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Body Odor Attractiveness and Ovarian Hormones in Women

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by

Mei Mei

Committee in charge:

Professor James Roney, Chair

Professor Nancy Collins

Professor Daniel Conroy-Beam

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The thesis of Mei Mei is approved.

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Nancy Collins

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Daniel Conroy-Beam

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James Roney, Committee Chair

August 2021

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ABSTRACT

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Previous literatures have shown that a woman's body odors during the fertile window (-5 to 0 days before ovulation) were rated by men as more attractive compared to odors outside the fertile window. However, few researches have looked at the underlying hormones that could be regulating this effect, and none have looked at the relationship between women's within-cycle shift in hormones and the within-cycle shifts in odor attractiveness. The current research examined the effects of estradiol and progesterone concentrations on women's odor attractiveness throughout the menstrual cycle. Forty-six donor women were instructed to wear an underarm pad overnight every five days for 30 days and provided saliva samples (assayed for estradiol and progesterone) in the morning of odor collection. These women also provided daily luteinizing hormone (LH) tests. A total of 66 men then rated the pleasantness, sexiness and intensity of the odor samples in five separate sessions. And the attractiveness ratings were regressed on donors' estradiol and progesterone concentrations. We found that odor samples during the donor women's late fertile window (-2 to 0 days before ovulation) were rated as more attractive. Additionally, we found no effect of estradiol or progesterone on odor attractiveness within women. However, a positive effect of estradiol and a null effect of progesterone on odor attractiveness were found between women, which offer support to the position that men

have evolved to attend to women's general reproductive condition, rather than detecting women's ability to conceive at that specific time. Since none of the hormones measured in this study can account for the late fertile window effect, further investigation is needed to explain this shift in odor attractiveness during the late fertile window.

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I. Introduction

In many mammalian species, olfactory cues can communicate important information to males regarding the reproductive status of females. The odor attractiveness of female mammals is strongly affected by their ovarian hormones. Researchers have shown that in meadow voles, ovariectomy makes the odors of female unappealing to males, but scent attractiveness is restored following an injection of estradiol (Ferkin & Johnston, 1993). Researches with rhesus macaques have shown a similar effect on the odor attractiveness of ovariectomized females. Odor attractiveness increases after an injection of estradiol, and subsequently decrease after a progesterone injection (Michael & Keverne, 1968; Michael & Keverne, 1970; Michael, Keverne & Bonsall, 1971). Male stump-tailed macaques also have been found to have positive testosterone responses to the odors of late follicular females (Cerda-Molina et al., 2006). These studies provided strong evidence that in many mammalian species, males can detect ovulation in female through odor cues, and these odor cues are regulated by estradiol and progesterone concentration.

In humans, however, the relationship between odor attractiveness, ovulation and ovarian hormones are less clear. Women's odor samples collected during the late follicular phase (the 'fertile window' when conception is possible) are on average rated as more attractive than samples collected from the luteal phase (Doty et.al, 1975; Gildersleeve, Haselton, & Pillsworth, 2012; Havlicek et al., 2006; Kuukasjärvi et al., 2004; Singh & Bronstad, 2001; Thornhill et.al, 2003). Men also have testosterone increases after smelling women's odors collected from the late follicular but not the luteal phase (Cerda-Molina et al., 2013; Miller & Maner, 2010; Miller & Maner, 2011). However, two independent studies (Roney & Simmons, 2012; Strom et al., 2012) found no change in men's testosterone after

exposed to ovulatory odors. Additionally, a recent study showed that between women, high estradiol and low progesterone concentration predict body odor attractiveness for odor samples collected near ovulation (Lobmaier et al., 2018). However, apart from the Lobmaier et al. (2018) study that tested the between-women effect of hormones, none of the previous research has looked directly at the relationship between hormones and odor attractiveness. Furthermore, no prior studies have examined the relationship between women's within-cycle shift in odor attractiveness and the within-cycle shifts in estrogen and progesterone concentrations.

Ovarian hormones fluctuate in a systematic manner across the menstrual cycle (see Figure 1). Estradiol rises during the follicular phase, peaks in the late follicular phase (the fertile window, -5 to 0 days before ovulation), drops just prior to ovulation, and then rises to a second peak during the luteal phase. Progesterone stays low during the follicular phase and rises following ovulation, peaking in the luteal phase. Thus, drops in odor attractiveness when comparing the fertile window to the luteal phase could be caused by the drop in estradiol or the rise in progesterone across these cycle regions (or by other signals). The present study provides the first direct evidence on this question.

A positive effect of estradiol, and a negative effect of progesterone on odor attractiveness would support the idea that odors provide direct clues of women's ovulatory timing. However, if odor attractiveness is coupled to estradiol but not progesterone, then this raises the possibility that some women's luteal phase odors may be more attractive than some other women's late follicular odors due to one woman having higher levels of estradiol throughout the cycle. This explanation is important to consider because estradiol and progesterone vary between-women, or within-women between-cycles, and tend to be elevated across the cycle in cycles with higher fertility (Lipson & Ellison, 1996). As shown

in Figure 1, if woman A is experiencing a particularly fertile cycle, she may have higher luteal phase estradiol (point A) than woman B's fertile window estradiol (point B). Thus, if odor attractiveness tracks estradiol only, it should be higher at point A in Fig. 2 than at point B, which is inconsistent with the hypothesis that female body odors provides clear clues of ovulatory timing.

Progesterone, on the other hand, only has one peak in the luteal phase. If progesterone effectively shuts down odor attractiveness, however, then fertile window samples should consistently smell better than luteal phase samples, regardless of cycle variability in fertility. Thus, a negative effect of progesterone on odor attractiveness would suggest that odors are cues of present fecundity (the fertile window), but a null or positive effect of progesterone might suggest that odors are cues of general reproductive status (e.g., this woman is having an ovulatory cycle, or secretes higher estradiol in general).

In the current research, we examined the effects of estradiol and progesterone on women's odor attractiveness. We hypothesized, in accordance with prior research, that men would rate odors collected during the fertile window as more attractive than those collected during other phases of the cycle. We also hypothesized that estradiol would positively predict odor attractiveness but progesterone would be unrelated to a women's odor attractiveness. This is because human pair bonding may have caused the evolution of preferences for cues of general reproductive condition, indexed by estradiol, over cues of whether a woman can conceive on the day in question.

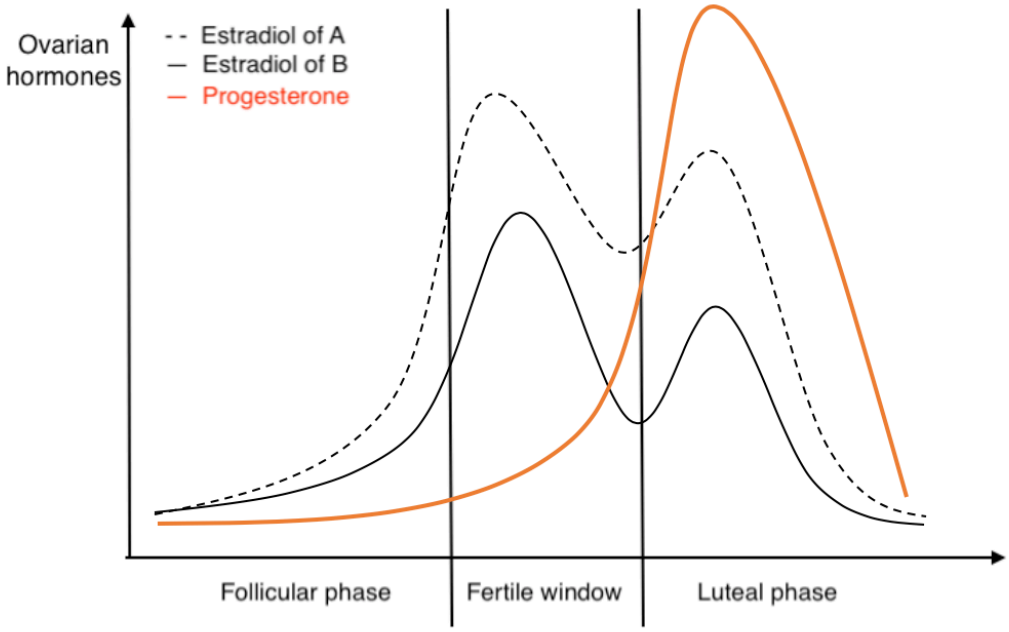

Figure 1. Change in estradiol and progesterone of women A and women B in a cycle

II. Methods

A. Participants

A total of 46 female donors and 66 male raters were recruited from University of California, Santa Barbara. The female donors were all naturally cycling (e.g., had not used any form of hormonal contraception in the previous three months) and between 18 and 25 years old (M = 20.231, SD = 1.308). Over the course of 30 days, donors collected odor samples every five days for a total of 6 samples per woman and received up to $180 in compensation. The male participants received partial course credit for their participation.

B. Sample collection

After obtaining informed consent, the women were given detailed instructions on the process of sample collection and materials required for sample collection. The materials include cotton pads, saliva collection tubes, LH tests, clean T-shirts for them to wear during the night of odor collection and unscented soap for them to shower with. The donor women were instructed to wear underarm cotton pads overnight every five days over a period of 30 days. The morning after collection nights, they were asked to put the pad in the corresponding freezer bag, which was stored temporarily in their home freezers. The donors were given standard instructions for avoiding contaminating odors on collection nights (e.g., washing with unscented soap and refraining from use of deodorants). When they completed all six samples, participants delivered the freezer bags to the lab, which were then stored in a -40 C freezer. Additionally, the donor women completed daily surveys on their mood, sleep, food intake, as well as questions about the completion of the odor and saliva collection, and their compliance to the procedure.

The female participants also provided saliva samples on odor collection days (assayed for estradiol and progesterone) using the passive drooling method, and completed daily luteinizing hormone (LH) tests. LH tests have been shown to be a highly valid and reliable way of measuring ovulation (Gangestad et al 2016), with 97% accuracy in ultrasound-verified ovulation (Guermandi et al, 2001) Positive LH tests indicate ovulation within about 24 hours (Testart and Frydman, 1982); odor samples that fall between four days before and one day after a positive LH test were considered fertile window samples.

C. Sample rating

Odor samples were rated across five rating sessions, with 10 to 17 male raters in each session. In each session, 9-10 individual stations were set up, each with the 6 samples from the same donor women. Each rater rated the odors of only 9-10 women (54-60 samples) to mitigate effects of scent fatigue. In order to counterbalance the order effect, the station order and sample order within stations for individual raters were generated in advance using Latin squares (Grant, 1948) and recorded on the rating sheets. A Latin Square is a n × n array filled with n numbers, each occurring exactly once in each row and exactly once in each column. Depending on the total number of stations, station order was generated using a 9 × 9 or 10 × 10 Latin Square, with each row of the Latin Square representing a unique station order. The order of odor samples within each station was randomized using a 6 × 6 Latin Square. The odor samples were thawed 3 hours in advance and placed in labeled glass jars. After informed consent, male raters were given a rating sheet with and were asked to start at a particular station following the order indicated on their rating sheet. Within each station, raters were asked to follow the order on the rating sheet and rate each odor sample for pleasantness, sexiness and intensity using 7-point Likert scales. They were instructed to

open the lid of each glass jar, take a deep sniff at the sample, close the lid and write down their ratings before moving on to the next sample. When the participants had finished rating all the samples from the same station, they moved on to next station indicated on their rating sheet.

III. Results

Multilevel modeling was used to test the fertile window effect and to investigate whether changes in women's hormones predict changes in their odor attractiveness. Analyses were conducted using R version 3.5.3, lmerTest version '3.1.0' (Kuznetsova et al., 2013). To create current hormone values for our analyses, hormone values of each sample were centered on subject-specific means and rescaled so that all values falls between −0.5 to 0.5. This was done following Jones et al. (2018) to facilitate convergence in the linear mixed models, and merely involves dividing values by a constant such that it does not alter any statistical results. To create mean hormone values for our analyses, hormone levels were averaged across all samples for each woman, then centered on the grand mean, and rescaled using the same scaling method as above. Pleasantness and sexiness were combined to create an attractiveness composite, since these ratings were highly correlated ($r = 0.743$, $p < 0.001$).

We performed two types of statistical analyses treating either women (donor) or men (rater) as the unit of analysis. When women are used as the unit of analysis, ratings from different male raters were combined to create an average rating for each odor sample. This allows us to look at the within-cycle and between-women effect of hormones separately, as while as looking at variables on the women's level (e.g. relationship status). Models treating men as the unit of analysis, on the other hand, does not differentiate between odor samples from different women, which means that the model cannot separate the within-cycle and between women effect of hormones. However, using men as the unit of analysis allow us to look at variables on the men's level (e.g. men's SOI score). The results of both type of analyses are reported below.

Women as the unit of analysis

The inter-rater reliability of most sessions was high, with ICCs ranging from 0.61 to 0.84 on all measures. One exception being Session 4 sexiness rating, with an ICC of 0.36. Since the intraclass correlation coefficients were reasonable, a mean rating was calculated for each odor sample by averaging across the rating of every individual rater.

To test the fertile window effect, cycle days were binned into days during fertile window (days -5 to 0), and days outside the fertile window. These cycle day bins were then entered at level one of a multilevel modeling as a predictor variable, and random intercepts and random slopes were specified for donor woman. Among the 46 donor women, 28 had an ovulatory cycle and were included in this model. Only marginally significant effect of fertile window was found on odor attractiveness ($b = 0.178$, $t = 1.999$, $p = 0.060$). However, as shown in Figure 2, there was a clear spike in odor attractiveness during day -2 to 0 (the late fertile window). An exploratory test with 16 out of the 46 donor women who had a late fertile window sample revealed a significant effect of late fertile window on odor attractiveness: Samples collected during the late fertile window were significantly more attractive than samples collected outside the late fertile window ($b = 0.372$, $t = 3.153$, $p = 0.005$). Additionally, no effect of fertile window ($b = 0.090$, $t = 0.833$, $p = 0.406$) or the late fertile window ($b = 0.212$, $t = 1.392$, $p = 0.177$) were found on odor intensity.

To test hormonal predictors of odor attractiveness, a multilevel model was constructed with current estradiol, current progesterone, and their interactions entered at level one as predictors. Mean estradiol, mean progesterone, and relationship status of donor women were entered as level two as predictors, and assessed in a separate model. Random intercepts and random slopes were specified for donor woman in the Level-1 models. No effects of current

estradiol (b = 0.333, t = 0.911, p = 0.363) or current progesterone (b = -0.176, t = - 0.455, p = 0.649) were found on the attractiveness composite within women. The estradiol-progesterone interaction was also not significant (b = 1.440, t = 0.926, p = 0.355). However, in the model with mean hormone values, a positive effect of mean estradiol was found on odor attractiveness (b = 0.202, t = 2.224, p = 0.032), suggesting that samples from women with higher mean estradiol were rated as significantly more attractive, controlling for relationship status. Mean progesterone, on the other hand, had no effect on attractiveness (b = -0.140, t = -1.219, p = 0.231), and there was no significant interaction between mean estradiol and progesterone on odor attractiveness (b = 0.148, t = 1.335, p = 0.189). Relationship status had a positive effect on odor attractiveness (b = 0.248, t = 2.782, p = 0.009) such that the odor samples from the donor women who were in a relationship were rated as significantly more attractive than samples from donor women not in relationships. A marginally significant interaction effect was found for within women estrogen and progesterone on odor intensity (b = -4.863, t = -2.154, p = 0.053), but none of the other terms were significant (Table 2).

To test the robustness of our effects, we conducted the same analyses on the attractiveness composite of our data excluding group 4, as the ICC on sexiness is low (0.36) for this session. The results remain virtually identical (Table 3).

Control variables like participants' mood, food intake and any illnesses during the process of the experiment are also entered in a model to check for any possible effect on odor attractiveness. With the exception of the positive effect of self-assurance on odor attractiveness (b = 0.175, t = 2.308, p = 0.022), none of the control variables have significant effect on the attractiveness composite.

Men as the unit of analysis

Similar to the analysis using women as the unit of analysis, cycle days were entered at level one of a multilevel modeling as a predictor variable, and random intercepts and random slopes were specified for male rater to test the fertile window effect. A significant fertile window effect was found: samples collected during fertile window were on average significantly more attractive than samples collected outside the fertile window ($b = 0.16076$, $t = 5.949$, $p < 0.001$). A separate model reveals a significant late fertile window effect: Samples collected during the late fertile window were significantly more attractive than samples collected outside the late fertile window (estimate = 0.40114, $t = 11.445$, $p < 0.001$). Additionally, a marginally significant late fertile window ($b = 0.189$, $t = 1.903$, $p = 0.057$) effect on odor intensity were found. There is no effect of fertile window ($b = -0.012$, $t = -0.159$, $p = 0.874$) on odor intensity.

To explore which hormone might be regulating this fertile window effect, we constructed a separate multilevel model was with estradiol, progesterone, and their interactions entered at level one as predictors. We found a positive effect of estradiol (estimate = 0.07487, $t = 4.517$, $p < 0.001$), suggesting that at mean progesterone concentration, odor samples with higher estradiol concentration were rated as more attractive. A marginally significant negative effect of progesterone (estimate = -0.03613, $t = -1.760$, $p = 0.0786$) was also found: at mean estradiol concentration, odor samples with lower progesterone concentration were rated as more attractive. Finally, the significant interaction effect suggests that as estradiol level increases, the negative effect of progesterone concentration on odor attractiveness became weaker (estimate = 0.02909, $t = 2.176$, $p = 0.0296$). A significant interaction effect was found for estrogen and progesterone on odor intensity ($b = -0.115$, $t = -4.111$, $p < 0.001$), but the main effect of estradiol ($b =$

0.039, t = 1.324, p = 0.186) or progesterone (b = -0.016, t = -0.403, p = 0.687) was not significant.

Men's SOI score (attitude, behavior, desire, and a composite score) are also entered into the above models as control variables to check for any possible effect on odor attractiveness. None of the control variables have significant effect on the attractiveness composite, and none of them altered the results reported above.

IV. Discussions

Across many mammalian species, males found female body odor during the fertile period of the ovulatory cycle more attractive. And this effect seems to be driven by a positive effect of estradiol and negative effect of progesterone on female body odor. Some past literatures have found the same fertile window effect in human females, but few has examined the underlining hormones that might be regulating this effect. Hence, the current study is the first to look at within cycle shifts in hormones and within cycle shifts in odor attractiveness.

We partially replicated the fertile window effect found in previous studies using men as the unit of analysis (Doty et.al, 1975; Havlicek et al., 2006; Kuukasjärvi et al., 2004; Singh & Bronstad, 2001; Thornhill et.al, 2003). However, this effect was not significant using women as the unit of analysis. Among the previous studies on this line of work, two of them (Doty et al., 1975; Singh and Bronstad, 2001) performed statistical analysis treating men (rater), instead of women, as the unit of analysis. When men (raters) are used as the unit of analysis, the results cannot be generalized to other women odor donors. This suggest that if one of the donor women smells better in her fertile window days than none fertile window day by chance alone, the results might be affected and it will look like there's a fertile window effect when there is none. Using women as the unit of analysis, on the other hands, means that the results are generalizable to other donor women and is therefore a statistically more powerful test. We found significant late fertile window effect using both men and women as the unit of analysis is consistent with Gildersleeve et al (2012), suggesting that this shift in odor attractiveness might be more specific to the late fertile window, namely two to zero days prior to ovulation, when fecundity is the highest (Wilcox et al, 2000).

The positive effect of mean estradiol and the null effect of mean progesterone using women as the unit of analysis supported our hypothesis. Higher mean estradiol indicate that the woman is currently in a more fertile cycle, and she will be in more fertile cycles in the near future. This provide evidence to the idea that female body odor are cues of general reproductive status. However, no effect of estradiol was found within women, which might be because the within women change in estradiol was not large enough to detect. It's also possible that estradiol has a long-term effect, or a lagged effect on odor, instead of an immediate effect.

One limitation of the current study is that it didn't measure the within women, between cycle variability. The donor women were only asked to provide odor samples for a period of 30 days. Therefore, we did not test whether odor attractiveness is higher in a more fertile cycle than a less fertile cycle of the same woman. Nonetheless, the study is important for its ability to provide the first evidence ever regarding the hormonal predictors of within-cycle shifts in women's odor attractiveness. The study also posed some new questions regarding the cycle phase shifts in odor attractiveness, as none of the hormones we measured in this study, namely estradiol and progesterone, can account for this shift in odor attractiveness during the late fertile window. It is possible that other hormones that peak in the late fertile window—such as luteinizing hormone or oxytocin (Engel et.al, 2019) might drive this effect, but more research is needed to assess this. Finally, the presence of a between-woman effect of estradiol and the lack of effect within women might be as such: long-term exposure to higher estradiol might increases odor attractiveness, while the day-to-day fluctuations have smaller effects. Another possibility is that healthier women smell better (Griep, 1997) and they also produce more estradiol. This is relevant to men's long-term mate choice, since men should be preferring healthier mates as a result of the higher paternal investment in

long term mating. Unlike in short-term mating, where men can be indiscriminate in their mate choice.

In conclusion, consistent with Lobmaier et al. (2018), a between-women effect of estradiol was found, suggesting that odor attractiveness might be signaling general reproductive status. However, the presence of the late fertile window effect suggests that there might also be some information about within-cycle fertility in female body odor, which cannot be explained by the two hormones measured in this study. Therefore, further investigation is needed regarding which hormones are regulating this late fertile window effect.

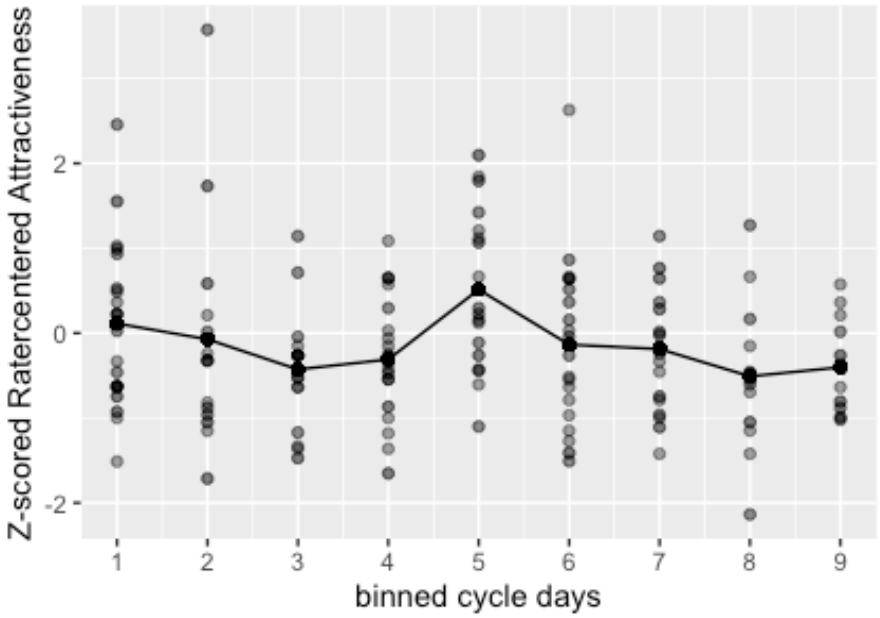

Figure 2. Cycle days shift in ratercentered ratings of the sexy-pleasant composite; 1 = <-11, 2 = -11 ~ -9, 3 = -8 ~ -6, 4 = -5 ~ -3, 5 = -2 ~ 0, 6 = 1 ~ 3, 7 = 4 ~ 6, 8 = 7 ~ 9, 9 = >9

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Appendix

Table 1: Within-woman and between-women effect of hormone on attractiveness composite

	b	SE	t	p	95%CI
Fertile window	0.178	0.089	1.999	0.060	[0.0015, 0.355]
Late FW	0.372	0.118	3.153	0.005	[0.138, 0.614]
Current E	0.334	0.366	0.911	0.363	[-0.457, 1.059]
Current P	-0.176	0.387	-0.455	0.649	[-0.961, 0.533]
Current E×P	1.438	1.553	0.926	0.355	[-1.773, 4.519]
Mean E	0.202	0.091	2.224	0.032	[0.032, 0.381]
Mean P	-0.140	0.115	-1.219	0.231	[-0.382, 0.066]
Mean E × P	0.148	0.111	1.335	0.189	[-0.071, 0.353]
Relationship	0.248	0.089	2.782	0.008	[0.070, 0.433]

Table 2: Within-woman and between-women effect of hormone on odor intensity

	b	SE	t	p	95%CI
Fertile window	0.090	0.108	0.833	0.406	[-0.123, 0.303]
Late FW	0.212	0.152	1.392	0.177	[-0.089, 0.523]
Current E	0.239	0.469	0.511	0.610	[-0.650, 1.163]
Current P	0.021	0.483	0.044	0.965	[-0.940, 0.920]
Current E×P	-4.863	2.257	-2.154	0.053	[-9.535, -0.431]
Mean E	-0.031	0.166	-0.184	0.855	[-0.325, 0.311]
Mean P	-0.088	0.211	-0.417	0.679	[-0.499, 0.285]
Mean E × P	-0.161	0.202	-0.801	0.428	[-0.538, 0.238]
Relationship	-0.153	0.154	-0.994	0.324	[-0.426, 0.151]

Table 3: Within-woman and between-women effect of hormone on attractiveness composite, excluding session 4

	b	SE	t	p	95%CI
Fertile window	0.076	0.102	0.747	0.463	[-0.160, 0.289]
Late FW	0.334	0.148	2.262	0.025	[0.041, 0.610]
Current E	0.309	0.430	0.717	0.474	[-0.519, 1.087]
Current P	-0.367	0.431	-0.853	0.395	[-1.197, 0.475]
Current E×P	1.843	1.634	1.128	0.261	[-1.352, 5.260]
Mean E	0.228	0.107	2.130	0.042	[0.026, 0.423]
Mean P	-0.175	0.129	-1.356	0.189	[-0.420, 0.089]
Mean E × P	0.126	0.115	1.095	0.283	[-0.104, 0.355]
Relationship	0.233	0.107	2.188	0.039	[0.027, 0.453]