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Current Opinion in Psychology

Human ovulation cues

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In most mammals, cues of impending ovulation — including changes in appearance and sexual behavior — mark the fertile phase within the ovulatory cycle. Such cues were long thought to have been completely concealed in humans. However, research over the past two decades has overturned this assumption, revealing subtle but detectable cues of ovulation to which observers respond both behaviorally and hormonally. We review research in this area over the last several years. Cues of ovulation in human females include attractive changes in scent, voice, and appearance. Women also appear to be more receptive and solicitous toward sexually attractive prospective mates when fertile within the cycle. We discuss reasons why human ovulation cues are subtle and outline questions for future research.

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Current Opinion in Psychology 2016, **7**:120–125

This review comes from a themed issue on **Evolutionary psychology**

Edited by **Steven W Gangestad** and **Joshua M Tybur**

For a complete overview see the Issue and the Editorial

Available online 29th August 2015

http://dx.doi.org/10.1016/j.copsyc.2015.08.020

Introduction

Male attraction to cues of ovulation

Fertility — the probability of conceiving from sex — varies across the mammalian ovulatory cycle, peaking just before ovulation and falling to zero immediately afterwards (see Figure 1). Ovulation is triggered by dramatic changes in hormones, with wide-ranging effects on female physiology and, possibly, their social interactions.

If there are outward signs of ovulation, males who find them attractive will have a reproductive advantage over males who do not. So, have males evolved to detect ovulation? Across diverse species, female scents, behaviors, and appearance become more attractive to males approaching ovulation [1]. For example, in chimpanzees and baboons, fertile females exhibit sexual swellings — marked increases in the volume and redness of their perineal skin — that are attractive to males. Female orangutans and gorillas instead exhibit subtle cues of ovulation [2]. Female gorillas, for example, have subtle labial swellings just before ovulation [3]. In addition, across diverse species, changes in scents mark fertility, and some males can even discern fertile from non-fertile cycles on the basis of scent (see review in [4]). In sum, ovulation cues are common among mammals, including our closest primate relatives, but vary in magnitude and mode of expression.

Assumption of concealed ovulation in humans

Scientists have long claimed that human sexuality was 'emancipated' from hormonal control during evolution [2,5]. However, new evidence indicates that human sexuality is influenced by the ovulatory cycle in nuanced ways [6,7••]. Here, we focus on key findings challenging the view that human ovulation is *completely concealed*. We also discuss reasons why ovulation cues exist and are so subtle that scientists almost missed them entirely.

Typical methods

Studies in this area typically involve within-woman comparisons of high-fertility and low-fertility scents, photos, vocal recordings, and other stimuli. Women who use hormonal contraceptives, which disrupt the cycle, are excluded. It remains common to estimate women's fertility by counting from their menstrual onset, but the most rigorous studies use hormonal measures.

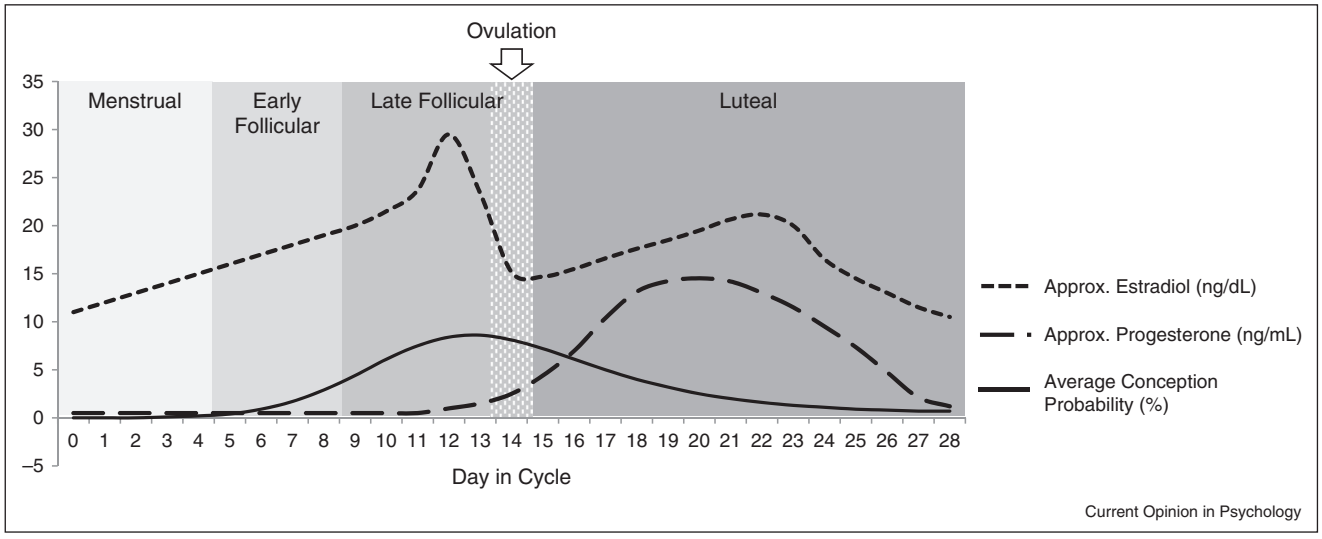
Evidence of human ovulation cues

Other-rated attractiveness

Evidence across a large variety of species indicates that female scents become more attractive approaching ovulation (see [8•]). Likewise, studies have found that women's natural body scents collected at high fertility (confirmed by luteinizing hormone tests) are rated by men as more attractive and less intense than samples collected at low fertility [8•]. Two recent replications showed the same pattern when *women* rated women's scent samples ([9]; Gildersleeve et al., unpublished data).

Women's facial and vocal attractiveness might also increase as they approach ovulation. In a particularly rigorous study, 202 women provided photos, audio recordings, and saliva samples twice within the cycle [10••]. Women's faces were rated as less attractive when their progesterone was high, consistent with them being

Figure 1



Conception probability (fertility, probability of conceiving from an act of sexual intercourse), estradiol (ng/dL), and progesterone (ng/mL) values across the phases of the human ovulatory cycle. Average conception probability estimates are from Wilcox *et al*. (2001). Approximate hormone values are based on values reported in Garver-Apgar *et al*. (2008) but have been smoothed for ease of presentation.

at low fertility. In contrast, women's voices were rated as more attractive when their progesterone was low and estradiol was high, consistent with them being at high fertility (also see [11]).

Behavioral changes

In many mammalian species, females become more *receptive* to sexual advances by favored males or even actively *solicitous* when fertile [2,12]. For example, only when fertile do female rats traverse electrified grids to access males (e.g., [13]). Are women more receptive or solicitous when fertile?

In two French studies, women approached by an attractive male confederate at high fertility were more likely to consent to a dance at a nightclub [14] and to a request for their phone number [15]. Likewise, women interacting with charismatic male confederates flirted more when fertile [16•].

Women might also engage in behaviors that help them distance themselves from *undesired* partners or individuals who might attempt to influence constrain their mating decisions at high fertility. A study of women's cell phone records found that women decreased their calls to their fathers, but not to their mothers, when fertile [17].

Women might also engage in attractiveness-enhancing behaviors when fertile. In one study, women were videotaped dancing to pop music twice within their cycle. Men rated women's dance as more attractive at high fertility than at low fertility [18]. In addition, several studies have shown that women wear more attractive clothing [19] and red and pink, specifically, at high fertility [20,21]. One 35-day study also found that women increased their grooming and styling efforts on fertile days of the cycle [22].

Social and hormonal responses in others to women's ovulation cues

Women report that their partners are more jealous at high relative to low fertility [23,24], suggesting that men might detect changes in their partners across the cycle (e.g., [23–25]).

Also, a recent study examined men's testosterone responses to 'rivals' across their partner's cycle [26••]. Couples completed two sessions, first involving a close interaction to expose the male partner to possible cues of his partner's fertility. Male partners then viewed profiles of men portrayed as competitive or as non-competitive, whom they were told their partner would rate for attractiveness. Men's post-test testosterone was higher at high than at low fertility only if they viewed competitive 'rivals.'

In another study, women collected underarm and vulvar scents at high fertility and low fertility [27•]. Men reported their interest in sex and provided saliva samples before and after smelling a high-fertility or low-fertility scent sample. Men exposed to high-fertility scents exhibited increased sexual interest and testosterone thereafter. Men exposed to low-fertility scents exhibited no change in sexual interest and decreased testosterone.

A recent study suggests that *women* also respond hormonally to fertile body scents [9]. Women who smelled