

Attractiveness of women's body odors over the menstrual cycle: the role of oral contraceptives and receiver sex

Seppo Kuukasjärvi,^a C. J. Peter Eriksson,^b Esa Koskela,^a Tapio Mappes,^a Kari Nissinen,^c and Markus J. Rantala^d

^aDepartment of Biological and Environmental Science, P.O. Box 35, FIN-40014, University of Jyväskylä, Finland, ^bDepartment of Mental Health and Alcohol Research, National Public Health Institute, P.O. Box 719, FIN-00101, Helsinki, Finland, ^cDepartment of Mathematics and Statistics, University of Jyväskylä, P.O. Box 35, FIN-40351, Jyväskylä, Finland, and ^dDepartment of Biology, University of California, Riverside, California 92521, USA

It is a long held assumption that women have concealed ovulation, which means that men do not know when women's menstrual cycles are in their most fertile phase. Recent empirical results have provided evidence that ovulation may not be totally concealed from pair-bonded males, but the generality and the mechanisms of the finding demand further study. To examine the possible adaptive value of the phenomenon, it is necessary to study whether the ability to detect ovulation is confined to males. We studied these questions in an experiment in which male and female raters rated the sexual attractiveness and intensity of T-shirts' odors worn by 42 women using oral contraceptives (pill users) and by 39 women without oral contraceptives (nonusers). Males rated the sexual attractiveness of nonusers highest at midcycle. However, female raters showed only a nonsignificant trend for this relationship. Neither sex rated attractiveness of the odors of pill users according to their menstrual cycle. The results indicate that men can use olfactory cues to distinguish between ovulating and nonovulating women. Furthermore, the contrasting results between pill users and nonusers may indicate that oral contraceptives demolish the cyclic attractiveness of odors. Together, these findings give more basis for the study of the role of odors in human sexual behavior. *Key words:* body odor, concealed ovulation, *Homo sapiens*, human, oral contraceptives, reproductive status, sexual selection. [*Behav Ecol* 15:579–584 (2004)]

Almost all primate females have periodical oestrus, when they attract males by advertising ovulation or their most fertile phase by sexual swellings or scents (see Baker and Bellis, 1995). Human females lack conspicuous visual signals advertising ovulation, and sexual intercourse can occur throughout the menstrual cycle. Thus, it has been supposed that human males cannot detect the timing of ovulation; that is, they are unaware of women's reproductive status and women have an adaptation of "concealed ovulation" (Alexander and Noonan, 1979; Baker and Bellis, 1995; Buss, 1994, 1999; Cartwright, 2000; Sillén-Tullberg and Møller, 1993; Thornhill and Palmer, 2000). However, if concealed ovulation was an adaptation of ancestral women, ancestral men would have had a chance to counter-adapt against it. One could expect that during human evolutionary history, sexual selection would have favored men who could detect timing of ovulation, because these men would have gained reproductive advantages. For example, men could have optimized their mating effort by channeling courtship or mate guarding toward women in the ovulatory phase.

One possible way for men to detect the timing of ovulation is through odors that could signal the reproductive status of women. Doty et al. (1975) showed that in both men's and women's opinion, the pleasantness of vaginal odors was less unpleasant and the intensity of odors was weaker in pre-ovulatory and ovulatory phases than in menstrual, early luteal, and late luteal phases. However, the study did not support the hypothesis that humans could use vaginal odors to determine

the general time of ovulation. Poran (1995) examined odor changes during the menstrual cycle by conducting an experiment in which subjects were seven couples who had long-term relationships. Body odors of women were collected from saliva, vagina, underarms, and loin, and the result was that men rated the odors of their mates from ovulatory phase more pleasant and long-lasting than the odors from other phases. Unfortunately, because men did not rate the odors of all women, men's preference could have been derived from learning.

If men do have an adaptation of detecting the timing of ovulation, they should be able to prefer ovulating women in the situation in which they can compare the attractiveness of odors between different women. This kind of a between-subjects design (group of ovulating women compared with a group of nonovulating women) was used in Thornhill and Gangestad (1999). In the study men rated the odor pleasantness and sexiness of T-shirts worn by women, but the ratings did not differ between the luteal and follicular phases. Singh and Bronstad (2001) used a within-subjects design, in which they collected follicular and luteal phase odors from the same women, and men compared them during the rating procedure. The results showed that men prefer the body odors of a woman in the ovulatory phase, which led investigators to suggest that ovulation may not be totally concealed from pair-bonded males. However, the study left open the question whether the cues signaling ovulation are perceptive enough that men can use them when given a choice between several women in different phases of the menstrual cycle.

We conducted a T-shirt experiment using a similar experimental design and methods to those of Thornhill and Gangestad (1999). Our aim was to study whether men can use olfactory cues to discriminate between potential partners,

Address correspondence to S. Kuukasjärvi. E-mail: sepelius@st.jyu.fi.
Received 22 March 2003; revised 14 April 2003; accepted 18 April 2003.

preferring women according to their reproductive status. To examine whether men prefer women because of their fertility, we included in our study a group of women that were using oral contraceptives. Furthermore, to study whether the possible ability to detect timing of ovulation is sex-specific, we also included women as raters.

METHODS

Study participants

The study was carried out at the Department of Biological and Environmental Science of the University of Jyväskylä in Finland. The participants were all volunteers and mainly students in biology and psychology. Eighty-two women wore a T-shirt for two consecutive nights directly on the skin, after which 31 male and 12 female raters rated the sexual attractiveness and intensity of the shirt's odors. As the possible attractiveness of women's body odors might have a hormonal basis, we selected both users and nonusers of oral contraceptive pills for the study. The participants were told that the purpose of the study was to investigate whether odors affect human sexual selection, but they were not informed of the exact hypothesis. The odor ratings were carried out in three trials during three consecutive weeks in March 1999. Each trial consisted of new T-shirts wearers (26, 28, and 28 wearers randomly assigned per week, respectively), whereas the T-shirt raters were always the same. The three trials did not differ in respect to the cycle length, day of menstrual cycle, or age of T-shirt wearers (one-way ANOVA, p for all $> .05$). Therefore, study week was not used as a separate factor in the statistical analyses.

Collection of women's body odors

As in many previous human odor studies, body odors of women were collected by T-shirts (see Gangestad and Thornhill, 1998; Rikowski and Grammer, 1999; Singh and Bronstad, 2001; Thornhill and Gangestad, 1999; Wedekind and Furi, 1997). The unworn white cotton T-shirts were prepared by washing them with nonperfumed soap powder and keeping them in odorless plastic freezing bags after drying. Each woman received one T-shirt, a package of soap powder to wash her bedclothes before the experiment, a perfume-free soap for personal hygiene, and odorless liquid soap for hair cleaning. Women were informed about the T-shirt experiment procedure, and they were provided detailed instructions of behavioral restrictions to avoid disturbing scents. The instructions included refraining from (1) using perfumes, perfumed deodorants, and perfumed soap powder; (2) eating odor-producing food such as garlic, onion, strong spices, herbs, cabbage, celery, asparagus, yogurt, and lamb; (3) smoking cigarettes, drinking alcohol, and using drugs; and (4) sleeping with another human and sexual activity. When a woman did not wear her shirt, she stored it in an odorless freezing bag. The women returned their shirts in the freezing bags in the second morning between 0800–1000 h, and they were asked to honestly report possible violations of the instructions. One woman reported that she had not followed our instructions, and her shirt was excluded from the study. Women were also asked whether they use contraceptive pills, and to report the first date of their last menstrual bleeding and their mean cycle length. These enabled us to calculate on which day of the menstrual cycle the experiment had taken place.

There was no difference in the age of participants between normally ovulating women (mean = 23.2, range = 16–49, SE = 0.78, $n = 41$) and pill-using women (mean = 22.5, range = 17–32, SE = 0.48, $n = 39$, two-sample t test: $t = -0.73$, $df = 78$, $p > .5$). Use of contraceptive pills changed the cycle length of

women (nonusers: mean = 30.1 days, range = 25–42, SE = 0.53, $n = 42$; pill users: mean = 28.1 days, range = 24–30, SE = 0.14, $n = 39$, two-sample t test: $t = -3.57$, $df = 46.5$, $p < .001$). When we analyzed the sexual attractiveness and intensity of odors in relation to menstrual cycle, every woman's day of menstrual cycle was corrected by her cycle length with an equation: $[(28/\text{cycle length}) \times \text{day of menstrual cycle}]$.

Odor rating sessions

The odor rating sessions were arranged at the same day the women returned their T-shirts. The shirts were conserved in 4-l glass jars, which were labeled and sealed. In addition to the shirts worn by women, three clean shirts that had not been worn were included in the sample (one shirt per week). The participants and supervising researchers did not know who had worn the T-shirts or other information about the wearers. The participants sat at tables while the glass jars were randomly circulated between the tables. During a rating procedure, a participant opened a jar and smelled a shirt by holding it beneath his or her nose. Then he or she rated the odors of the shirt for sexual attractiveness (range, 1–10; 5 = neutral, 10 = highest) and intensity (range, 1–10) and wrote the ratings on a questionnaire. After this, he or she closed the jar and passed it to the next rater. To measure the repeatabilities (see below), a second rating session with changed labels and randomized order of shirts was arranged. The sessions lasted approximately for half an hour with a 15-min break between them.

Repeatabilities

The repeatabilities of shirt ratings were calculated from the one-way ANOVA comparing T-shirts over the both rating sessions (see Lessells and Boag, 1987). The repeatabilities (R) were as follows: for attractiveness (males: $R = .85$, ANOVA $F_{83,2399} = 12.613$, $p < .001$; females: $R = .62$, ANOVA $F_{83,814} = 4.252$, $p < .001$) and for intensity (males: $R = .74$, ANOVA $F_{83,2398} = 6.629$, $p < .001$; females: $R = .47$, ANOVA $F_{83,813} = 2.803$, $p < .001$).

Statistical analyses

The correlations of ratings between the two rating sessions were high (attractiveness, males: $r = .91$, $p < .001$, $n = 84$; females: $r = .82$, $p < .001$, $n = 84$; intensity, males: $r = .91$, $p < .001$, $n = 84$; females: $r = .81$, $p < .001$, $n = 84$). Therefore, mean attractiveness and intensity ratings of the first and the second rating sessions for each rater were used when analyzing the odor characteristics in relation to menstrual cycle. There was no statistically significant correlation between sexual attractiveness and intensity of the odors (males: $r = .10$, $p = .367$, $n = 84$; females: $r = .03$, $p = .779$, $n = 84$). Consequently, we treated these as separate variables in all the analyses.

We analyzed the attractiveness and intensity of body odors along menstrual cycle with a linear mixed model specified for the mean ratings of the T-shirts. In the first stage of analysis, the model contained all the effects involved in the experimental design. That is, the main effects of the sex of the rater (SEX) and the use of contraceptive pills of the wearer (PILL), as well as their interaction (SEX \times PILL), were included as fixed effects. Because the same T-shirts were smelled by both male and female raters, the shirt effect was included in the model as a random effect nested within the pill effect. Thus, the design is similar to the repeated-measures design with the T-shirts as subjects, PILL as a between-subjects factor, and SEX as a within-subject factor. We also wanted to examine the effect of the day of menstrual cycle on the responses. Within the

Table 1
Significance test results for the fixed effects on the sexual attractiveness of body odors (full model)

Effect	df	F	p
SEX	1, 75	2.588	.112
DAY	1, 75	0.431	.514
DAY ²	1, 75	0.792	.376
PILL	1, 75	2.517	.117
SEX × DAY	1, 75	0.422	.518
SEX × DAY ²	1, 75	0.312	.578
SEX × PILL	1, 75	0.011	.918
PILL × DAY	1, 75	5.896	.018
PILL × DAY ²	1, 75	7.080	.010
SEX × PILL × DAY	1, 75	1.949	.167
SEX × PILL × DAY ²	1, 75	3.659	.060

See Methods for the details of the model.

menstrual cycle, this effect was expected to be of quadratic form: the levels of attractiveness and intensity are highest in the ovulatory phase (middle of the cycle) and decrease toward the beginning and end of the cycle. Because the preliminary data analyses seemed to support this hypothesis, we added the linear (DAY) and quadratic (DAY²) effects of the day into the model as covariates. No evidence on higher-order effects was found. Finally, we added the two-way and three-way interactions of the covariates with PILL and SEX to account for the possible variation of the day effect over the four PILL × SEX groups.

This full model (in the sense that it contains all possible interactions in the design) was first estimated and evaluated. Then we hierarchically simplified the model as far as possible by removing the nonsignificant effects one by one, starting from the most complex least significant interactions. The model that could not be simplified any more without dropping a significant effect or violating the hierarchy principle (i.e., nonsignificant lower-order effects cannot be removed if a significant higher-order interaction of the same factors is present) was selected as the final one.

The model was built in this stepwise way independently for both attractiveness and intensity. In each step the estimation and significance testing was carried out by the MIXED procedure of SAS software (SAS Institute, 1999b), using the restricted maximum likelihood (REML) method (Patterson and Thompson, 1971) with related *F* tests. In our case these agree with the usual *F* tests of the repeated-measures ANOVA. The degrees of freedom for the *F* tests were calculated by the method of Kenward and Roger (1997).

The estimates of the fixed effects in the final model were used in calculating the estimated second-order polynomial regression of the responses on the day of menstrual cycle in each PILL × SEX group. These calculations were performed by the SAS/IML software (SAS Institute, 1999a).

RESULTS

Sexual attractiveness

The results of the full model significance tests for the fixed effects on the sexual attractiveness are given in Table 1. The variance component of the random T-shirt effect was highly significant ($Z = 5.55, p < .001$), which is natural in this kind of design. Following the hierarchy principle, we removed two interactions, SEX × PILL × DAY and SEX × DAY, from the full model to obtain the final model, giving the test results

Table 2
Significance test results for the fixed effects on the sexual attractiveness of body odors (final model)

Effect	df	F	p
SEX	1, 77	18.625	<.001
DAY	1, 75	0.431	.514
DAY ²	1, 75	0.792	.376
PILL	1, 75	2.517	.117
SEX × DAY ²	1, 77	0.290	.592
SEX × PILL	1, 77	4.999	.028
PILL × DAY	1, 75	5.896	.018
PILL × DAY ²	1, 75	7.080	.010
SEX × PILL × DAY ²	1, 77	5.068	.027

See Methods for the details of the model.

presented in Table 2. The removal of the two effects did not affect the significance of the T-shirt effect ($Z = 5.55, p < .001$).

The results in Table 2 show several significant interactions. Two of these, SEX × PILL × DAY² and PILL × DAY², suggest that there exists a quadratic effect of the day of menstrual cycle on the sexual attractiveness, although it varies over the four SEX × PILL groups. The significant interaction PILL × DAY gives rise for the linear effect varying with the use of contraceptive pills.

To clarify these findings, we calculated the second-order polynomial regressions in each SEX × PILL group, in which the mean attractiveness (*y*) was regressed on the linear and quadratic effect of the day of menstrual cycle (*x* and *x*², respectively). The estimated equations and their statistical significances for each group are as follows (standard errors of the parameter estimates are given in parentheses): (1) normally ovulating women, rated by male raters (*n* = 42)— $y = 4.888 (0.318) + 0.127 (0.059)x - 0.005 (0.002)x^2, F_{2,81.3} = 3.62, p = .031, R^2 = .150$; (2) women using contraceptive pills, rated by male raters (*n* = 39)— $y = 5.492 (0.363) - 0.073 (0.057)x + 0.003 (0.002)x^2, F_{2,81.3} = 1.23, p = .299, R^2 = .106$; (3) normally ovulating women, rated by female raters (*n* = 42)— $y = 4.440 (0.318) + 0.127 (0.059)x - 0.005 (0.002)x^2, F_{2,81.3} = 2.72, p = .072, R^2 = .056$; and (4) women using contraceptive pills, rated by female raters (*n* = 39)— $y = 5.350 (0.363) - 0.073 (0.057)x + 0.002 (0.002)x^2, F_{2,81.3} = 0.83, p = .438, R^2 = .057$.

The regressions are presented graphically in Figure 1. The main finding is that the shape of the regression curve is clearly related to the use of contraceptive pills. Some minor variation is related to the sex of the rater. The regression is significant only in the case of normally ovulating women, rated by men (Figure 1a, Equation 1 above). The statistical significance of the regression 1 (and especially the quadratic term therein) indicates that males rated the sexual attractiveness of normally ovulating women's (nonusers) body odors highest near mid-cycle (maximum value of regression curve = 12.7 days).

In the case of normally ovulating women, rated by women (Figure 1c, Equation 3 above) the regression is not significant at the 5% level ($p = .072$). However, the magnitudes of the regression coefficients in Equation 3 are large compared with the corresponding standard errors, and testing their significances separately by *t* test gives $p = .035$ and $p = .024$ for the linear and quadratic effect, respectively. The conflicting results from the *F* and *t* tests are not easy to interpret and may be caused by the intercorrelation of the linear and quadratic effects in the equation. The attractiveness ratings by women for the body odors of normally ovulating women (Equation 3) also reached the maximum value at 12.7 days.

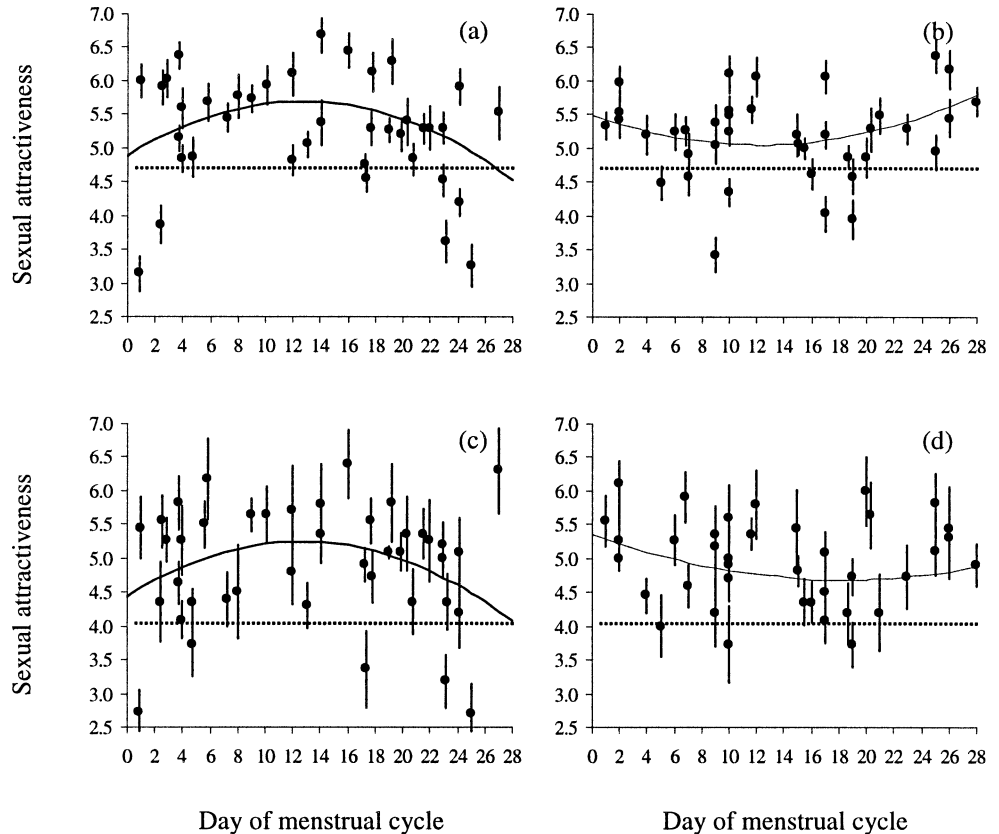


Figure 1

Sexual attractiveness of women's body odors with respect to day of menstrual cycle. The points represent the mean (\pm SE) attractiveness values of T-shirts scored by raters (31 men and 12 women). The dotted lines represent the mean ratings for clean T-shirts. The data is transformed by using the equation $[(28/\text{cycle length}) \times \text{day of menstrual cycle}]$. (a) Normally ovulating women, rated by males. (b) Women using contraceptive pills, rated by males. (c) Normally ovulating women, rated by females. (d) Women using contraceptive pills, rated by females. For statistics, see Results.

The main effect of the sex of the rater as well as its interaction with the use of pills were significant (Table 2), suggesting that when the effect of the day of menstrual cycle is averaged out, male raters tend to rate the sexual attractiveness of odors higher than female raters did, the difference being larger for odors of normally ovulating women. The use of contraceptive pills did not have a main effect on the attractiveness ratings (Table 2). The effect of using pills were tested also directly with *t* test, and no difference was found between the groups (nonusers: mean = 5.11, SE = .11; pill users: mean = 5.07, SE = 0.11, $t_{75} = 0.27$, $p = .785$).

Intensity

Outside the T-shirt random effect ($Z = 5.50$, $p < .001$) induced by the design, the mixed model analysis of the intensity of women body odors did not reveal any statistically significant effects of the specified factors or covariates (Table 3): the hierarchical model building scheme would have yielded a model consisting only of the intercept. Thus, we found no evidence of the day, the use of pills, or the sex of the rater affecting on the intensity of odor. However, to illustrate the results, we give the estimated polynomial regression equations for the intensity of odors in the four SEX by PILL groups (1) normally ovulating women, rated by male raters ($n = 42$)— $y = 4.320 (0.505) - 0.100 (0.671)x + 0.004 (0.048)x^2$, $F_{2,89.6} = 1.03$, $p = .362$, $R^2 = .049$; (2) women using contraceptive pills, rated by male raters ($n = 39$)— $y = 3.950 (0.505) - 0.058 (0.080)x + 0.002 (0.003)x^2$, $F_{2,89.6} = 0.35$, $p = .702$, $R^2 = .029$; (3) normally ovulating women, rated by female raters ($n = 42$)— $y = 4.058 (0.505) - 0.031 (0.671)x + 0.002 (0.048)x^2$, $F_{2,89.6} = 0.83$, $p = .438$, $R^2 = .026$; and (4) women using contraceptive pills, rated by female raters ($n = 39$)— $y = 3.838$

$(0.505) - 0.017 (0.080)x + 0.001 (0.003)x^2$, $F_{2,89.6} = 0.04$, $p = .961$, $R^2 = .003$.

DISCUSSION

In our study, male raters preferred odors of women whose menstrual cycles were near ovulatory phase. This finding indicates that men can use olfactory cues to detect the reproductive status of women. Female raters showed a trend for this relationship, suggesting that women may also have the ability to detect the reproductive status of other women. Moreover, as neither males nor females rated attractiveness of the odors of pill users according to the day of menstrual cycle, it implies that the attractiveness of women's body odors may have a hormonal basis.

Although we did not measure the day of menstrual cycle of the study participants precisely (e.g., by a real-time ultrasonography), it is probable that women (nonusers) in midcycle were ovulating. However, there is clinical evidence that all ovulations do not occur exactly during the midcycle, and there exists much variation in the timing of ovulation even among women with regular menstrual cycles. It has been estimated that only about 30% of women are in their fertile window (which consists of the day of ovulation and the 5 days before it) entirely between days 10 and 17, with the most fertile period being on days 12 and 13 (Wilcox et al., 2000). This may partially explain why in our study there is no steep increase in the sexual attractiveness during the midcycle.

Our findings concerning male raters are in agreement with the study of Singh and Bronstad (2001). In their study, women who were not using hormonal contraceptives wore a T-shirt for three consecutive nights during their follicular (ovulatory) phase. They also wore another T-shirt for three consecutive

nights during their luteal (nonovulatory) phase. Men then rated sexiness, pleasantness, and intensity of the shirts' odors, comparing always the shirts from the same woman consecutively. Singh and Bronstad (2001) concluded that men rated the odors of shirts worn during the follicular phase as more pleasant and sexy than the odors of shirts worn during the luteal phase. Our results extend their results to any social situation in which it is possible to judge the sexual attractiveness of body odors. However, our results do not support the study of Thornhill and Gangestad (1999), who used in their study a between-subject design similar to us. In their study, men rated the odor pleasantness and sexiness of T-shirts worn by women, and the ratings did not differ between the luteal and follicular phases.

In the current study, neither males nor females rated attractiveness of the odors of pill users according to the day of menstrual cycle. Furthermore, because the attractiveness ratings for nonusers and pill users did not differ significantly from each other, it seems that oral contraceptives do not make odors unattractive but only demolish the cyclicity of attractiveness of odors. However, although we are not aware of any other differences between the two groups than either using the pill or not, the pill was not subject to manipulation, leaving open the possibility that, for example, level of sexual activity was different in pill users and nonusers. Still, oral contraceptives without question affect hormonal levels of users. There are steroid hormones (e.g., estradiol) with blood concentrations that change cyclically during the fertile menstrual cycle, peaking in the preovulatory phase (Nelson, 2000). Most oral contraceptives (so-called combination pills) inhibit the secretion of luteinizing hormone (LH) and follicle-stimulating hormone (FSH) from the pituitary gland in the midcycle (Usathanondh, 1995). This prevents ovulation and inhibits the secretion of estrogens and progesterone from the ovarian follicle and corpus luteum (Nelson, 2000). However, the steroid hormones are not directly responsible for the body odor. Humans have apocrine sweat glands (e.g., in the axillae, anogenital region and mammary areola), which start after the puberty to secrete odorless steroids that are composed from steroid hormones. A part of human body odors are developed when bacteria on the skin convert these steroids into odorous compounds (Doty, 1981; Kohl and Francoeur, 1995). Thus, although there were only one steroid hormone with blood concentration that peaks strongly during or just before ovulation, it is possible that several odorous compounds are responsible for the final sexual attractiveness of body odors.

Because the intensity of odors did not depend on the day of menstrual cycle, use of oral contraceptives, or the sex of the rater, it would be tempting to conclude that the quantity of odorous compounds would be constant during the menstrual cycle and it would be only the quality of odorous compounds that changes in the normally ovulating women. However, this conclusion is not valid because it is unknown whether the ratings for body odors were based solely on the stimulation of main olfactory epithelium. It is not necessary for pheromones to have a detectable odor, because they can be perceived also through the vomeronasal organ (VNO). Virtually all humans have a pair of VNOs in the anterior nasal septum (Garcia-Velasco and Mondragon, 1991; Stensaas et al., 1991), and human VNO is also functional (Grosser et al., 2000). In other mammals other than human, stimulation of VNO with pheromones activates hypothalamic and limbic structures and results in changes of social and sexual behavior and modulation of neuroendocrine reflexes (see Monti-Bloch et al., 1998). In humans, pheromones may modulate a mood state rather than trigger a stereotyped behavioral or emotional responses (Jacob and McClintock, 2000). Consequently, an

Table 3
Significance test results for the fixed effects on the intensity of body odors (full model)

Effect	df	F	p
SEX	1, 75	0.868	.354
DAY	1, 75	0.874	.353
DAY ²	1, 75	1.310	.256
PILL	1, 75	0.213	.646
SEX × DAY	1, 75	2.493	.119
SEX × DAY ²	1, 75	2.238	.139
SEX × PILL	1, 75	0.140	.710
PILL × DAY	1, 75	0.063	.803
PILL × DAY ²	1, 75	0.160	.690
SEX × PILL × DAY	1, 75	0.164	.687
SEX × PILL × DAY ²	1, 75	0.068	.795

See Methods for the details of the model.

interesting and still open question is whether pheromones are involved in the sexual attractiveness of body odors.

We did not measure the major histocompatibility complex (MHC) types of the study participants. MHC is a group of genes that is important in immune recognition and has products that also affect body odor (for a review, see Penn and Potts, 1999). For example, Wedekind and Furi (1997) showed in their T-shirt experiment that both sexes preferred the body odors of individuals whose MHC genes were dissimilar to their own, independently of the gender of a T-shirt wearer and a rater. The reason to that preference in humans is probably inbreeding avoidance (Penn and Potts, 1999; Reusch et al., 2001; but see Jacob et al., 2002). Another reason could be improving the heterozygosity of offspring in order to get better immunocompetence against many different parasites (Penn and Potts, 1999). Accordingly, MHC preferences could have affected the ratings of individual raters in the current study. However, it seems quite unlikely that MHC preferences would have, for instance, biased ratings of sexual attractiveness for nonusers systematically toward midcycle. The sample sizes used in our study were reasonable, and the collection of body odors was random in respect to study participants.

Men could use several indirect and imperfect cues rather than one direct cue to detect ovulation (see Burt, 1992; Buss, 1999, Symons, 1995). For example, there exists evidence that asymmetry of women's paired soft tissue (fingers, ears, and breasts) is lowest on the day of ovulation (Manning et al., 1996; Scutt and Manning, 1996). On the other hand, women's ability to attract men during their ovulation may be as important as men's ability to detect women's signals. Grammer (1996) showed that ovulating women were touched by men more often than were nonovulating women, and they also exposed more their skin and wore tighter and shorter clothes. Accordingly, the relative importance of women's odors as signals of their reproductive status is currently unknown and requires well-designed experiments.

No statistically significant relationship was found between odor attractiveness and day of menstrual cycle by women raters. However, the nonsignificant trend (and statistical significance of linear and quadratic terms, see Results) suggests that women may still be able to use olfactory cues to detect the reproductive status of other women. Recent evidence suggests that women can use odors in their mate selection. For instance, near their ovulatory phase, women have been found to prefer the body odors of symmetrical men (Gangestad and Thornhill, 1998; Rikowski and Grammer, 1999). However, at present we have no obvious adaptive explanation supporting the interpretation that also females

could detect the reproductive status of other women. If the ability of a woman to detect ovulation has no costs for the bearer and it has coevolved with men's ability, it could have survived during evolution. Still, communication through pheromones can also work in female-female interactions (Stern and McClintock, 1998) and clearly deserves more study.

To conclude, our results support the view that the body odors of an ovulating woman increase her attractiveness to men. This "the scent of ovulation" could increase a man's probability to fertilize a woman and might therefore be an adaptation of men. When all the earlier and present evidence is summarized, we conclude that although human ovulation may not be as conspicuous as in some primates, it is not either concealed. The unconcealed ovulation should be taken into consideration in theoretical and empirical studies of human sexual behavior in the future.

We thank R.V. Alatalo, A. Grapputo, O. Huitu, M. Koivula, J.S. Kotiaho, and J. Mappes for constructive criticism and J. Raatikainen and K. Tynkkynen for assistance. Special thanks go to all participants of the study. The study was supported by the Academy of Finland (research grant to T.M., no. 63789).

REFERENCES

- Alexander RD, Noonan KM, 1979. Concealment of ovulation, parental care, and human social evolution. In: *Evolutionary biology and human social behavior: an anthropological perspective* (Chagnon NA, Irons W, eds). North Scituate, Massachusetts: Duxbury Press; 402–435.
- Baker RR, Bellis MA, 1995. *Human sperm competition: copulation, masturbation and infidelity*. London: Chapman & Hall.
- Burt A, 1992. "Concealed ovulation" and sexual signals in primates. *Folia Primatol* 58:1–6.
- Buss DM, 1994. *The evolution of desire: strategies of human mating*. New York: HarperCollins.
- Buss DM, 1999. *Evolutionary psychology: the new science of the mind*. Boston: Allyn & Bacon.
- Cartwright J, 2000. *Evolution and human behavior*. Cambridge, Massachusetts: MIT Press.
- Doty RL, 1981. Olfactory communication in humans. *Chem Senses* 4: 351–376.
- Doty RL, Ford M, Preti G, Huggins GR, 1975. Changes in the intensity and pleasantness of human vaginal odors during the menstrual cycle. *Science* 190:1316–1318.
- Gangestad SW, Thornhill R, 1998. Menstrual cycle variation in women's preferences for the scent of symmetrical men. *Proc R Soc Lond B* 265:927–933.
- Garcia-Velasco J, Mondragon M, 1991. The incidence of the vomeronasal organ in 1000 human subjects and its possible clinical significance. *J Steroid Biochem Mol Biol* 4B:561–563.
- Grammer K, 1996. The human mating game: the battle of the sexes and the war of signals. In: *The human behavior and evolution society annual conference*, Northwestern University, Evanston, Illinois, USA, June 29, 1996.
- Grosser BI, Monti-Bloch L, Jennings-White C, Berliner DL, 2000. Behavioral and electrophysiological effects of androstadienone, a human pheromone. *Psychoneuroendocrinology* 25:289–299.
- Jacob S, McClintock MK, 2000. Psychological state and mood effects of steroidal chemosignals in women and men. *Horm Behav* 37: 57–78.
- Jacob S, McClintock MK, Zelano B, Ober C, 2002. Paternally inherited HLA alleles are associated with women's choice of male odor. *Nat Genet* 30:175–179.
- Kenward MG, Roger JH, 1997. Small sample inference for fixed effects from restricted maximum likelihood. *Biometrics* 53:983–997.
- Kohl JV, Francoeur RT, 1995. *The scent of eros: mysteries of odor in human sexuality*. New York: Continuum.
- Lessells CM, Boag PT, 1987. Unrepeatable repeatabilities: a common mistake. *Auk* 104:116–121.
- Manning JT, Scutt D, Whitehouse GH, Leinster SJ, Walton JM, 1996. Asymmetry and the menstrual cycle in women. *Ethol Sociobiol* 17: 129–143.
- Monti-Bloch L, Diaz-Sanchez V, Jennings-White C, Berliner DL, 1998. Modulation of serum testosterone and autonomic function through stimulation of the male human vomeronasal organ (VNO) with pregna-4,20-diene-3,6-dione. *J Steroid Biochem Mol Biol* 1–6: 237–242.
- Nelson RJ, 2000. *An introduction to behavioral endocrinology*. Sunderland: Massachusetts: Sinauer Associates.
- Patterson HD, Thompson R, 1971. Recovery of inter-block information when block-sizes are unequal. *Biometrika* 58:545–554.
- Penn D, Potts WK, 1999. The evolution of mating preferences and major histocompatibility complex genes. *Am Nat* 153:145–164.
- Poran NS, 1995. Cyclic attractivity of human female odors. *Adv Biosci* 93:555–560.
- Reusch TBH, Häberli MA, Aeschlimann PB, Milinski M, 2001. Female sticklebacks count alleles in a strategy of sexual selection explaining MHC polymorphism. *Nature* 414:300–302.
- Rikowski A, Grammer K, 1999. Human body odour, symmetry and attractiveness. *Proc R Soc Lond B* 266:869–874.
- SAS Institute, 1999a. *SAS/IML user's guide*, version 8. Cary, North Carolina: SAS Institute.
- SAS Institute, 1999b. *SAS/STAT user's guide*, version 8, vol. 2. Cary, North Carolina: SAS Institute.
- Scutt D, Manning JT, 1996. Symmetry and ovulation in women. *Hum Reprod* 11:2477–2480.
- Sillén-Tullberg B, Möller AP, 1993. The relationship between concealed ovulation and mating systems in anthropoid primates: a phylogenetic analysis. *Am Nat* 141:1–25.
- Singh D, Bronstad PM, 2001. Female body odour is a potential cue to ovulation. *Proc R Soc Lond B* 268:797–801.
- Stensaas LJ, Lavker RM, Monti-Bloch L, Grosser BI, Berliner DL, 1991. Ultrastructure of the human vomeronasal organ. *J Steroid Biochem Mol Biol* 4B:553–560.
- Stern K, McClintock MK, 1998. Regulation of ovulation by human pheromones. *Nature* 392:177–179.
- Symons D, 1995. Beauty is in the adaptations of the beholder: the evolutionary psychology of human female sexual attractiveness. In: *Sexual nature, sexual culture* (Abramson PR, Pinkerton SD, eds). Chicago: University of Chicago Press; 80–118.
- Thornhill R, Gangestad SW, 1999. The scent of symmetry: a human sex pheromone that signals fitness? *Evol Hum Behav* 20:175–201.
- Thornhill R, Palmer CT, 2000. *A natural history of rape: biological bases of sexual coercion*. Cambridge: MIT Press.
- Usathanondh R, 1995. Conception control. In: *Kistner's gynecology: principles and practice* (Ryan KJ, Berkowitz RS, Barbieri RL, eds). St. Louis, Missouri: Mosby; 532–570.
- Wedekind C, Furi S, 1997. Body odour preferences in men and women: do they aim for specific MHC combinations or simply heterozygosity? *Proc R Soc Lond B* 264:1471–1479.
- Wilcox AJ, Dunson D, Baird DD, 2000. The timing of the "fertile window" in the menstrual cycle: day specific estimates from a prospective study. *BMJ* 321:1259–1262.