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Scent of a Woman: Men's Testosterone Responses to Olfactory Ovulation Cues

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Abstract

Adaptationist models of human mating provide a useful framework for identifying subtle, biologically based mechanisms influencing cross-gender social interaction. In line with this framework, the current studies examined the extent to which olfactory cues to female ovulation—scents of women at the peak of their reproductive fertility—influence endocrinological responses in men. Men in the current studies smelled T-shirts worn by women near ovulation or far from ovulation (Studies 1 and 2) or control T-shirts not worn by anyone (Study 2). Men exposed to the scent of an ovulating woman subsequently displayed higher levels of testosterone than did men exposed to the scent of a nonovulating woman or a control scent. Hence, olfactory cues signaling women's levels of reproductive fertility were associated with specific endocrinological responses in men—responses that have been linked to sexual behavior and the initiation of romantic courtship.

Keywords

human mating, evolution, fertility, hormones, olfaction

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What factors influence human sexual attraction? What determines when and toward whom someone will direct romantic interest? The psychological literature reveals a complex network of factors that can affect mating preferences and the initiation of romantic courtship (Aron, Norman, Aron, McKenna, & Heyman, 2000; Beck & Clark, 2009; Gangestad, Haselton, & Buss, 2006; Kenrick, Li, & Butner, 2003). Many studies of human mating focus on overt evaluative processes that people use to make important mating-related decisions (e.g., evaluation of observable traits possessed by a potential partner; cf. Eastwick & Finkel, 2008). The current research, in contrast, adds to an emerging literature suggesting that human mating is guided, in part, by relatively subtle processes that occur at fundamental levels of biology.

Evolutionary perspectives suggest that some of the subtle factors affecting human mating may be similar to those that shape the mating behavior of other animals (Buss, 1989). Across a number of species, for example, the odors emitted by an animal can have a substantial impact on the mating behaviors of its conspecifics (Scordato & Drea, 2007; Ziegler, Schultz-Darken, Scott, Snowdon, & Ferris, 2005). Recent evidence suggests that subtle scents may play an important role in mating-related processes in humans as well (Singh & Bronstad, 2001; Thornhill et al., 2003).

In the current research, we evaluated whether scents that signal a woman's level of reproductive fertility directly

influence mating-related biological processes in men. We predicted that olfactory cues to female ovulation would influence men's levels of testosterone—a hormone known to mediate men's mating behavior.

Mating-Related Olfactory Processes

Across many sexually reproducing species, females are fertile only during the brief period of time surrounding estrus or ovulation. For many animals, olfaction serves as a key medium by which female fertility promotes male mating behaviors. Evidence for this type of chemosensory signaling exists in numerous species, ranging from rodents (Pankevich, Baum, & Cherry, 2004) to primates (Ziegler et al., 2005).

Recent studies indicate that olfactory processes might play an important role in human mating as well (Thornhill & Gangestad, 1999). Although traditionally it has been assumed that human female ovulation is concealed (Burley, 1979), recent evidence suggests that changes in a woman's fertility across the menstrual cycle may be perceived via olfactory cues. In particular, a small number of studies indicate that men

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subjectively evaluate the odors of women close to ovulation as more pleasant than the odors of women far from ovulation (Havlíček, Dvořáková, Bartoš, & Flegr, 2006; Singh & Bronstad, 2001).

To serve as a functional chemosensory signaling device, however, cues to ovulation should have effects in men that go well beyond subjective assessments of odor pleasantness. Indeed, olfactory cues to female ovulation might be expected to promote specific physiological responses in men—responses that are linked closely with mating-related processes.

The Role of Testosterone

The neuroendocrine system is a key biological system involved in mating. In males of numerous species, testosterone levels are sensitive to cues indicating potential mating opportunities, and high levels of testosterone promote heightened interest in mating (Batty, 1978; Roney, Lukaszewski, & Simmons, 2007). Moreover, an extensive animal-research literature indicates that male testosterone levels are influenced by chemosensory signals emitted by females (Cerdeña-Molina et al., 2006; Scordato & Drea, 2007) and particularly by cues to female estrus or ovulation (Ziegler et al., 2005).

No published studies have examined whether, in humans, men's testosterone levels are responsive to olfactory ovulation cues. However, some suggestive evidence does indicate that men's testosterone levels are responsive to mating-related cues more generally. Some studies, for example, suggest that men display increases in testosterone after watching a sexually arousing film (e.g., Stoleru, Ennaji, Cournot, & Spira, 1993). Two recent studies also found testosterone increases among men who had just interacted with an attractive woman (Roney, Mahler, & Maestripieri, 2003; Roney et al., 2007).

Consistent with an adaptationist model of human mating, our hypothesis is that testosterone levels in men are responsive to female ovulation cues. Moreover, given the literature on animal chemosensory signaling, we propose that olfaction may serve as one means by which men's testosterone levels are influenced by female ovulation cues.

Overview of the Current Studies

In two studies, men were exposed to the odors of women at varying points during their menstrual cycles. Salivary testosterone levels were assessed subsequently. Our primary hypothesis was that men exposed to the odors of women near ovulation would display higher levels of testosterone than men exposed to odors of women relatively far from ovulation.

Study I

Method

Participants. Thirty-seven undergraduate men (age range: 18–23 years) participated for course credit. Two participants

were excluded because they did not provide enough saliva for their testosterone to be measured. To prepare for the experiment, participants were asked to refrain from activities known to affect hormone levels: eating food or drinking caffeinated beverages or alcohol for 2 hr prior to testing, exercising for 12 hr prior to testing, and smoking for 6 hr prior to testing.

Odor collection. Four women not on hormonal contraceptives (age range: 18–19 years) participated in return for course credit and \$10. In a pretesting session, these women indicated that they had regular menstrual cycles of approximately 28 days in length. Odor collection procedures were similar to those used in previous studies (Singh & Bronstad, 2001). The date of onset of menstrual blood flow counted as Day 0; women wore a T-shirt during the nights of Days 13, 14, and 15 (late follicular phase, near ovulation) and then wore a different T-shirt during the nights of Days 20, 21, and 22 (luteal phase, far from ovulation). During each day, the T-shirt was placed into a sealed freezer bag. To reduce extraneous odors, during each 3-day session, women showered with unscented soap and shampoo and refrained from using perfumes, deodorants, and antiperspirants; eating odor-producing food (e.g., chili, garlic, pepper, vinegar, asparagus); smoking cigarettes, drinking alcohol, and using drugs; and engaging in sexual activity or sleeping in the same bed as someone else. After each 3-day session, women returned the T-shirt to the experimenter and reported on whether they had refrained from the aforementioned activities; all women adhered to the instructions. In addition, a trained research assistant smelled the T-shirts and confirmed that none smelled of extraneous odors (e.g., perfume, smoke). Shirts were kept in a freezer when not in use. All shirts were used within 6 days of being worn.

Odor smelling. Participants arrived between 12:00 p.m. and 4:30 p.m. and were told that the study's purpose was to examine the relationships among scent, hormones, and social cognition. Participants were informed that they would smell a T-shirt worn previously by a woman; ovulation was not mentioned. Each participant was randomly assigned to one particular T-shirt. T-shirts were assigned so that for each T-shirt supplier, the T-shirt worn during ovulation and the T-shirt worn during nonovulation were smelled by a similar number of men (within 1; e.g., if 3 men smelled supplier A's T-shirt worn during ovulation, 2–4 men smelled supplier A's T-shirt worn during nonovulation).

Prior to smelling the T-shirts, participants provided a baseline saliva sample by spitting into a collection vial (approximately 4 ml per sample). Each participant was then instructed to put his nose to the opening of a plastic bag containing a T-shirt and to take three large inhalations. The potency of the smell was increased by repeating this procedure 5 and 10 min following the first odor exposure. Fifteen minutes after the first inhalation, participants provided another saliva sample. This time delay was included because changes in testosterone typically require 15 min before being detectable in saliva.

Both experimenters and participants were blind to the phase of the shirt supplier's menstrual cycle. Eighteen participants were randomly assigned to smell a shirt worn close to ovulation (Days 13–15), and 17 participants were assigned to smell a shirt worn far from ovulation (Days 20–22).

Testosterone measurement. We used a conventional approach for assaying salivary hormones. Saliva samples were frozen at -20°C . To precipitate mucins, we thawed the samples and centrifuged them at 3,000 rpm for 10 min. The supernatant was stored in 250- μl aliquots at -20°C until assayed. Commercially available solid-phase radioimmunoassay kits were used to measure concentrations of testosterone in nanograms per deciliter. All samples were processed in duplicate using a high-throughput, automated gamma counter. The lower limit of sensitivity of the radioimmunoassay kits was 0.2 ng/dl. Intra- and interassay coefficients of variation were 4.21% and 5.03%, respectively.

Results

To predict participants' testosterone levels after smelling the women's T-shirts (postsmell testosterone), we performed an analysis of covariance. Phase of the shirt supplier's menstrual cycle (T-shirt condition: ovulation vs. nonovulation) served as the independent variable. Baseline testosterone (presmell testosterone) served as a covariate, and did not differ between participants in the two T-shirt conditions, $t(33) = 1.13, p = .27$. There was an effect of presmell testosterone level, $F(1, 32) = 96.33, p < .001, p_{\text{rep}} > .99, \eta_p^2 = .75$, such that higher presmell testosterone was associated with higher postsmell testosterone. In addition, results revealed the expected effect of the T-shirt supplier's menstrual-cycle phase, $F(1, 32) = 13.45, p = .001, p_{\text{rep}} = .99, \eta_p^2 = .30$. Controlling for presmell testosterone, postsmell testosterone was substantially higher in men exposed to the odor of a woman close to ovulation ($M = 9.34, SE = 0.33$) than in men exposed to the odor of a woman far from ovulation ($M = 7.60, SE = 0.34$).

To examine raw-score change in testosterone, we performed a mixed-model analysis of variance with measurement occasion (presmell vs. postsmell testosterone) as a within-subjects variable and T-shirt condition (ovulation vs. nonovulation) as a between-subjects variable. Results revealed a main effect of measurement occasion, $F(1, 33) = 10.81, p = .002, p_{\text{rep}} = .98, \eta_p^2 = .25$, with testosterone decreasing from the first to the second sample. However, this effect was qualified by the predicted interaction between measurement occasion and T-shirt condition, $F(1, 33) = 12.12, p = .001, p_{\text{rep}} = .99, \eta_p^2 = .27$. Follow-up contrasts revealed that postsmell testosterone was significantly lower than presmell testosterone among men in the nonovulation condition, $F(1, 33) = 22.26, p < .001, p_{\text{rep}} > .99, \eta_p^2 = .40$. However, no difference between presmell and postsmell testosterone was observed among men in the ovulation condition, $F(1, 33) = 0.02, p = .89, p_{\text{rep}} = .20, \eta_p^2 < .01$ (see Table 1).

Table 1. Mean Raw Salivary Testosterone Levels (ng/dl) in Studies 1 and 2

Study and condition	Presmell	Postsmell
Study 1		
Ovulation	9.72 (3.05)	9.77 (3.41)
Nonovulation	8.73 (2.12)	7.14 (1.68)*
Study 2		
Ovulation	10.58 (3.81)	9.86 (3.92)
Nonovulation	10.44 (3.65)	8.36 (3.75)*
Control	10.86 (5.75)	9.01 (4.88)*

Note: Standard deviations are given in parentheses. *F* tests were used to compare presmell and postsmell testosterone values in each condition.

* $p < .05$.

Discussion

Study 1 provides preliminary evidence that exposure to olfactory ovulation cues influences men's testosterone levels. Men exposed to the scent of a woman near ovulation had higher testosterone levels than men exposed to the scent of a woman far from ovulation.

Given that the difference between conditions was driven partially by a decrease in testosterone among men in the nonovulation condition, it was unclear whether this difference reflected responses to cues of high fertility (ovulation) or to cues of low fertility (nonovulation). Therefore, in Study 2, we included a control condition in which some men smelled a T-shirt not worn by anyone. This allowed us to test whether the differences in testosterone were caused by cues signaling fertility or by cues signaling lack of fertility.

Study 2 included two additional design enhancements. First, we obtained more accurate assessments of when women wore T-shirts relative to their day of ovulation, which allowed for a more rigorous test of our hypotheses. Second, to link our work to previous research (Havlicek et al., 2006; Singh & Bronstad, 2001), we asked men to provide subjective ratings of odor pleasantness.

Study 2

Method

Participants. Sixty-eight undergraduate men (age range: 18–23 years) participated for course credit. Two participants were excluded because they did not provide enough saliva for their testosterone to be measured. Three men were excluded because they were assigned to a T-shirt worn by a woman who did not adhere to instructions (see the Odor Collection section). As in Study 1, prior to testing, participants were asked to refrain from activities that affect hormone levels.

Odor collection. Eleven women (age range: 18–21 years) who were not on hormonal contraceptives and had regular menstrual cycles participated in return for course credit and

\$10. Procedures were identical to those in Study 1 with two exceptions. First, the order in which the women wore the T-shirts was counterbalanced. Five women first wore a T-shirt during the nights of Days 20 to 22 (luteal phase) and then wore another T-shirt on Days 13 to 15 (late follicular phase); six women wore T-shirts in the reverse order. Second, we tracked the women over the course of their menstrual cycles and assessed both when they began their menstrual cycle prior to supplying T-shirts and when they began their next menstrual cycle after supplying T-shirts. This allowed us to obtain more complete information about their true menstrual-cycle length and to identify more accurately their period of peak fertility. As in Study 1, all women were instructed to refrain from activities that might influence odors. One woman indicated that she had used drugs during both T-shirt sessions; her data were excluded from analyses.

Odor smelling. Procedures for smelling the T-shirt were identical to those in Study 1, with two exceptions. The first is that we included a control condition in which some participants smelled a T-shirt not worn by anyone. Thus, participants were randomly assigned to one of three conditions: (a) ovulation (smelling a T-shirt worn by a woman on Days 13–15), (b) non-ovulation (smelling a T-shirt worn by a woman on Days 20–22), or (c) control (smelling a T-shirt that had never been worn by anyone). All men (including those in the control condition) were told that the T-shirt had been worn by a woman. The second difference from Study 1 is that, after providing saliva samples, participants again smelled the T-shirt and provided ratings of how pleasant (from 1, *very unpleasant*, to 7, *very pleasant*) and intense (from 1, *very weak*, to 7, *very strong*) the odor was.

Testosterone measurement. Hormone analyses were the same as in Study 1. The lower limit of sensitivity of the radioimmunoassay kits was 0.2 ng/dl. Intra-assay and interassay coefficients of variation were 4.79% and 4.93%, respectively.

Results

T-shirt condition (ovulation, nonovulation, control) served as the independent variable and presmell testosterone as a covariate in an analysis of covariance predicting participants' testosterone levels after smelling a T-shirt. Presmell testosterone did not differ among the three conditions, $F(2, 60) = 0.05, p = .96$. As in Study 1, there was a main effect of presmell testosterone, $F(1, 59) = 231.48, p < .001, p_{\text{rep}} > .99, \eta_p^2 = .80$, such that higher presmell testosterone was associated with higher post-smell testosterone. Consistent with our hypothesis, results also revealed a main effect of T-shirt condition, $F(2, 59) = 3.12, p = .05, p_{\text{rep}} = .88, \eta_p^2 = .10$ (see Fig. 1). Controlling for presmell testosterone, postsmell testosterone was substantially higher in men exposed to the odor of a woman close to ovulation ($M = 9.89, SE = 0.42$) than in men exposed to the odor of a woman far from ovulation ($M = 8.50, SE = 0.39$), $F(1, 59) = 5.85, p = .02, p_{\text{rep}} = .93, \eta_p^2 = .09$, and was (marginally) higher in

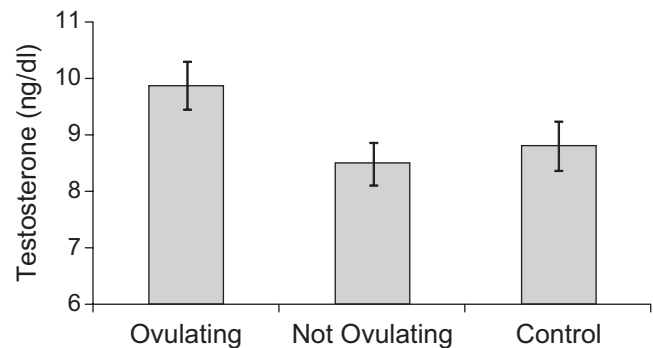


Fig. 1. Results from Study 2: postsmell testosterone levels (controlling for presmell testosterone levels) among men exposed to the odor of a woman close to ovulation, the odor of a woman far from ovulation, or a control odor. Error bars represent standard errors.

men exposed to the odor of a woman close to ovulation than in men who smelled a control T-shirt ($M = 8.81, SE = 0.43$), $F(1, 59) = 3.16, p = .08, p_{\text{rep}} = .84, \eta_p^2 = .05$. An a priori contrast comparing testosterone levels in the ovulation condition with levels in the other two conditions was significant, $F(1, 59) = 5.76, p = .02, p_{\text{rep}} = .93, \eta_p^2 = .09$. There was no difference in postsmell testosterone between participants in the nonovulation and control conditions, $F < 1$.

To examine raw-score change in testosterone, we performed a mixed-model analysis of variance. As in Study 1, there was a main effect of measurement occasion, $F(1, 60) = 37.16, p < .001, p_{\text{rep}} > .99, \eta_p^2 = .38$, such that testosterone decreased from the first to the second sample. However, as in Study 1, this effect was qualified by the predicted (marginally significant) interaction between measurement occasion and condition, $F(2, 60) = 2.76, p = .07, p_{\text{rep}} = .85, \eta_p^2 = .09$. Follow-up contrasts revealed that postsmell testosterone was significantly lower than presmell testosterone for participants in the non-ovulation condition, $F(1, 60) = 25.91, p < .001, p_{\text{rep}} > .99, \eta_p^2 = .30$, and the control condition, $F(1, 60) = 16.01, p < .001, p_{\text{rep}} > .99, \eta_p^2 = .21$. However, there was no difference between presmell and postsmell testosterone for participants in the ovulation condition, $F(1, 60) = 2.57, p = .12, p_{\text{rep}} = .79, \eta_p^2 = .04$ (see Table 1).

To be consistent with recent techniques in the literature designed to more rigorously assess effects of ovulation (Garver-Apgar, Gangestad, & Thornhill, 2008; Puts, 2006), we performed analyses in which we used women's actual menstrual-cycle lengths to more accurately identify their true day of ovulation. Compared with the luteal phase, the length of the follicular phase tends to be more variable and accounts for more of the variance across women in overall cycle length (Fehring, Schneider, & Raviele, 2006). Thus, to be consistent with previous studies, we placed women on a "standard" 28-day cycle by adjusting the follicular phase to take into account each woman's actual cycle length; the luteal phase was held constant at 14 days. That is, if a woman was in the last 14 days of her cycle (the luteal phase), her standardized-cycle day was equal to 28 (the standard cycle length) minus

her actual cycle length plus her actual cycle day (e.g., Day 21 of a 30-day cycle would be calculated as $28 - 30 + 21 =$ standardized-cycle day 19). If a woman was not in the last 14 days of her cycle (i.e., she was in the follicular phase), her standardized-cycle day was calculated as 14 times the quantity of her actual cycle day divided by her actual cycle length minus 14, so that Day 8 of a 30-day cycle would be calculated as $[8/(30 - 14)] * 14 =$ standardized-cycle day 7. (This procedure is described in detail elsewhere; see Garver-Apgar et al., 2008). This enabled us to identify more precisely when (relative to ovulation) the women wore the T-shirts.

We predicted that men's postsmell testosterone would vary as a curvilinear function of women's menstrual cycle (cf. Kuukasjärvi et al., 2004). That is, we expected men to have the highest testosterone levels after smelling a T-shirt worn on the (estimated) day of actual ovulation, and lower testosterone levels as the time (earlier or later) from ovulation increased. To evaluate this prediction, we analyzed data from men in the two conditions in which T-shirts were worn by women (data from the control condition were excluded for this analysis). We regressed men's postsmell testosterone on presmell testosterone, and on linear and quadratic functions of the estimated day on which the woman wore the T-shirt relative to ovulation. As Figure 2 shows, there was a significant quadratic effect, $\beta = -0.18$, $p = .04$, $p_{\text{rep}} = .89$, $r_p^2 = .10$, such that postsmell testosterone was highest when men smelled a T-shirt worn by a woman on her estimated day of ovulation; postsmell testosterone was lower when men smelled a T-shirt worn by a woman earlier or later in her cycle.

Ancillary analyses evaluated men's ratings of odor pleasantness and intensity. Consistent with previous findings (Kuukasjärvi et al., 2004), there was a significant curvilinear effect for odor pleasantness, $\beta = -0.35$, $p = .03$, $p_{\text{rep}} = .91$, $r_p^2 = .11$, such that odor pleasantness ratings were highest when men

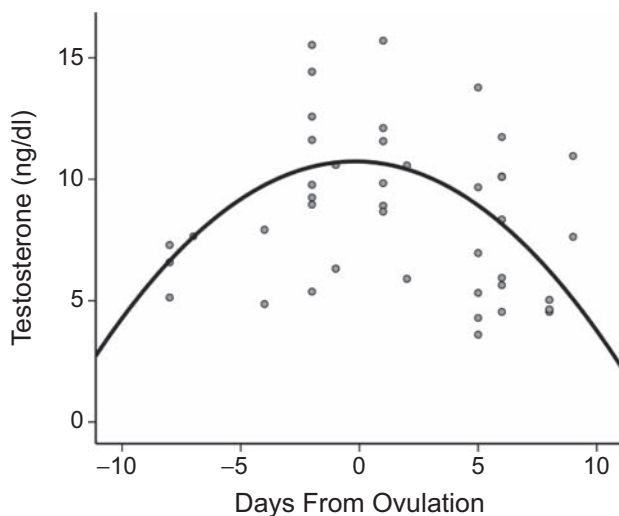


Fig. 2. Results from Study 2: postsmell testosterone levels (controlling for presmell testosterone levels) among men exposed to a woman's odor, as a function of the woman's estimated days from ovulation.

smelled a T-shirt worn by a woman midcycle (around her estimated day of ovulation). No linear or curvilinear effects on ratings of odor intensity were found, $ps > .34$. Additional analyses revealed a marginally significant correlation between postsmell testosterone (controlling for presmell testosterone) and ratings of odor pleasantness, $r = .22$, $p = .09$, $p_{\text{rep}} = .82$, such that higher testosterone was associated with higher ratings of odor pleasantness.

Discussion

Findings from Study 2 provide further evidence that olfactory ovulation cues influence men's testosterone levels. Men exposed to the scent of a woman close to ovulation had higher testosterone levels than both men exposed to the scent of a nonovulating woman and men exposed to a control scent. This suggests that cues to reproductive fertility (rather than lack of fertility) were the primary factor influencing men's endocrinological responses. Indeed, men who smelled a T-shirt worn by a woman on her estimated day of ovulation responded with higher testosterone levels than men who smelled a T-shirt worn by a woman earlier or later in her cycle. Additionally, consistent with previous findings, our results showed that men perceived women's odors to be most pleasant right around the time of ovulation. Furthermore, perceived pleasantness was (marginally) correlated with heightened testosterone levels in men.

General Discussion

The current studies provide evidence that men's testosterone levels are responsive to chemosensory cues indicative of a woman's reproductive fertility. Although previous studies have indicated that men subjectively rate the odors of women close to ovulation as particularly pleasant (Singh & Bronstad, 2001), the present research is the first to provide direct evidence that olfactory cues to female ovulation influence biological responses in men. Findings suggest not only that men are sensitive to chemosensory cues to female ovulation, but also that this sensitivity is manifested in specific endocrinological processes known to promote mating in humans and other species.

In neither study did ovulatory cues increase testosterone in men. Rather, they prevented the decrease in testosterone observed in the control conditions. The general decrease observed in the current studies could reflect the fact that testosterone follows a strong circadian pattern in men, decreasing throughout the day (Dabbs, 1990). Previous studies have documented such a general decrease in testosterone across an experimental session (e.g., Mazur, Susman, & Edelbrock, 1997; Schultheiss, Wirth, & Stanton 2004; Schultheiss et al., 2005). However, other studies have documented a general increase in testosterone over an experimental session (e.g., Carré & McCormick, 2008; Schultheiss, Campbell, & McClelland, 1999). The inconsistencies may result from a number of methodological factors, including whether testosterone is measured via blood or salivary samples, and how and when samples are

obtained from participants; common techniques used to stimulate saliva flow (e.g., chewing gum), for example, can artificially increase testosterone values (Granger, Shirtcliff, Booth, Kivlighan, & Schwartz, 2004). Assuming that methodological factors influencing testosterone change scores apply equally across experimental conditions, comparisons of relative changes in testosterone across conditions can provide a useful picture of stimulus-driven endocrinological effects.

Some studies in rodents and primates have found androgen increases after exposure to female scent cues (e.g., Cerda-Molina et al., 2006). Others have instead documented differences in testosterone levels across conditions (e.g., Ziegler et al., 2005), as we did in the current studies. In humans, some studies have documented increases in testosterone in men interacting with an attractive woman or watching a sexual film (Roney et al., 2007; Stoleru et al., 1993). That no increase was observed in our studies could reflect the fact that scent is likely to be a more subtle stimulus than direct social interaction or watching an erotic film. Nevertheless, cross-condition comparisons in the current studies revealed a clear and replicable pattern in which cues of ovulation led to higher testosterone levels than did control cues.

These findings fit with adaptationist theories of human mating. Across a range of species, males tend to pursue sexual encounters with females during females' periods of peak fertility. The current research provides evidence for a chemosensory signaling mechanism potentially mediating romantic courtship behavior. Although we did not observe increases in testosterone in these studies, the relatively higher testosterone levels arising from exposure to ovulatory scents suggest that those scents might lead men to respond with greater mate-seeking behaviors than they would otherwise. In addition, high testosterone levels are associated with competitiveness, dominance, and risk seeking (Mazur & Booth, 1998; Vermeersch, T'Sjoen, Kaufman, & Vincke, 2007), all traits typically valued by women (Sadalla, Kenrick, & Vershure, 1987), particularly women near their period of peak reproductive fertility (Gangestad, Garver-Apgar, Simpson, & Cousins, 2007; Gangestad, Simpson, Cousins, Garver-Apgar, & Christensen, 2004). The higher testosterone levels observed after exposure to female ovulatory cues could be associated with an increased tendency to display these traits. Additional research is needed to evaluate these possibilities empirically.

Our overarching interest in this research was to identify the immediate physiological consequences of exposure to important reproductive cues. The dependent measures we used therefore captured relatively direct, early-in-the-stream male responses to ovulatory cues. Although a sizable literature indicates that testosterone is linked to mating-related behavior in males, the current study is limited by the fact that we did not examine behavioral responses to olfactory ovulation cues.

There are a number of intervening factors that could influence and interact with initial hormonal responses to shape downstream forms of behavior and social interaction. Men already committed to a long-term relationship, for example,

might down-regulate their responses to other women's olfactory signals (cf. Maner, Gailliot, & Miller, 2009; McIntyre et al., 2006). Among committed men, higher testosterone levels during peak periods of partner fertility could be associated with vigilance to detect potential sexual interlopers (cf. Haselton & Gangestad, 2006), rather than with increased interest in new mates.

In the current studies, men were told that they were being exposed to the scent of a woman; whether this awareness is necessary to produce hormonal responses remains to be determined (cf. Li, Moallem, Paller, & Gottfried, 2007). Indeed, a useful direction for future research will be to evaluate contextual factors that influence behavioral and endocrinological responses to ovulatory cues.

The amount of circulating testosterone, by itself, is not the only factor influencing testosterone's impact on behavior; the number and sensitivity of testosterone receptors also play an important role (Canoine, Fusani, Schlinger, & Hau, 2007). Future studies are needed to examine more closely the extent to which such factors ultimately shape how initial changes in men's endocrinological systems correspond with more downstream forms of behavior and decision making.

The current research provides evidence that ovulatory cues are detectable via chemosensory signaling and, moreover, that these cues are linked with functionally relevant endocrinological responses in men. The capacity for these endocrinological responses to promote mating-related behaviors provides several intriguing directions for future research. At a broader theoretical level, this research illustrates the utility of examining men's and women's reproductive lives through the lens of adaptationist thinking. These studies not only uncovered a previously hidden undercurrent of human mating, but also illustrate the utility of merging evolutionary theories with scientific literatures on animal chemosensory signaling and behavioral neuroendocrinology. This theoretical integration provides a powerful framework for understanding a range of human social processes.

Declaration of Conflicting Interests

The authors declared that they had no conflicts of interests with respect to their authorship and/or the publication of this article.

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