

Original Article

Men Smelling Women: Null Effects of Exposure to Ovulatory Sweat on Men's Testosterone

James R. Roney, Department of Psychological and Brain Sciences, University of California at Santa Barbara, Santa Barbara, CA, USA. Email: roney@psych.ucsb.edu (Corresponding author).

Zachary L. Simmons, Department of Psychological and Brain Sciences, University of California at Santa Barbara, Santa Barbara, CA, USA.

Abstract: Males of many species, humans included, exhibit rapid testosterone increases after exposure to conspecific females. Female chemical stimuli are sufficient to trigger these responses in many nonhuman species, which raises the possibility of similar effects in humans. Recently, Miller and Maner (2010) reported that smelling T-shirts worn by women near ovulation can trigger testosterone responses in men; however, men were aware that they were smelling women's scents, and thus mental imagery associated with that knowledge may have contributed to the hormone responses. Here, we collected axillary sweat samples from women on days near ovulation. In a crossover design, men who were not explicitly aware of the specific stimuli smelled the sweat samples in one session and water samples in a second session. There were no differences in testosterone responses across the experimental conditions. Our null findings suggest that the relevant chemical signal is not found in axillary sweat, and/or that knowledge of the stimulus source is necessary for hormone responses. These results thus suggest boundary conditions for the effects reported in Miller and Maner (2010), and recommend further research to define the precise circumstances under which men's testosterone may respond to chemosensory cues from women.

Keywords: testosterone, chemical communication, ovulation, human mating, evolution, olfaction

Introduction

Males of many vertebrate species exhibit rapid increases in testosterone after non-tactile exposure to potential mates (e.g., Amstislavskaya and Popova, 2004; Bonilla-Jaime, Vazquez-Palacios, Arteaga-Silva, and Retana-Marquez, 2006; Purvis and Haynes, 1974), and recent studies have demonstrated similar hormonal responses in young men after brief

social interactions with young women (Roney, Lukaszewski, and Simmons, 2007; Roney, Mahler, and Maestripieri, 2003; Roney, Simmons, and Lukaszewski, 2010; van der Meij, Buunk, van de Sande, and Salvador, 2008). Chemosensory stimuli such as female urine or vaginal secretions are sufficient to trigger these testosterone increases in many nonhuman species (e.g., Cerda-Molina, et al., 2006; James, Nyby, and Saviolakis, 2006; Macrides, Bartke, Fernandez, and D'Angelo, 1974; Ziegler, Schultz-Darken, Scott, Snowdon, and Ferris, 2005), which at least raises the possibility of similar chemical communication in humans.

Recently, Miller and Maner (2010) reported that testosterone was higher in men who had sniffed T-shirts worn by women on days close to ovulation compared to men who had smelled shirts worn by women during the luteal phase or to men who had smelled unworn shirts. Ovulatory shirts were also judged to smell more pleasant, and pleasantness ratings were marginally correlated with testosterone responses. The male perceivers in these studies were explicitly told that they were smelling shirts worn by women, however, and this knowledge may have led the men to visualize sexual images in response to the more pleasant-smelling odors. In addition, in a subsequent article (Miller and Maner, 2011) reporting additional results from the same studies, the authors revealed that male participants in at least one of the studies were told as part of the cover story that the women wearing the T-shirts were asked to “relive in her mind an emotionally arousing event” (p. 300). Male subjects were asked to rate the degree to which they thought the shirt wearer was feeling angry, happy, scared, or sexually aroused. Men who smelled T-shirts worn by women near ovulation provided higher sexual arousal ratings (perhaps because these shirts also smelled more pleasant). This implies that men in this condition were more likely to have imagined a sexually aroused woman, and such imagery may have contributed to the differences in testosterone responses between the experimental groups. Consistent with such a role for sexual thoughts, research has shown that imagining a sexual encounter can prime testosterone increases in women (Goldey and van Anders, 2011), and mere discussion of sexual topics was associated with increases in luteinizing hormone in men (LaFerla, Anderson, and Schalch, 1978).

The above considerations leave ambiguous the causal role of chemical stimuli in affecting men's testosterone responses. On one model, specialized neural structures containing receptors for specific ovulatory chemicals may trigger neuroendocrine responses upon chemoreception of those chemicals. Alternatively, men may visualize women when they are explicitly told that they are smelling odors from them, and may generate more arousing images when exposed to more pleasant odors; on this account, hormone responses depend on the instructions given to perceivers, and do not necessarily reflect the output of mechanisms designed to produce endocrine reactions to specific chemical stimuli.

Because the present research was completed before publication of the Miller and Maner (2010) paper, it was not specifically designed to test replication of its findings, but nonetheless employed a design that may provide additional evidence regarding men's hormonal responses to chemical cues from women. In this study, we collected axillary sweat samples from women on days near ovulation, and then compared men's testosterone responses after exposure to these samples vs. after exposure to plain water. Importantly, men were not explicitly aware that they were smelling stimuli from women. There are

therefore at least two important differences between this study and the Miller and Maner (2010) study: the use of sweat samples vs. whole T-shirts as stimuli, and the absence of male participants' explicit knowledge that they were smelling stimuli from women. If testosterone responses are found under the conditions of the present study, that outcome would suggest that the effects demonstrated in Miller and Maner (2010) generalize across stimulus collection techniques and likely do not require conscious thoughts about women for their occurrence. Conversely, however, if testosterone responses are not found, that outcome would raise questions regarding the generalizability of these effects across stimulus collection techniques and perceivers' states of knowledge regarding the sources of the chemical stimuli.

Materials and Methods

Participants

Stimulus donors were 10 women from the University of Texas, Austin. Mean age was 19.11 ($SD = 1.27$). Participants were recruited conditional on not using hormonal contraception, absence of prescription or recreational drug use, and self-report of regular menstrual cycles 25-35 days in length. Donors were paid \$25.

Stimulus perceivers were 40 heterosexual men from the University of California, Santa Barbara (UCSB). Mean age was 20.15 ($SD = 2.20$). Participants were recruited conditional on being non-smokers and free from illnesses that could interfere with olfaction. Participation was in exchange for partial course credit. Three men completed only one of the two testing sessions, leaving a final sample size of $n = 37$.

Design and Procedure

The procedures described below were approved by the UCSB and University of Texas Institutional Review Boards, and were in compliance with the Code of Ethical Principles for Medical Research Involving Human Subjects of the World Medical Association (Declaration of Helsinki).

Stimulus Collection

To verify that samples were collected near ovulation, we used a commercially available test of the luteinizing hormone (LH) surge (Clearblue Easy Ovulation Test Kit). Women came to the lab beginning three days before their estimated day of ovulation (based on backward counting from the estimated end of the cycle, with day -15 the estimated day of ovulation) and completed the urine applicator test each day until the LH surge was detected. Positive tests were obtained for all women, and stimulus collection was scheduled for the day after the LH surge. Because the LH surge reliably precedes ovulation by about one day (e.g., Guida et al., 1999; Hoff, Quigley, and Yen, 1983), this procedure ensured that all samples were collected during high fertility days of the cycle.

Women were provided non-deodorant soap for showering on the day of stimulus collection, and were instructed to avoid scented hygiene products and odorous foods beginning the night before and extending through the time of stimulus collection. Upon arrival at the lab, a sterile gauze pad was affixed under each arm with medical tape; donors

then put on a sterile T-shirt supplied by the investigators. The women next took a brisk walk around the psychology building (temperatures ranged from 80 – 100° F; 27 – 38 C) until they had broken a sweat and maintained it for five minutes. Gauze pads were removed and frozen at -80 C until being shipped on dry ice to UCSB, at which time they were again stored at -80 C before being thawed for presentation to the male perceivers (the time from thaw to presentation was about one hour).

Stimulus Presentation

The presentation phase employed a crossover design in which all men were exposed to both the experimental condition (sweat samples) and the control condition (water) in separate sessions that were counterbalanced for order. In the experimental condition, men inhaled from 10 plastic squeeze bottles, each of which contained a gauze pad worn by a separate donor woman; in the control condition, 10 different bottles contained unworn gauze pads to which water had been added. Aside from the difference in gauze pads, all other procedures were identical across the two conditions.

Participants took part in the two sessions at the same time of day spaced approximately one week apart. Up to ten men were tested per session, separated by cubicles. Sessions were administered by a male experimenter who was blind to condition. As part of the informed consent process, participants were told that they might be exposed to a number of odors (e.g., lilac, cucumber, pine), including sweat, in a study designed to investigate the relationship between olfaction and mood. Two baseline saliva samples were collected (via passive drool into polypropylene vials) 15 minutes apart while participants completed demographic surveys and the short version of the Profile of Mood States (POMS-B; McNair, Lorr, and Droppleman, 1992). Participants were then asked to place the nozzle of one of the 10 squeeze bottles close to their nostril and inhale deeply while squeezing the bottle. After repeating this a second time, the odor in the bottle was rated for pleasantness, intensity, familiarity, and liking (1-7 Likert scale). A 90 second break followed, after which the same process was repeated until all 10 bottles had been sampled. Further saliva samples were then collected 15, 30, 45, and 60 minutes after completion of the odor rating task. The POMS was completed immediately after the odor rating task, and again 30 and 60 minutes later. After the final POMS completion, participants provided a free response listing of all scents that they detected in the bottles. Participants played a computerized billiard game as a filler activity between ratings; the game was set to practice mode (participants simply attempted shots on a virtual pool table), such that there was no feedback regarding winning or losing. Debriefing occurred at the end of the second session.

Hormone Assays

Saliva samples were stored at -80 C until being shipped on dry ice to the Biomarkers Core Lab at the Yerkes National Primate Research Center in Atlanta, GA. Testosterone was assayed via RIA in triplicate using procedures described in Roney et al. (2007). Intra- and inter-assay CVs were 7.64% and 6.03%, respectively.

Data Analyses

To measure testosterone responses to the respective stimuli, we computed area under the curve (AUC) with respect to baseline (see Pruessner, Kirschbaum, Meinlschmid, and Hellhammer, 2003). The two testosterone values obtained before the stimulus presentation were averaged ($r = 0.89$) and served as the baseline; the AUC measures the overall magnitude of change relative to this baseline across the four post-stimulus saliva samples. The AUC values were analyzed using linear mixed regression models in SPSS v19. The independent variables were experimental condition (sweat vs. water), session (first or second), and sequence (sweat first or water first); the latter two variables are necessary to obtain unbiased estimates of the within-subject effect of condition in a crossover design given the possibility of session and carry-over effects (see Jones and Kenward, 2003). Given that hormone reactivity often depends on baseline values, baseline testosterone was added as a covariate to the regression models. Mood effects (assessed as AUC with respect to baseline for composite “mood disturbance” (see McNair et al., 1992) from the POMS) and odor ratings were also analyzed with mixed regression models.

Results

Table 1 presents results of the mixed regression model predicting testosterone AUC responses. There was no within-subject effect of exposure to sweat vs. water ($p = 0.35$). Higher baseline testosterone was associated with smaller post-stimulus changes in testosterone, as expected; the null result for experimental condition was nonetheless robust to removal of this covariate ($p = 0.28$). Given the absence of session and sequence effects (see Table 1), a paired t -test comparing AUC in response to water and sweat will approximate the effect of condition and perhaps be more intuitive to some readers. This test also yielded a null result, $t(36) = 1.10$, $p = 0.28$. The power of a paired t -test is approximately 90% to detect a moderate effect size ($d \approx 0.50$) given our sample size. A random effect for the subject-level intercept was also included in the model, since there was significant variance in intercepts between participants (Wald $Z = 1.97$, $p = 0.049$); however, no statistical conclusions were changed by omission of this effect and parameter estimates were virtually identical with or without this term in the model.

Table 1. Linear mixed regression model predicting testosterone response (AUC)

Variable	Parameter Estimate	Standard Error	t -value	Effect Size (r)	p -value
Intercept	-0.08	0.22	-0.35	0.04	0.73
Condition	0.17	0.18	0.96	0.17	0.35
Session	-0.06	0.18	-0.32	0.06	0.75
Sequence	0.35	0.28	1.27	0.23	0.21
Baseline T	-0.40	0.12	-3.29	0.40	0.002

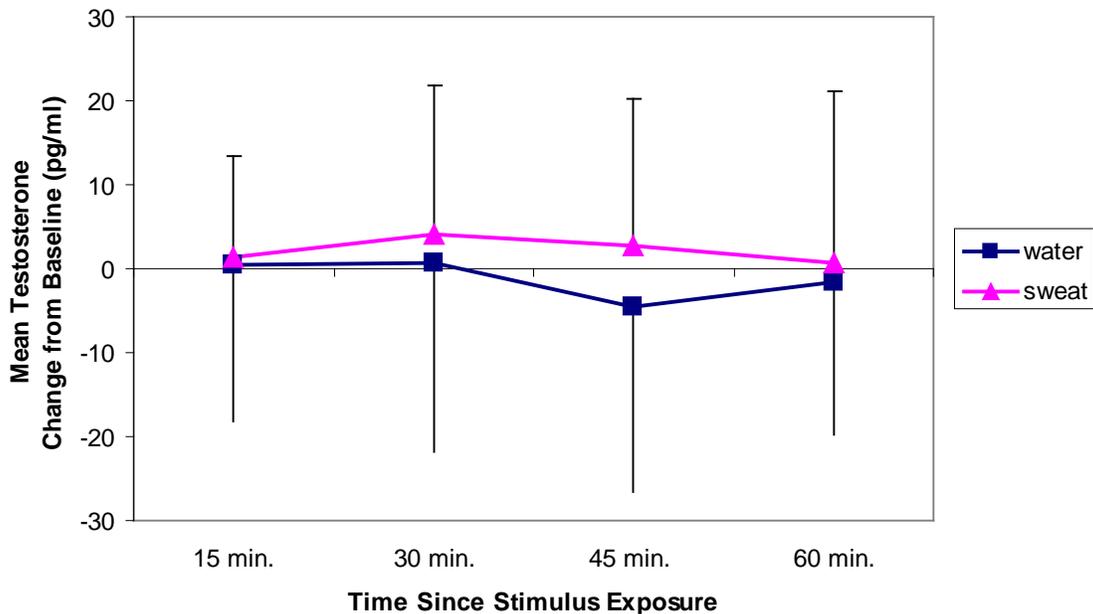
Note: T = testosterone. AUC and baseline T were standardized, making parameter estimates interpretable in SD units. Condition is coded water = 0 and sweat = 1.

Figure 1 presents the average testosterone change from baseline across the two

conditions for each post-stimulus time of saliva collection. The pattern was in the direction of more positive change in testosterone after exposure to ovulatory sweat samples, but the differences between conditions were small relative to the standard deviations. Miller and Maner (2010) measured testosterone responses 15 minutes after odor exposure; we constructed a linear mixed model predicting testosterone change from baseline at post-15 minutes, with the same predictor variables as in Table 1. As expected from Figure 1, there was no effect of experimental condition ($p = 0.97$).

Mean odor ratings in each session were computed for each subject; because mean pleasantness and liking ratings were highly correlated ($r = 0.90$), we combined them into a composite attractiveness rating. Ratings were standardized relative to the grand mean to allow for interpretation of parameter estimates in standard deviation units. Linear mixed models controlling for sequence and session revealed no effect of condition on attractiveness ratings ($b = 0.08, p = 0.68$), greater intensity ratings for sweat vs. water ($b = 0.29, p = 0.04$), and greater familiarity ratings for sweat vs. water ($b = 0.32, p = 0.04$). A linear mixed model revealed no effect of experimental condition on standardized AUC for “total mood disturbance” as measured by the POMS ($b = -0.08, p = 0.59$).

Figure 1. Mean change from baseline (pg/ml) for salivary testosterone after exposure to sweat samples or water



Note: Error bars are +1 SD for the sweat condition and -1 SD for the water condition.

Participants’ lists of detected odors were coded yes/no for any references to human stimuli (e.g., sweat, body odor). These references occurred in 35 and 51 percent of the sessions in which participants had smelled water and sweat, respectively; a binary mixed logistic regression model revealed that the within-subject effect of experimental condition on the likelihood of having guessed exposure to human stimuli was not statistically significant ($b = 0.77; p = 0.15; \text{Exp}(b) = 2.15$), despite the pattern of greater detection in

the sweat condition. In addition, the free response listings contained references to nonhuman odors (e.g., fruits, pine, mint, rubber, alcohol) more often than to human odors – these references occurred in 54 and 68 percent of the control and experimental sessions, respectively – and in 81 percent of the cases in which a human odor was listed, at least one other odor was also recorded. As such, the participants generally appeared to be in a state of uncertainty regarding the nature of the stimuli. Whether subjects reported having detected human odors had no effect on testosterone AUC responses, whether tested as a main effect or an interaction with experimental condition in mixed regression analyses ($p > 0.15$).

Although participants did not differentially detect human stimuli across the two conditions, there was evidence that they were more likely to detect odors in general in the sweat condition: participants reported having smelled nothing in 41 percent of the control sessions but in only 22 percent of the experimental sessions; a binary mixed logistic regression model revealed a marginally significant, within-subject effect of experimental condition on the likelihood of having reported detection of any scent ($b = 1.13$, $p = 0.067$, $\text{Exp}(b) = 3.10$). Exclusion of the cases in which men detected no odors in the sweat condition did not reverse the null effect of experimental condition on testosterone responses ($p = 0.32$), nor did general odor detection predict testosterone AUC responses either as a main effect or as an interaction with condition ($p > 0.75$). In sum, participants tended to detect more odors in the sweat condition, but were uncertain regarding the precise identity of those odors; in addition, testosterone responses were not moderated by whether men reported detection of human or other odors.

Finally, as part of the background surveys completed during collection of the baseline saliva samples, participants indicated when they had last exercised. Miller and Maner (2010) instructed men not to exercise for at least 12 hours before taking part in their study. Controlling for time since last exercise in the present study did not reverse the null effect of experimental condition on testosterone responses ($b = 0.23$, $p = 0.20$); likewise, exclusion of the 14 men who indicated last exercise less than 12 hours ago had no effect on the parameter estimate for experimental group ($b = 0.19$, $p = 0.40$; compare Table 1).

Discussion

Unlike Miller and Maner (2010), we did not find more positive testosterone responses in men after exposure to ovulatory chemical stimuli than after exposure to control stimuli. Importantly, our study was not an exact replication of the Miller and Maner (2010) study, and so should not be construed as a direct replication failure. Nonetheless, the discrepancy in findings raises important issues regarding which differences in methods may have led to the distinct outcomes.

We note first a number of strengths of our study design that, if anything, should have improved the chances of positive findings. We confirmed the timing of ovulation via LH tests, for instance, collected a larger number of baseline and post-test saliva samples, and employed a more statistically powerful crossover design in which the same men took part in all experimental conditions. Our use of gauze pads that were frozen and then thawed is unlikely to explain discrepancies between the studies, both because experiments have

shown that this process does not affect reactions to human axillary stimuli (Lenochova, Roberts, and Havlicek, 2009) and because Miller and Maner (2010) also froze their stimuli. In addition, higher ratings of intensity and familiarity in the sweat condition support successful chemoreception of the axillary stimuli. As such, low power, mis-estimations of ovulatory timing, or failures of chemoreception are all unlikely explanations for our failure to detect significant effects.

One clear difference between the study designs was our use of axillary sweat collected on gauze pads as stimuli, as opposed to the use of worn T-shirts as stimuli in Miller and Maner (2010). In principle, a chemical signal of ovulatory timing could be absent from axillary secretions but present elsewhere on the skin; arguing against this, however, are findings that axillary secretions collected near ovulation are rated more pleasant and sexy than such secretions collected at other times in the menstrual cycle (Gildersleeve, Haselton, Larson, and Pillsworth, 2012; Havlicek, Dvorakova, Bartos, and Flegr, 2006). Nonetheless, even in the studies that have collected axillary secretions, participants have worn gauze pads under their arms for longer periods of time than in the present study, and without active stimulation of sweating; as such, we cannot rule out the possibility that the use of axillary sweat as stimuli may have removed or attenuated the crucial cues necessary for elicitation of testosterone responses. If our use of axillary samples instead of T-shirts was in fact the cause of our null findings, this would at the very least raise questions as to whether the effects demonstrated in Miller and Maner (2010) are robust across alternative methods of stimulus collection and presentation.

A second difference between the studies concerns the male participants' knowledge of the stimulus source. As explained in the Introduction, male participants in Miller and Maner (2010) were explicitly told that they were smelling shirts worn by women, and this knowledge may have triggered mental images that contributed to the observed hormonal responses. In the present study, men appeared to be in a state of uncertainty regarding the identity of the odor stimuli: men were not significantly more likely to report detection of human odors in the experimental as opposed to the control condition, and participants generally reported detection of nonhuman odors more often than detection of human odors. Even in cases in which men reported detecting sweat or body odor, there was never any reference to women's scents in particular, such that there is little reason to think that the male participants were visualizing women. Differential likelihood of having visualized women thus stands as another possible explanation for the discrepant findings between the two studies: perhaps chemoreception of ovulatory cues is by itself insufficient to trigger a neuroendocrine response in human males, which may instead require additional stimuli, such as visual images triggered by knowledge of the stimulus source. The need for additional, contextual cues for elicitation of responses to chemical stimuli has precedent in research on humans, as women's physiological and mood responses to putative human chemosignals have been shown to be dependent on sex of the experimenter (Jacob, Hayreh, and McClintock, 2001). The requirement of additional inputs beyond chemoreception itself does not refute the possible information content of chemical stimuli, of course, but does suggest possible differences from some nonhuman species in which testosterone appears to respond to chemoreception alone (see below).

The possible absence of a direct neuroendocrine response to chemoreception of

ovulatory cues is consistent with specific aspects of human neuroanatomy. In many nonhuman species, males' testosterone responds to female chemical stimuli in isolation (e.g., Macrides et al., 1974; Pfeiffer and Johnston, 1994). In rodents, ablation of a structure called the vomeronasal organ (VNO) has been shown to eliminate male hormonal responses to female urine or vaginal secretions but not to interactions with actual females (Coquelin, Clancy, Macrides, Noble, and Gorski, 1984; Pfeiffer and Johnston, 1994); as such, the VNO appears to mediate direct neuroendocrine responses to chemoreception of cues from females. Importantly, evidence suggests that the human homologue of the VNO is vestigial and without functional connections (e.g., Bhatnagar and Smith, 2010; Frasnelli, Lundstrom, Boyle, Katsarkas, and Jones-Gotman, 2011). If so, then human males could be expected to respond like VNO-lesioned nonhuman males: with an absence of hormonal responses to female chemical stimuli presented in isolation, despite reactive hormone increases after interactions with actual females. Results from the present study combined with previous research on men's testosterone responses to social interactions with women (Roney et al., 2003, 2007, 2010; van der Meij et al., 2008) are consistent with this pattern. The argument that the effects reported in Miller and Maner (2010) may require more than just chemoreception of female stimuli, then, is bolstered by evidence that the specific neural structure mediating direct effects of chemoreception in nonhuman species appears to be non-functional in humans.

In conclusion, we found no evidence that exposure to women's ovulatory, axillary sweat could trigger reactive testosterone increases in men who were uncertain of the source of the stimuli. These results raise questions regarding the generalizability of the effects reported in Miller and Maner (2010) across stimulus collection methods and perceiver states of knowledge. Importantly, a direct effect of chemoreception in the absence of conscious knowledge of the stimulus source has yet to be demonstrated in humans. An ideal future study could experimentally manipulate perceivers' knowledge of the stimulus source in a design that employs the stimulus collection methods used in Miller and Maner (2010). Given financial constraints, we are unlikely to complete such a study in the near future, but we encourage others to do so.

Acknowledgements: This research was supported by a UCSB Academic Senate Grant to James Roney. Sponsors were in no way involved in any aspect of study design, analysis, or publication. We thank Kristina Durante for collection of the sweat samples, and are grateful to Inverness Medical Innovations, Inc. (now Alere, Inc.) for their generous donation of the Clearblue® Easy Ovulation Test Kits to Dr. Durante.

Received 31 July 2012; Revision submitted 10 September 2012; Accepted 11 September 2012

References

Amstislavskaya, T. G., and Popova, N. K. (2004). Female-induced sexual arousal in male mice and rats: Behavioral and testosterone response. *Hormones and Behavior*, *46*, 544-550.

- Bhatnagar, K. P., and Smith, T. D. (2010). The human vomeronasal organ: Part VI: A nonchemosensory vestige in the context of major variations of the mammalian vomeronasal organ. *Current Neurobiology*, *1*, 1-9.
- Bonilla-Jaime, H., Vazquez-Palacios, M., Arteaga-Silva, M., and Retana-Marquez, S. (2006). Hormonal responses to different sexually related conditions in male rats. *Hormones and Behavior*, *49*, 376-382.
- Cerda-Molina, A. L., Hernandez-Lopez, L., Chavira, R., Cardenas, M., Paez-Ponce, D., Cervantes-De la Luz, H., et al. (2006). Endocrine changes in stump-tailed macaques (*Macaca arctoides*) as a response to odor stimulation with vaginal secretions. *Hormones and Behavior*, *49*, 81-87.
- Coquelin, A., Clancy, A. N., Macrides, F., Noble, E. P., and Gorski, R. A. (1984). Pheromonally induced release of luteinizing hormone in male mice: Involvement of the vomeronasal system. *The Journal of Neuroscience*, *4*, 2230-2236.
- Frasnelli, J., Lundstrom, J. N., Boyle, J. A., Katsarkas, A., and Jones-Gotman, M. (2011). The vomeronasal organ is not involved in the perception of endogenous odors. *Human Brain Mapping*, *32*, 450-460.
- Gildersleeve, K. A., Haselton, M. G., Larson, C. M., and Pillsworth, E. G. (2012). Body odor attractiveness as a cue of impending ovulation in women: Evidence from a study using hormone-confirmed ovulation. *Hormones and Behavior*, *61*, 157-166.
- Goldey, K. L., and van Anders, S. M. (2011). Sexy thoughts: Effects of sexual cognitions on testosterone, cortisol, and arousal in women. *Hormones and Behavior*, *59*, 754-764.
- Guida, M., Tommaselli, G. A., Palomba, S., Pellicano, M., Moccia, G., Di Carlo, C., and Nappi, C. (1999). Efficacy of methods for determining ovulation in a natural family planning program. *Fertility and Sterility*, *72*, 900-904.
- Havlicek, J., Dvorakova, R., Bartos, L., and Flegr, J. (2006). Non-advertised does not mean non-concealed: Body odour changes across the human menstrual cycle. *Ethology*, *112*, 81-90.
- Hoff, J. D., Quigley, M. E., and Yen, S. S. C. (1983). Hormonal dynamics at mid-cycle: A reevaluation. *Journal of Clinical Endocrinology and Metabolism*, *57*, 792-796.
- Jacob, S., Hayreh, D. J. S., and McClintock, M. K. (2001). Context-dependent effects of steroid chemosignals on human physiology and mood. *Physiology & Behavior*, *74*, 15-27.
- James, P. J., Nyby, J. G., and Saviolakis, G. A. (2006). Sexually stimulated testosterone release in male mice (*Mus musculus*): Roles of genotype and sexual arousal. *Hormones and Behavior*, *50*, 424-431.
- Jones, B., and Kenward, M. G. (2003). *Design and analysis of cross-over trials*. Boca Raton, FL: Chapman & Hall/CRC.
- LaFerla, J. J., Anderson, D. L., and Schalch, D. S. (1978). Psychoendocrine response to sexual arousal in human males. *Psychosomatic Medicine*, *40*, 166-172.
- Lenochova, P., Roberts, S. C., and Havlicek, J. (2009). Methods of human body odor sampling: The effect of freezing. *Chemical Senses*, *34*, 127-138.
- Macrides, F., Bartke, A., Fernandez, F., and D'Angelo, W. (1974). Effects of exposure to vaginal odor and receptive females on plasma testosterone in the male hamster.

Neuroendocrinology, 15, 355-364.

- McNair, D. M., Loor, M., and Droppleman, L. F. (1992). *Manual for the profile of mood states*. San Diego, CA: Educational and Industrial Testing Service.
- Miller, S. L., and Maner, J. K. (2010). Scent of a woman: Testosterone responses to olfactory ovulation cues. *Psychological Science*, 21, 276-283.
- Miller, S. L., and Maner, J. K. (2011). Ovulation as a male mating prime: Subtle signs of women's fertility influence men's mating cognition and behavior. *Journal of Personality and Social Psychology*, 100, 295-308.
- Pfeiffer, C. A., and Johnston, R. E. (1994). Hormonal and behavioral responses of male hamsters to females and female odors: Roles of olfaction, the vomeronasal system, and sexual experience. *Physiology & Behavior*, 55, 129-138.
- Pruessner, J. C., Kirschbaum, C., Meinlschmid, G., and Hellhammer, D. H. (2003). Two formulas for computation of area under the curve represent measures of total hormone concentration versus time-dependent change. *Psychoneuroendocrinology*, 28, 916-931.
- Purvis, K., and Haynes, N. B. (1974). Short-term effects of copulation, human chorionic gonadotropin injection and non-tactile association with a female on testosterone levels in the male rat. *Journal of Endocrinology*, 60, 429-439.
- Roney, J. R., Lukaszewski, A. W., and Simmons, Z. L. (2007). Rapid endocrine responses of young men to social interactions with young women. *Hormones and Behavior*, 52, 326-333.
- Roney, J. R., Mahler, S. V., and Maestripieri, D. (2003). Behavioral and hormonal responses of men to brief interactions with women. *Evolution and Human Behavior*, 24, 365-375.
- Roney, J. R., Simmons, Z. L., and Lukaszewski, A. W. (2010). Androgen receptor gene sequence and basal cortisol concentrations predict men's hormonal responses to potential mates. *Proceedings of the Royal Society of London: Biological Sciences*, 277, 57-63.
- van der Meij, L., Buunk, A. P., van de Sande, J. P., and Salvador, A. (2008). The presence of a woman increases testosterone in aggressive dominant men. *Hormones and Behavior*, 54, 640-644.
- Ziegler, T. E., Schultz-Darken, N. J., Scott, J. J., Snowdon, C. T., and Ferris, C. F. (2005). Neuroendocrine response to female ovulatory odors depends upon social condition in male marmosets, *Callithrix jacchus*. *Hormones and Behavior*, 47, 56-64.