**Human Ovulation Cues**

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**Highlights**

* Recent research reveals cues of ovulation in women that observers can detect.
* These include attractive changes in women’s scents, voices, and appearance.
* Observers respond to human ovulation cues behaviorally and hormonally.
* Nonetheless, it is likely that women have evolved to suppress ovulation cues.
* We outline research questions that will help to address lingering mysteries.

**Abstract**

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 towards sexually attractive prospective mates when fertile within the cycle. We discuss reasons why human ovulation cues are subtle and outline questions for future research.

**Human Ovulation Cues**

**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](#_ENREF_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](#_ENREF_2)]. Female gorillas, for example, have subtle labial swellings just before ovulation[[3](#_ENREF_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](#_ENREF_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](#_ENREF_2),[5](#_ENREF_5)]. However, new evidence indicates that human sexuality is influenced by the ovulatory cycle in nuanced ways [[6](#_ENREF_6),[7](#_ENREF_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- 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](#_ENREF_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](#_ENREF_8)]. Two recent replications showed the same pattern when *women* rated women’s scent samples ([[9](#_ENREF_9)]; Gildersleeve, Fales, & Haselton, 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](#_ENREF_10)]. Women’s faces were rated as less attractive when their progesterone was high, consistent with them being 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](#_ENREF_11)]).

*Behavioral changes*

In many mammalian species, females become more *receptive* to sexual advances by favored males or even actively *solicitous* when fertile [[2](#_ENREF_2),[12](#_ENREF_12)]. For example, only when fertile do female rats traverse electrified grids to access males (e.g., [[13](#_ENREF_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 [[14](#_ENREF_14)] and to a request for their phone number [[15](#_ENREF_15)]. Likewise, women interacting with charismatic male confederates flirted more when fertile [[16](#_ENREF_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](#_ENREF_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](#_ENREF_18)]. In addition, several studies have shown that women wear more attractive clothing [[19](#_ENREF_19)] and red and pink, specifically, at high fertility [[20](#_ENREF_20),[21](#_ENREF_21)]. One 35-day study also found that women increased their grooming and styling efforts on fertile days of the cycle [[22](#_ENREF_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](#_ENREF_23),[24](#_ENREF_24)], suggesting that men might detect changes in their partners across the cycle (e.g., [[23-25](#_ENREF_23)]).

 Also, a recent study examined men’s testosterone responses to “rivals” across their partner’s cycle [[26](#_ENREF_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](#_ENREF_27)]. Men reported their interest in sex and provided saliva samples before and after smelling a high- 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](#_ENREF_9)]. Women who smelled women’s high-fertility T-shirts displayed higher post-test testosterone than did women who smelled low-fertility T-shirts (marginally significant). This pattern reached significance among women who themselves displayed estrogen and progesterone profiles, consistent with being in the fertile phase of the cycle.

 Notably, studies examining changes in women’s [[28](#_ENREF_28)] and men’s testosterone [[29](#_ENREF_29)] have often included small numbers of scent samples (from 10 women at most [[28](#_ENREF_28),[30](#_ENREF_30)]), which could vary in attractiveness and other characteristics by chance alone. These studies also have not treated female scent donors as the unit of statistical analysis, thus prohibiting inferences about whether other high- and low-fertility samples would have similar social and hormonal effects (discussed in [[7](#_ENREF_7)]).

*Ovulation cues: Effect sizes and robustness*

In sum, many findings are consistent with the existence of detectable ovulation cues. Effect sizes have typically ranged from small to medium, though these estimates could be conservative given error in measuring women’s fertility within the cycle [[31](#_ENREF_31),[32](#_ENREF_32)]. (Here, we report effect sizes in Hedges’s *g*, which is interpreted identically to Cohen’s *d* but is less biased[[33](#_ENREF_33)].) For example, the high-fertility increase in women’s flirtation with a charismatic confederate is about a third of a standard deviation (0.31 [[16](#_ENREF_16)]). The increase in women’s scent attractiveness is about half of a standard deviation (*g* = .55 [[34](#_ENREF_34)]). The increase in men’s testosterone in response to fertile scents is apparently larger, at just under half of a standard deviation to two standard deviations (*g* = .42 to 2.04 [[27](#_ENREF_27)]).

However, there are some notable non-replications of key findings (e.g., in men’s testosterone in response to fertile body scents [[35](#_ENREF_35)]). A meta-analysis including these non-replications and additional unpublished data indicates that overall effects are nonetheless statistically robust [[36](#_ENREF_36)]. Thus, ovulation cues are likely subtler in humans than in many other mammals but probably still have meaningful social consequences.

**Why do Human Ovulation Cues Exist?**

 What evolved function, if any, have ovulation cues historically served for women? One possibility is that evolutionary forces favored ovulation cues in women to *signal* their fertility to men, thus promoting mating and conception. This seems unlikely, however, given high levels of sexual interest among men (see [[37](#_ENREF_37)] for an extended discussion).

We think the *opposite* is more plausible (see Box 1). Evolution might have favored the concealment of ovulation to reduce unwanted male sexual advances or aggression from other females, while encouraging current mates to invest throughout the cycle. Along these lines, the *leaky cues hypothesis* proposes that cues of ovulation are incidental byproducts of physiological changes that trigger ovulation [[37](#_ENREF_37),[38](#_ENREF_38)], which women’s bodies cannot fully conceal without compromising fertility. Once ovulation cues—however subtle—are “leaked” from the system, evolution can favor a male ability to detect them.

Another possibility is that women have evolved to signal their overall reproductive quality in order to attract desirable long-term mates [[39](#_ENREF_39)]. Estradiol levels could indicate overall reproductive quality and also vary across the cycle, peaking just prior to ovulation. Therefore, any estradiol-dependent signals of overall reproductive quality will incidentally increase at high fertility. Thus, cues of ovulation are still “leaked” but within the context of constant signaling of overall reproductive quality.

Notably, these explanations best account for shifts in women’s *physical* attractiveness (e.g., scent). Shifts in women’s receptivity and solicitousness might instead reflect shifts in women’s mating motivations (see [[7](#_ENREF_7),[40](#_ENREF_40)]).

**Conclusion**

 The studies we have reviewed overturn the conventional wisdom that human sexuality is vastly different from that of other mammals. Women also appear to experience high-fertility increases in their attractiveness, receptiveness, and solicitousness, though these changes have likely been modified during human evolution [[37](#_ENREF_37)]. We encourage theoretical and empirical work to better understand the evolutionary origins—and possible social consequences—of these cycle shifts (see Table 1). Such work will refine and add nuance to our understanding of human sexuality, relationship dynamics, and aspects of human evolution that unite and differentiate us from other species.

**Box 1 -- Why are Human Ovulation Cues Subtle?**

Human ovulation cues appear to be present but subtle. For example, scent cues of ovulation in humans, though they appear to exist, are not likely to be discernable by males across vast distances, as they are in other primate species [[37](#_ENREF_37)]. This raises the question, *why*?

 *Increasing paternal investment*

Concealing clear cues of ovulation might have facilitated the evolution of human pair bonding and biparental childrearing. If female ovulation is non-obvious, male partners must be near their partner throughout the cycle to be certain of their genetic relation to their children [[5](#_ENREF_5),[41](#_ENREF_41)]. In turn, increased paternity certainty increases the benefits to men of investing in their partner and children, further reinforcing pair bonding. Related to this idea, the *extended sexuality hypothesis* proposes that women have evolved to have sex throughout the cycle (rather than in the fertile window alone) in order to promote paternal investment [[42](#_ENREF_42)].

Relatedly, if ovulation were obvious, socially dominant males could have attempted to monopolize mating opportunities with fertile females. However, non-dominant males might offer benefits to women, such as investment in their children. Therefore, the concealment of cues of ovulation might have enabled women to pursue non-dominant males[[43](#_ENREF_43)]. In turn, increased male investment could help to explain a variety of notable human features, such as heavily dependent young, short inter-birth intervals, and large family sizes (reviewed in [[44](#_ENREF_44)]).

*Preserving female choice*

Current male partners cannot mate guard constantly and therefore may benefit by guarding their female partner primarily during her fertile period (when a failure to do so could result in her conceiving with another male). Thus, the concealment of cues of ovulation might have enhanced females’ freedom to choose the *genetic* fathers of their offspring [[37](#_ENREF_37),[38](#_ENREF_38)]. For example, some human females might historically have reproductively benefitted by pursuing a “mixed” mating strategy, securing investment from long-term partners but acquiring genetic benefits from surreptitious sexual affairs with other men at high fertility [[7](#_ENREF_7),[37](#_ENREF_37)].

*Avoiding aggression from other females*

Lastly, concealing ovulation cues might have helped women avoid aggression from other women. A recent study of chacma baboonsdemonstrated that females were most likely to become the target of female-female aggression—which can be deadly—when displaying sexual swellings and receiving attention from a male [[45](#_ENREF_45)]. In humans, women rate other women’s high-fertility body odors as more attractive than their low-fertility odors ([[9](#_ENREF_9)]; Gildersleeve et al., unpublished data) and appear to experience increased testosterone in response to fertile body odors [[28](#_ENREF_28)], though perhaps only when fertile themselves [[9](#_ENREF_9)]. This could facilitate aggression, though evidence to date is inconclusive [[9](#_ENREF_9)]. Moreover, aggression against fertile females might be most pronounced in species exhibiting clear visual fertility cues (e.g., swellings).

**Table 1: Future Research Directions**

|  |  |
| --- | --- |
| **Unresolved Issues** | **Suggestion for Future Work** |
| *Methods.* (1) Studies of subtle ovulation cues require sufficient power. (2) Research designs that imprecisely estimate fertility within the cycle cannot speak to the true magnitude of ovulation cues (see [[32](#_ENREF_32)]); (3) methods have been highly variable, prompting criticism that flexibility in analytic procedures has increased the false positive rate (see [[46](#_ENREF_46)]).  | (1 & 2) Conduct within-women studies to detect subtle cycle shifts. Ideally, include hormonal confirmation (e.g., LH tests) or concrete benchmarks of cycle position (e.g., prospectively assessed menstrual onset; see [[32](#_ENREF_32)] for details, including recommended *N*s based on power analyses). Conduct analyses that treat cycling women (rather than responders) as the unit of statistical analysis to justify inferences about the general magnitude of ovulation cues or their effects on others (see [[8](#_ENREF_8)]). (3) Work to achieve agreed-upon methodological standards to facilitate cross-study comparisons and avoid “false positive” criticisms. |
| *Hormonal mediators.* Few studies have examined specific hormonal mediators of ovulation cues. Hormonal mediators can help to adjudicate between alternative explanations for the existence of ovulation cues and unite the human and non-human literatures. | Assay hormones, preferably at multiple times across the cycle. |
| *Effects of hormonal contraceptives (HCs)*. (1) HCs appear to eliminate changes in women’s attractiveness and social behavioracross the cycle[[47](#_ENREF_47)]. However, the effects of HCs on *overall* attractiveness, receptivity, solicitousness, and relationship dynamics are largely unknown, despite potentially important consequences for women’s well-being. (2) HC use is often confounded with other factors, such as relationship status. (3) Moreover, HCs differ in dosage and form of estrogen and progestin and dosage schedule. Different formulations could have different effects. | (1) Compare naturally-cycling and HC-using women both across the cycle and overall, ideally, through randomized controlled trials. (2) Account for possible confounds (see Christina M Larson, PhD dissertation, UCLA, 2014). (3) Examine effects of different HC formulations (Grebe et al., unpublished data). |
| *How do men versus women respond to ovulation cues?* Few studies have examined women’s responses to ovulation cues in other women. It remains unknown whether women increase their competitive responses to women who are in the fertile window. | Compare men’s and women’s responses to high- and low-fertility stimuli, and test between competing explanations for women’s ability to detect ovulation cues. |
| *Ovulation cues in the wild.* Most studies isolate putative ovulation cues and study their effects on unacquainted individuals in the laboratory. The effects in women’s ongoing relationships – both with women and men – is unknown.  | Conduct studies examining changes across the cycle in romantic partner’s perceptions of women’s attractiveness, receptivity, and solicitousness; in their responses to their partner; in their hormones; and so on.  |

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This meta-analysis evaluated evidence for shifts across the ovulatory cycle in women’s mate preferences. Results showed that women prefer purported indicators of genetic quality (e.g., body masculinity) more on fertile than non-fertile days of the cycle. These shifts were present when women evaluated men’s short-term sexual desirability or attractiveness but absent when they evaluated men’s long-term desirability. These results remained statistically significant after adjusting for possible publication bias.

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In this lab study, men rated samples of women's natural body odor collected at high- and low-fertility points within the ovulatory cycle (confirmed by luteinizing hormone tests). Men rated women's high- fertility body odor as sexier and more pleasant but slightly less intense than their low-fertility body odor.

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In this study, women provided vocal recordings, facial photos, and hormone samples twice within their cycles--when their estradiol and progesterone were at their respective peaks. Men rated both women's photos and vocal recordings as more attractive when their progesterone was low, consistent with them being in the follicular phase. Also, men rated women's vocal recordings as more attractive when their progesterone was low but estradiol was high, consistent with them being in the late follicular phase, when fertility is maximal.

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In this experiment, women interacted with confident and sexy (but unreliable) “cads” and kind and caring (but uncharismatic) “dads” at high and low fertility within the cycle, as confirmed by luteinizing hormone tests. Women were more flirtatious with the “cads” than with the “dads” only at high fertility; no such difference was observed at low fertility.

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In this study, romantic couples completed lab sessions at high and low fertility within the female partner’s cycle. At both sessions, the couple completed an interaction to expose the male partner to possible ovulation cues in his female partner. The male partner then viewed profiles of putative male rivals portrayed as either highly competitive or non-competitive. Men exposed to highly competitive rivals exhibited a greater testosterone response to the manipulation at high than at low fertility, whereas men exposed to non-competitive rivals showed no such pattern.

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In this study, researchers used a nebulizer to expose men to underarm and vulvar odors collected from women in the high-fertility phase or in the low-fertility premenstrual phase (verified by estradiol and progesterone assays). Exposure to women’s fertile underarm and vulvar odors increased men’s testosterone and interest in sex, whereas exposure to premenstrual underarm and vulvar odors decreased men’s testosterone and had no effect on their interest in sex.

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Fig. 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.