, green chilli, pepperoni, pungent spices, herbs, strong cheeses, cabbage, celery, asparagus, yoghurt, and lamb; (3) drinking alcohol or using recreational drugs; (4) smoking tobacco; (5) engaging in sex with another person; or (6) sleeping with another person. Each participant was further instructed to place the T-shirt in a plastic bag (provided by us and identified with an arbitrary code number) during the day, when not worn, and return the shirt, in the bag, the morning following the second night at 9 a.m. Of the 42 participants, 41 returned their shirts on time.

(b) Procedures for women

At 10 a.m. on the morning that the men returned their shirts, female participants began reporting in groups of up to six. Following informed consent, women were placed in separate rooms. Shirts had been separated into groups of approximately ten, and each group placed in a box. In addition to the 41 shirts worn by men, one clean shirt that had not been worn was included in the sample. Boxes were circulated through the sample of women present during a session. Some women therefore smelled shirts 1-10 first, other women smelled shirts 11-20 first, and still others smelled shirts 21-30 or 31-42 first. Although no attempt was made to fully randomize the order in which women smelled shirts, it is likely that no two women smelled them in precisely the same order. For each shirt, women were asked to open the plastic bag, smell the shirt, and rate it on three dimensions: (1) pleasantness, on a scale of 1 (very unpleasant) to 10 (very pleasant); (2) sexiness, on a scale of 1 (very unsexy) to 10 (very sexy); and (3) intensity, on a scale of 1 (not at all intense) to 10 (very intense). They were instructed to roll the top of the bag shut before putting it back in its box and moving onto the next shirt. All researchers presenting shirts to women for smelling were unaware of the symmetry scores of the men who had worn them. Women were not aware that the research concerned men's symmetry or their menstrual cycle variation.

Women were also given a brief questionnaire to fill out, which assessed the same background information we asked of the men in addition to two critical pieces of information: (1) whether the woman currently used a contraceptive pill; and (2) the first day of the woman's last menstrual period. We also asked women the typical length (in days) of their menstrual cycle. Unfortunately, many women answered this question with the typical duration of their menstrual bleeding.

In total, sessions lasted about 1 h. Sessions were run until noon of the day following the collection of the T-shirts.

(c) Data treatment: men

Multiple asymmetry measurements were checked for reliability. Intraclass correlations of the two measured signed asymmetries for individual traits ranged from 0.71 to 0.95: all $F_{41.42} \le 5.80$, p < 0.00001; mean intraclass r = 0.83. For unsigned asymmetries, these correlations ranged from 0.49 to 0.91: all $F_{41.42} \le 2.93$, p < 0.0005; mean intraclass r = 0.67.

Signed asymmetries were checked for directional or antiasymmetry (Palmer 1994). No right–left (RL) difference was significantly different from zero (all $|t_{41}| \le 1.54$, n.s.). No signed asymmetry exhibited significant platykurtosis. Mean g_2 was 0.63 and hence distributions were slightly leptokurtic, consistent with FA (Gangestad & Thornhill 1998).

To guard against the effects of large asymmetries due to injury, FA of traits that men reported to have injured were excluded in these analyses if they were greater than the mean (18 out of 420 observations; 4.3%). For measurement purposes, the mean FA for the trait was substituted in these instances (r with unadjusted FA=0.96). This practice essentially treats high asymmetry on injured traits as missing data by calculating FA on the basis of the uninjured traits (adjusted by the mean trait level of the missing trait).

An aggregated FA score was calculated in two different ways. First, each trait's absolute asymmetry was divided by the mean trait size ((R+L)/2) for that participant, and the FA of all ten characters was summed to yield an overall index (relative FA). Second, each trait's absolute asymmetry was standardized (divided by) the sample mean of trait size and summed to yield an overall index (absolute FA). These two measures correlated 0.99 with each other, and yielded nearly identical results (all correlations reported below to be within 0.02 of one another, with neither measure's correlations consistently higher than the other's). Thus, we report results for just one measure (the first) below. The intraclass correlation across the two measurements for the summed index was 0.65, $F_{41,42}$ =4.67, p<0.00001.

(d) Data treatment: women

Of the 52 participants, five reported a homosexual or bisexual orientation. Because this study examined attractiveness of scent in a heterosexual situation, analyses focused on the responses of the 47 exclusively heterosexual women. Of these, 17 currently used a pill or related contraceptive (e.g. DepoProvera) and one noted that she was post-menopausal. Of the remaining 29 participants, 28 provided a specific date for first day of their last menstruation. For these women, we estimated fertility risk (probability of conception following sex) on the basis of values reported in the medical literature (Jöchle 1973; illustrated in fig. 2 of Box 6.10 in Baker & Bellis 1995). The minimum value was 0.01, the maximum 0.40 (day 12). Nine women had a fertility risk of at least 0.15 (days 6-14). For convenience, we refer to this group as having 'high-fertility risk'. Within it, the mean fertility risk was estimated to be 0.28 (range = 0.18-0.40). The remaining women had a mean fertility risk of 0.02 (range=0.01-0.05). We refer to this group as having 'low-fertility risk'. The mean cycle length of normally cycling women who appropriately responded to this question was 27.1 days ($\mathcal{N}=12$, range=21-32). Three women reported to be on day 40 or more since their last menstruation, raising the possibility of pregnancy. Exclusion of these women did not alter the results.

The mean correlation between individual women's 'pleasantness' and 'sexiness' ratings was 0.82. Therefore, these ratings were averaged into a total attractiveness index for reported analyses. Analyses on specific ratings yielded highly similar results.

3. RESULTS

We performed two complimentary sets of analyses. The first treated men as the unit of analysis and examined

associations between men's FA and mean scent attractiveness ratings by different sets of women. The second treated women as the unit of analysis and examined variations in how individual women's ratings were associated with men's FA

Although unsigned FA tends to be non-normally distributed (Swaddle *et al.* 1994), Monte-Carlo analyses reveal that significance tests on parametric correlations involving FA are robust (Gangestad & Thornhill 1998*a*): hence, we performed standard parametric analyses.

(a) Individual men as the unit of analysis

For the first set of analyses, we split women into the two groups of normally ovulating women discussed above: high-fertility risk and low- fertility risk. Mean attractiveness ratings for each male's scent were calculated within each group. Each total index had a reasonably high internal consistency (α =0.75 and 0.79, respectively; Cronbach 1951), indicating that women's ratings tended to covary within groups. Our a priori prediction was that high-fertility risk women's ratings would correlate with men's FA and more so than low-fertility risk women's ratings. To control for experiment-wise error on multiple (2) tests, yet maintain sufficient power to test our directional hypothesis, we used a directed test and unbalanced Bonferroni-adjusted criterion values. Rice & Gaines (1994) recommend splitting the 0.05 p-value at 0.04 (for a predicted hypothesis) and at 0.01 (for an unpredicted test). Adjusting for multiple tests in this way yielded criterion one-sided p-values of 0.032 (for the predicted negative relationship for high-fertility risk women) and 0.005 (for the unpredicted relationship in either direction for highfertility risk women). The difference between the two correlations was tested with a directed test using a criterion p-value of 0.04 for the predicted direction (see Rice & Gaines 1994).

Men's FA did not predict the mean attractiveness ratings of low-fertility risk women, r = -0.02, n.s. (d.f. = 39). By contrast, men's FA significantly and negatively predicted the mean attractiveness ratings of high-fertility risk women, r = -0.31, p = 0.023. Hence, the more symmetrical the male contributing the shirt was, the more attractive its scent to the high-fertility risk women. These two correlations significantly differed from one another, $t_{38} = 2.72$, p = 0.005 (test for difference between dependent correlations; Cohen & Cohen 1975).

An issue that arises is whether the scent of symmetrical men is merely less repulsive to women during the high-fertility period of the cycle. Figure la shows the regression line of high-fertility women's mean ratings on men's FA. Also indicated is these women's mean rating of the clean T-shirt. As can be seen, the mean rating of the worn T-shirts' scents (4.64) was very similar to the rating of the scent of the clean T-shirt (4.50). The scents of about half of the shirts, then, were rated as more attractive than the scent of a clean shirt, which was rated slightly more negative than the mid-point of the scale (5.5). Figure lb shows the comparable regression line for low-fertility women. Their mean rating of the worn shirts (4.76) was somewhat higher than their rating of the clean shirt (4.21).

Low-fertility risk and high-fertility risk women's ratings were highly correlated, r=0.73, p<0.001. Clearly, then, a set of cues affected both sets of women is similar ways.

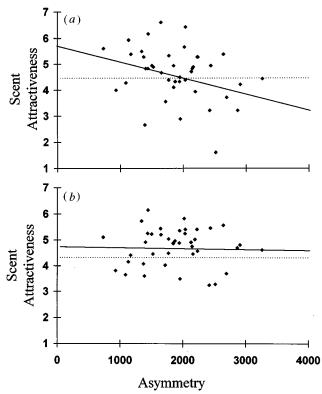


Figure 1. (a) Mean attractiveness ratings of men's scent made by high-fertility risk women as a function of men's asymmetry. The solid line is the best-fit least-squares regression line. The dotted line indicates the mean attractiveness rating given a clean, unworn T-shirt. $r\!=\!-0.31, p\!<\!0.03.$ (b) Mean attractiveness ratings of men's scent made by low-fertility risk women as a function of men's asymmetry. The solid line is the best-fit least-squares regression line. The dotted line is the mean attractiveness rating given a clean, unworn T-shirt. $r\!=\!-0.02,$ n.s.

Nonetheless, given the difference in correlation with men's FA, it appears that some variance in high-fertility risk women's evaluations was due to factors not affecting (or affecting to a lesser degree) low-fertility risk women's evaluations. To examine the association between men's FA and variation in women's ratings unique to the high-fertility risk group, we partialled low-fertility risk women's ratings out of the correlation between high-fertility risk women's ratings and men's FA. The partial r was -0.44, p < 0.005 (d.f. = 38).

Men reported the socio-economic status (SES) of their family origin on a five-point scale (5=upper class, 3=middle class, 1=lower class). Neither men's age nor their SES significantly correlated with men's FA (r=0.25 and -0.11, respectively, n.s.), the ratings made by high-fertility risk women (r=0.05 and 0.14, n.s.), or the ratings made by low-fertility risk women (r=0.06 and -0.02, n.s.). Partialling out men's SES and age resulted in a somewhat stronger correlation between FA and scent attractiveness ratings made by high-fertility risk women (partial r=-0.33, p<0.05, d.f.=37). The partial correlation between FA and ratings made by low-fertility risk women was near zero (-0.01, n.s.).

The internal consistency (α) of ratings made by women using contraceptive pills was 0.77. As expected, pill-using women's mean attractiveness ratings did not significantly

correlate with men's FA, r=-0.16, n.s. This correlation did not significantly differ from the correlation between high-fertility risk women's ratings and men's FA at the 0.10 level (two-tailed; t_{38} =1.72, p=0.09), nor from the correlation between normally ovulating, low-fertility risk women's ratings and men's FA (t_{38} =1.40, n.s.). On average, women gave the worn shirts an attractiveness rating of 5.02, compared to 4.68 for the clean shirt.

(b) Individual women as the unit of analysis

Because the above analyses could examine changes in women's scent preferences as a function of the menstrual cycle based only on rough and fixed categories of fertility risk, a second set of analyses treating individual women as the unit of analysis was performed. Each woman's attractiveness ratings were regressed on men's FA. The unstandardized regression slope that resulted reflected changes in an individual woman's ratings as a function of men's FA. Because a negative slope reflects preferences for the scent of symmetrical men, the sign of this regression slope was reversed to yield an estimate of 'preference for symmetry'.

Normally ovulating (non-pill using) women's preference for symmetry was correlated with the estimated fertility risk based on the day in the menstrual cycle that the women had reached. We predicted that this correlation would be positive (and hence applied a directed test where the criterion p-value=0.04; Rice & Gaines 1994). The correlation was highly significant, r=0.54, p=0.001(d.f. = 26). As figure 2 shows, the greater the fertility risk of a woman, the greater her preference for scent associated with male symmetry. The intercept of the leastsquares regression line is nearly zero, meaning that women with no fertility risk favoured the scents of neither symmetrical men nor asymmetrical men. As estimated fertility risk increased, however, women preferred the scents of symmetrical men. Owing to the fact that on most cycle days women have a near-zero probability of conception, fertility risk is a highly skewed variable. A randomization test (based on 50 000 random pairings of the variables), which makes no a priori distributional assumptions (e.g. Thomas & Poulin 1997) yielded a pvalue of 0.002.

To examine whether pill-using women show the same changes across the menstrual cycle, we correlated their preference for symmetry with the fertility risk they would have were they normally ovulating, based on the day they had reached in their menstrual cycles. The results revealed no significant correlation, r=-0.09, n.s. (d.f.=12). These findings suggest that changes in normally ovulating women's preferences across the menstrual cycle are due to changes that take place in connection with normal ovulation, and not to changes that are entrained with menstruation independent of normal ovulation.

To examine whether high-fertility risk women's ratings differed in mean level from those of the other groups, we performed an *a priori* comparison within a one-way ANOVA (e.g. Winer *et al.* 1991). Mean ratings by high-fertility risk women (4.64) did not differ from those made by normally cycling low-fertility risk women (4.76) and women using birth-control pills (5.02), t_{42} =0.88, n.s. No *post hoc* Scheffé comparisons were significant.

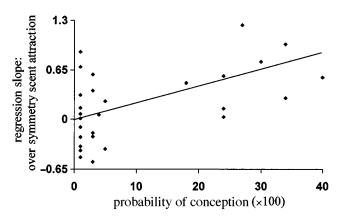


Figure 2. Women's preference for symmetry as a function of her probability of conception, based on actuarial values. Normally ovulating (non-pill-using) women only. Note: positive regression values reflect increased relative attraction to secent of symmetrical males. r=0.54, p<0.005.

(c) Intensity ratings

On average, across women, intensity and attractiveness ratings correlated (r=-0.14): this value, although small, was significantly different from zero, $t_{43}\!=\!2.09$, $p\!<\!0.05$ (unadjusted for experiment-wise error).

Because previous research has suggested that women's sensitivity to male scents varies across the menstrual cycle, we performed an *a priori* contrast between the mean intensity ratings made by high-fertility risk women (5.25) and those made by normally cycling, low-fertility risk women (4.77) and women using a contraceptive pill (4.37) (e.g. Winer *et al.* 1991). This contrast was not statistically significant (t_{41} =1.58, p=0.12, two-tailed test).

Men's FA did not predict mean intensity ratings for women in any group: high-fertility risk: r=0.08; normally ovulating, low-fertility risk: r=0.11; pill-using: r=0.03; all n.s. (d.f.=39). Moreover, women's fertility risk did not predict the extent to which their intensity ratings reflected men's symmetry within the group of normally ovulating women; r=-0.05, n.s. (d.f.=25). Finally, within this same group of women, mean intensity ratings did not predict the extent to which their attractiveness ratings reflected men's symmetry; r=-0.05, n.s. (d.f.=25). Thus, partialling out mean intensity rating from the correlation between women's fertility risk and their preference for symmetry did not alter the correlation; partial r=0.54, p<0.01 (d.f.=24).

Taken together, these findings suggest that the association between women's fertility risk and their preference for male symmetry is not mediated by a general increased sensitivity to smells during the fertile period. It should be noted, however, that a more objective measure of olfactory sensitivity may be needed to make this claim conclusively.

4. DISCUSSION

We explored changes in women's preferences for men's scent across the menstrual cycle. As predicted, normally ovulating women preferred the scent of symmetrical men during their period of peak fertility. Such women revealed no preference for symmetry or asymmetry during periods of low fertility.

These findings are consistent with other literature (e.g. Baker & Bellis 1995) indicating that women's sexual preferences (e.g. as revealed by their rate of EPCs) change across the menstrual cycle. They are also consistent with the notion that the changes occurring during the period of peak fertility have been 'designed' by natural selection to increase the probability of insemination by a male who, relative to other males, provides genetic benefits. Such an adaptation could have been selected for in the context of multiple mating (e.g. an in-pair partner and one or more extra-pair partners). Baker & Bellis (1995) suggest that female orgasm also evolved in the context of multiple mating (through sperm retention, giving an edge to the sperm of certain men over that of others). Consistent with this logic, we reported previously that females are also more likely to experience orgasm (particularly high sperm-retention orgasm) with symmetrical men (Thornhill et al. 1995). Thus, multiple lines of evidence suggest that there exist female adaptations designed to bias insemination by males who provide genetic benefits in the context of multiple mating. Nonetheless, we cannot definitely rule out all alternative interpretations of the sexual selection process involved, and therefore the 'good genes' sexual selection hypothesis awaits further tests.

For these findings to have occurred, women must be able to use a chemosensory signal in men's sweat or skin as a basis for discriminating between men who have and who have not experienced developmental instability. Because it would seem advantageous for all men (whether symmetrical or not) to signal developmental stability, the signal that women use to detect developmental stability in men's scent is presumably an honest one—i.e. asymmetrical men cannot fake it (Zahavi 1975; Grafen 1990). The current research does not address the precise nature of this signal. At least four possibilities may be entertained. (1) Androstenol levels may signal developmental quality (perhaps because of its association with other androgens such as testosterone or dehydroepiandrosterone; see Kohl & Francoeur 1995). It should be noted that men's androstenol levels decrease with age (Brooksbank 1962), yet we found no effect of men's age on scent attractiveness in this study. Possibly, a larger age range is needed to detect any association. (2) The concentration or type of bacteria on the skin that contributes to male scent (e.g. Gower & Ruperelia 1993) may differ as a function of male developmental stability and its correlate, a sound immune system (see Thornhill & Møller 1997). (3) Symmetrical and asymmetrical men may produce different fatty acids in sweat (which contribute to its pungent odour; e.g. Gower & Ruperelia 1993), perhaps due to differences in metabolism related to men's symmetry (e.g. Manning et al. 1997). Perhaps symmetrical men produce acids with odours that are less aversive to women near ovulation than those produced by asymmetrical men. (4) Symmetrical men may have particularly rare HLA genotypes. Wedekind et al. (1995) found that normally ovulating women tend to prefer the scent of men who possess dissimilar HLA genotypes and, hence, men with rare HLA alleles should be attractive to relatively many women (see also Wedekind & Furi 1997). Future research should address these and other potential mechanisms.

It should be noted that the scent of symmetrical men tended to be rated as near-neutral by high-fertility women, though still more attractive than the sweat of asymmetrical men, which was rated as aversive by these women. Hence, preference for symmetry may be owing to a lack of an aversive odour rather than the presence of a pleasant odour. Of course, any difference in pleasantness of odour could render a difference in female choice, as women might be expected to avoid sexual contact with men with aversive body odours. Hence, the presence or absence of an aversive odour could qualify as an important biological signal. Grammer (1993) found that women rate the smell of androstenone as near-neutral near ovulation, but as unpleasant during low-fertility periods of the menstrual cycle (consistent with the present findings), this being due to differences in production of andostenol or its derivative, androstenone. But the other possibilities we mention above are consistent with this aspect of our findings as well. One last note is that most women rated some men's odours on the sexy or pleasant side of the neutral point. Possibly, when a number of factors are all present (symmetry, HLA-dissimilarity, good hygiene), women find men's odours attractive. Because we did not measure all relevant factors (e.g. HLA similarity), we cannot address this issue with the present study. However, future work may address how these features work in concert to affect women's olfactory responses.

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As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute to production costs.