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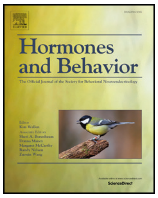

Endocrinology of human female sexuality, mating, and reproductive behavior

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ABSTRACT

Hormones orchestrate and coordinate human female sexual development, sexuality, and reproduction in relation to three types of phenotypic changes: life history transitions such as puberty and childbirth, responses to contextual factors such as caloric intake and stress, and cyclical patterns such as the ovulatory cycle. Here, we review the endocrinology underlying women's reproductive phenotypes, including sexual orientation and gender identity, mate preferences, competition for mates, sex drive, and maternal behavior. We highlight distinctive aspects of women's sexuality such as the possession of sexual ornaments, relatively cryptic fertile windows, extended sexual behavior across the ovulatory cycle, and a period of midlife reproductive senescence—and we focus on how hormonal mechanisms were shaped by selection to produce adaptive outcomes. We conclude with suggestions for future research to elucidate how hormonal mechanisms subserve women's reproductive phenotypes.

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1. Introduction

In some ways, women are typical female primates. In the broad arc of their lifespans, women reproduce at modest rates and engage in extensive parental investment—that is, they have a primate's characteristically slow life history (Jones, 2011). As in many other primates, humans also form complex social groups and evince sexually differentiated behaviors both during development and in adulthood (Wallen, 2005). Some of the earliest developing and most sexually differentiated components of human psychology are gender identity, which directs gendered socialization and behavior, and sexual orientation. Following puberty, the process of sexual maturation, women mate and gestate, nurse, and care for offspring.

Although human beings share many characteristics with nonhuman primates, we are unique in a number of ways. For instance, humans have a very long juvenile period and adult life span, both of which facilitate the acquisition of skills via cultural learning (Lancaster and Kaplan, 2009). Perhaps because of men's investment in offspring (which is unusual among male mammals), women also engage in an extraordinary level of mating competition (Campbell, 2013; Puts, 2010; Puts, 2016). That is, as benefits conferred by men often cannot be shared among women, variation in male mate quality is predicted to engender female competition over high-quality males. This competition sometimes involves aggression and threats of aggression but generally takes the form of mate attraction.

Unlike most female primates, women exhibit relatively cryptic fertile windows in their ovulatory cycles (Nunn, 1999), perhaps to prevent dominant males from monopolizing estrous copulations and thus to facilitate investment by subordinate males (Strassmann, 1981). However, there are several other adaptive explanations (see Haselton and Gildersleeve, 2016), as well as byproduct explanations (e.g. Havlíček et al., 2015; but see Roney et al., 2015), for the evolution of concealed ovulation in humans (see ESM). Women's sexual behavior is also unusual in that it extends across the ovulatory cycle. In most mammals, including primates (e.g., Deschner et al., 2004; Nadler et al., 1983), female sexual activity is heightened during the fertile period of the reproductive cycle (Beach, 1976; Dixson, 1998; Nadler et al., 1983; Thornhill and Gangestad, 2015). By contrast, evidence suggests that women's intercourse frequency tends to vary modestly and inconsistently, if at all, across the ovulatory cycle (Baker and Bellis, 1995; Clayton et al., 1999; Matteo and Rissman, 1984; Udry and Morris, 1968; Wilcox et al., 2004). In combination with concealed ovulation, extended sexuality may have evolved in part because it enabled ancestral women to recruit good genes surreptitiously from extra-pair males (Thornhill and Gangestad, 2015). However, the degree to which such “dual mating” played a role in the evolution of these traits is a matter of debate (see ESM).

In later years, women undergo a period of midlife reproductive senescence (Alberts et al., 2013; Derry, 2002; Kirkwood and Shanley, 2010; Pavelka and Fedigan, 1991), a life history transition during which fertility declines more rapidly than other aging processes (Kirkwood and Shanley, 2010), resulting in follicular depletion and permanent cessation of menstrual periods (Burger et al., 1995; Burger et al., 2008; Hulka and Meirik, 1996; Soules et al., 2001). Although an extended post-reproductive life stage has been observed in many mammalian species (for review, see Cohen, 2004), its ubiquity in humans appears to distinguish us from other primates (Levitis et al., 2013).

These components of sexual development, reproduction, and reproductive senescence are guided by hormones. Because they circulate throughout the body in the bloodstream, hormones are ideally suited for coordinating systemic responses to changes in the environment or bodily state. Such systemic changes may be classified into life historical, contextual, or cyclical changes according to the precipitating causes (Table 1). Hormone levels coordinate life history transitions such as prenatal sexual differentiation and puberty, as well as responding to and supporting others, such as pregnancy and nursing. Such hormonal effects depend on the stage of development, as well. Hormones also adjust resource allocation to mating and reproduction in response to contextual factors, such as caloric availability, psychosocial stress, and physical challenge. Finally, hormones exhibit cyclical fluctuations, which adjust behavior and physiology according to sleep-wake cycles and the ovulatory cycle.

In the current manuscript, we review evidence regarding how hormones orchestrate, coordinate, and regulate key components of human female sexual development, life history, and reproductive strategies, as well as how behaviors and the environment feed back onto hormone production. We focus on how these relationships were shaped by selection to produce adaptive outcomes. Sections are ordered roughly chronologically in relation to the timing of life history stages—early development, puberty, mating, sex drive, motherhood, and menopause—and throughout we emphasize how hormones coordinate life historical, contextual, and cyclic changes in women's reproductive anatomy, physiology, and behavior. Although much of what is known about these relationships in humans derives from clinical and laboratory-based research, we highlight field-based research wherever possible.

2. Early development: sexual orientation and gender identity

Two key elements of women's reproductive life history strategies are sexual orientation, the extent to which one is sexually attracted to men, women, or both (Hill et al., 2013; Rieger et al., 2005), and gender identity, one's feeling of being male, female, both, or neither (LeVay and Baldwin, 2009). It is becoming increasingly evident that sexual orientation and gender identity cannot be explained by gender socialization alone, and that prenatal events are instrumental in their development.

Consider the ideal experiment for investigating the role of gender socialization on psychosexual development: Begin with an infant of one sex and expose that child to a social environment typical of the opposite sex, including by changing the child's appearance so that others would perceive the child as the reassigned sex. Later, ascertain gender identity and sexual orientation (Bailey et al., 2016). The larger the role of gender socialization in psychosexual development, the more typical the child should be of the reassigned gender.

In fact, circumstances very close to this “ideal experiment” have occurred several times. Gender has been reassigned in several hormonally typical males whose penises were accidentally destroyed during circumcision, or were malformed due to cloacal exstrophy, in which the abdomen and penis develop abnormally. The medical community once believed that such males would be happier being reassigned as female, both surgically (via castration, penectomy, and vaginoplasty) and socially. For seven natal males whose gender was reassigned between birth and 17 months, adult gender identity and sexual orientation were later ascertained. In six of these seven cases, gender identity was male, indicating a strong influence of prenatal development but leaving room for postnatal factors, possibly including social environment. In all cases, sexual attraction was to females (Bailey et al., 2016). Given a population base rate of 1.1% of women being primarily attracted to women, the statistical odds of all seven individuals being attracted to women if prenatal development were irrelevant is less than 2 in 100 trillion (Bailey et al., 2016).

While differential treatment by parents and/or physicians may have played a role in the discordance between psychosexual development and gender of rearing in gender reassigned natal males, this is unsatisfying as a general explanation, as we know of no evidence that repeated interaction with physicians can produce this type of discordance. Rather, physicians and parents attempted to provide a female-typical, as opposed to atypical, social environment, which, if anything, tends to decrease discordance between psychosexual traits and gender of rearing (see, e.g., Callens et al., 2016). From this pattern of results, it would appear that postnatal gender socialization alone is generally

Table 1
Taxonomy of hormonal changes according to function, with examples of related research.

Type	Subtype	Example
Life historical	Early development	Elevated prenatal androgens predicted attraction to women (Hines et al., 2004)
	Puberty	Increased estrogens at puberty produce gynoid body fat distribution (Wells, 2007)
	Pregnancy	Placental estrogens and progesterone inhibit ovulation (Jones and Lopez, 2013)
	Mothering	Increases in oxytocin predicted more affectionate contact with offspring (Feldman et al., 2010)
	Nursing	Prolactin induces lactation and maternal behavior (Numan and Sheehan, 1997)
	Menopause	Sexual desire declined with estradiol levels across menopause (Dennerstein et al., 2002)
Contextual	Diet	Estradiol declined during caloric shortage (Wade and Schneider, 1992)
	Physical challenge	Testosterone rose prior to athletic competition (Edwards and Casto, 2013)
	Relationship status	Testosterone was elevated in single women (Kuzawa et al., 2010)
	Sexual behavior	Oxytocin peaked at orgasm (Blaicher et al., 1999)
	Stress	Elevated cortisol predicted early pregnancy loss (Nepomnaschy et al., 2006)
Cyclical	Circadian	Changes in testosterone predicted diurnal changes in attractiveness (Wheatley et al., 2014)
	Ovulatory	Estradiol predicted women's clothing choices (Haselton et al., 2007)

insufficient to produce female-typical sexual orientation and gender identity in individuals with male-typical prenatal androgenization.

The neural organization underlying sexual orientation (Balthazart, 2016) and gender identity (Hines et al., 2004) is directed in part by androgens. For instance, females exposed to elevated prenatal androgens due to congenital adrenal hyperplasia (CAH) report greater attraction to females (Hines et al., 2004; Meyer-Bahlburg et al., 2008) and less satisfaction with female sex assignment (Hines et al., 2004) compared to their unaffected female relatives. CAH is characterized by an enzyme deficiency causing precursors of cortisol to be shunted down the androgen pathway, resulting in the prenatal overproduction of androgens (Pang et al., 1980). CAH thus provides a “natural experiment” for examining the role of hormones in gender identity and sexual orientation. Although some studies have found that androgen levels in CAH females exceeded even those of control males during some stages of prenatal development (reviewed in Meyer-Bahlburg et al., 2008), the fact that XX CAH individuals may possess virilized, but not male-typical, genitalia suggests that overall androgen production is below the normal male range during critical periods of prenatal sexual differentiation.

Recent work on girls with CAH suggests that androgens organize gendered behaviors in part by influencing children's choice of male vs. female role models, and decreasing preference for objects that they observed, or were explicitly told, were “for girls” (Hines et al., 2016). However, these findings alone are insufficient to draw robust conclusions about the influence of hormones on human neural and behavioral organization, as females with CAH differ from unaffected females in other ways, including that their condition likely elicits different treatment from their parents and physicians.

Conversely, 46,XY individuals with complete androgen insensitivity syndrome (CAIS) exhibit female-typical gender identity and sexual attraction to men (Hines et al., 2003; Money et al., 1984; Wisniewski et al., 2000; Zucker et al., 1996). In CAIS individuals, testes develop, remain undescended in the abdominal cavity, and produce normal-to-high male levels of testosterone. However, due to completely nonfunctional androgen receptors (ARs), androgens do not influence gene transcription in their target tissues, and thus male-typical phenotypic features do not develop (Imperato-McGinley et al., 1982).

Looking across individuals raised as females but with differing exposure and/or sensitivity to androgens, one notes an apparent dose-response relationship, such that higher levels of early androgenization predict greater psychobehavioral masculinity for traits such as recalled feminine play in childhood (Callens et al., 2016) and adult sexual orientation (Fig. 1). However, it is important to note that these lines of evidence are potentially confounded with socialization in two ways. First, sex hormones may have direct effects on neural characteristics underlying other behavioral patterns, which then elicit psychosocial experiences that influence traits such as sexual orientation and gender identity (Bem, 1996; but see Pasterski et al., 2005). Though natural selection would probably not leave the development of a psychological trait as critical to fitness as sexual orientation to be shaped by the vagaries of gender socialization, gender identity may indeed be formed partly through the evaluation of one's own feelings and attitudes in relation to the characteristics of other members of society, as well as in response to social treatment influenced by the overall gender typicality of one's behavior. Second, the effects of sex hormones on outward appearance may influence gender socialization.

Recent work suggests that individuals with sex-atypical androgenization are generally content with their gender of rearing (Callens et al., 2016). Of 14 genetic males with male-typical prenatal androgenization but reassigned neonatally as female due to cloacal exstrophy, all exhibited marked-to-moderate male-typical interests and attitudes; however, five continued to identify as female by age 16 (Reiner and Gearhart, 2004). While it is difficult to imagine that the differences in gender socialization between, for example, girls with complete androgen insensitivity syndrome and those born male whose gender was reassigned could be so vast as to lead to nearly all of the former group being attracted to males and nearly all of the latter group being attracted to females, some role of socialization differences on sexual orientation cannot be ruled out definitively.

Another source of evidence that is not obviously confounded with socialization is the ratio of the lengths of the second and fourth fingers (2D:4D), a putative biomarker for prenatal androgen exposure

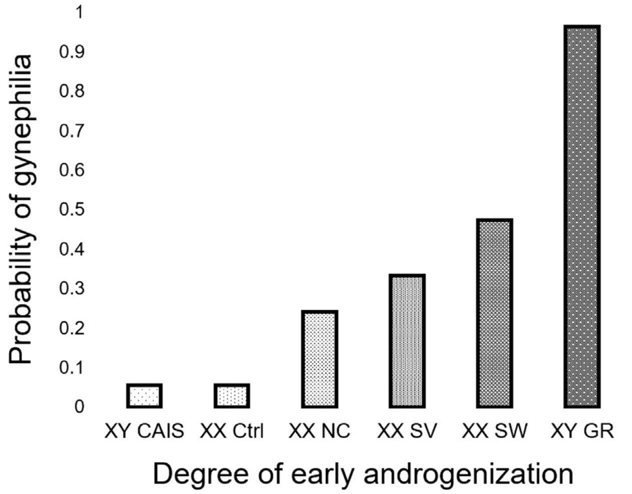

Fig. 1. Proportion of individuals experiencing attraction to women (gynephilia) as a function of early (prenatal and early postnatal) androgen signaling in individuals raised as females. Gynephilia is defined here as Kinsey 2–6 (regular attractions to and fantasies about women). Degree of androgenization refers to both exposure and sensitivity to androgens. Categories are rank-ordered. CAIS = complete androgen insensitivity syndrome (sexual orientation does not differ from female controls; Hines et al., 2003), Ctrl = women recruited without regard to diagnosis or sexual orientation (Gangestad et al., 2000), NC = non-classical CAH, SV = simple virilizing CAH, SW = salt-wasting CAH (Meyer-Bahlburg et al., 2008 for all CAH), GR = gender-reassigned natal males (Bailey et al., 2016).

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(Manning et al., 1998; Williams et al., 2000; Breedlove, 2010; Putz et al., 2004). While multiple factors likely contribute to variation in 2D:4D (Saino et al., 2007; Yang et al., 2009), evidence suggests that 2D:4D reflects early androgen signaling. For example, finger length ratios are sexually differentiated (lower in males) by the end of the first trimester of gestation (Galis et al. 2010; Malas et al., 2006), and are masculinized in females with CAH (Brown et al., 2002; Ciumas et al., 2009; Ökten et al. 2002; but see Buck et al., 2003). In addition, 46,XY AIS individuals have finger length ratios that are similar to those of typical women (Berenbaum et al., 2009). Finally, modulation of androgen and estrogen receptors in utero affects the development of a masculine and feminine 2D:4D ratio, respectively, in mice (Zheng and Cohn, 2011). Thus, digit ratios may provide a retrospective biomarker for early sex hormone signaling that can illuminate nonsocial factors influencing sexual orientation. Indeed, in a meta-analysis of the relationship between 2D:4D and sexual orientation in 16 independent samples comprising 1693 heterosexual women and 1014 lesbians, women reporting a homosexual orientation had more masculinized finger length ratios (Grimbos et al., 2010). Moreover, 2D:4D is masculinized specifically in lesbians with masculine gender presentation (Brown et al., 2002), and in natal females with male gender identity (Kraemer et al., 2009; Wallien et al., 2008).

Various lines of evidence demonstrate that androgens likely organize sexual orientation, gender identity, and other psychobehavioral traits in humans specifically through binding to ARs in the brain (Zuloaga et al., 2008), rather than aromatization and binding of estrogen to estrogen receptors (ERs), as in rodents (Bakker et al., 2006; Puts et al., 2006). First, alpha-fetoprotein binds estrogen and prevents it from entering and masculinizing the brain in rodents (Bakker et al., 2006; Puts et al., 2006), but has very low affinity for estrogen in humans (Swartz and Soloff, 1974). If brain masculinization were also ER-mediated in humans as in rodents, then ovarian estrogens would presumably cross the blood-brain barrier and masculinize the human female brain. Second, women with CAIS exhibit female gender identity (Mazur, 2005), sexual attraction to men (Hines et al., 2003), and feminine behavior, despite producing normal-to-high male levels of testosterone (Imperato-McGinley et al., 1982). This suggests that functional ARs rather than ERs are required to masculinize the human brain. Finally, human males with mutations rendering the aromatase enzyme dysfunctional typically present as normal males, despite the absence of aromatization in the brain or elsewhere (Grumbach and Auchus, 1999). Together, these data indicate that ER stimulation has a limited role, if any, in masculinizing the human brain and behavior.

As noted above, each of the studies of this kind is not without limitations. However, these various lines of evidence converge to suggest that hormones affect the brain and behavior in humans as they do in laboratory mammals where experimental hormonal manipulations are possible. For example, in laboratory rodents, androgen manipulations affect sexually differentiated sexual behaviors (Morris et al., 2004). Thus, while socialization likely plays important roles in the development of diverse aspects of gender-related behavior, central elements of our reproductive psychology appear less responsive to social manipulation. Prenatal events, probably involving androgen signaling, appear to drive gender development and sexual orientation.

3. Puberty

A next crucial life history transition is puberty, a process involving the coordination of psychological and anatomical changes associated with sexual maturation. As adolescents transition through puberty into adulthood, they must learn to navigate increasingly complex social relationships (Brown, 2004), including romantic and sexual relationships, in order to succeed in the competitive reproductive sphere. Due in part to the vast number of variables involved in its onset, there is no definitive “beginning” to puberty (Bronson and Rissman, 1986; Dorn and Biro, 2011; Wilson, 1992). Rather, puberty involves a cascade of events that prepare the body, including the brain, for the capacity to reproduce, including the emergence of physical and psychological traits that function in mating interest and behavior, choosing mates, and mating competition (Grumbach, 2002; Grumbach and Styne, 1998).

Pubertal development is comprised of two distinct developmental stages, adrenarche and gonadarche. Adrenarche is an early stage of sexual maturation in which the adrenal cortex begins to secrete dehydroepiandrosterone (DHEA), which is then converted into testosterone and estradiol. DHEA levels begin to increase as early as 6 years of age in typically developing children (Counts et al., 1987; De Peretti and Forest, 1976; Ducharme et al., 1976) but increase sharply at age 10 (the approximate age at which individuals of both sexes tend to report first experiencing sexual attractions; McClintock and Herdt, 1996). Gonadarche typically begins later, between 9 and 13 years, and involves the activation of the hypothalamic-pituitary-gonadal (HPG) axis. The HPG axis is fundamentally influenced by secretion of gonadotropin releasing hormone (GnRH) from the hypothalamus. This activation then signals the synthesis and secretion of the pituitary gonadotropins: luteinizing hormone (LH) and follicle stimulating hormone (FSH) (Dorn and Biro, 2011; Sisk and Foster, 2004; Sisk and Zehr, 2005). LH and FSH act on target cells in the ovaries to direct the production of ova and the secretion of steroid hormones (e.g. estradiol and progesterone), which also participate in follicle maturation (Sisk and Foster, 2004).

From here, steroid hormones stimulate a cascade of physical changes, including rapid height and weight growth, as well as the emergence of secondary sex characteristics such as breasts, fat deposition on the buttocks and hips, and pubic hair, particularly as girls approach the onset of menarche (Frisch, 1994; Grumbach and Styne, 1998; Lanska et al., 1984; Lassek and Gaulin, 2007; Marshall and Tanner, 1969, 1970; Pond, 1981; Sellers et al., 1992). Estrogen inhibits the accumulation of fat in the abdominal region and stimulates fat deposits in the lower half of the body (Singh, 1993), producing the gynoid body shape typical of fertile women (Björntorp, 1991; Pawlowski, 2001; Singh, 1993).

In tandem, puberty brings about profound changes in psychology and the brain (Dahl, 2004; Scherf et al., 2013; Silk et al., 2013). The complex interplay of LH, FSH, and steroidal hormones is simultaneously influenced by neuroendocrine feedback loops from the brain, which are believed to facilitate sexual behavior in adolescence (Schulz et al., 2004; Sisk and Foster, 2004), and perhaps the development of adult mating preferences (Saxton et al., 2009), as well as emerging perceptual sensitivity for facial cues related to sexual interest and contempt (Motta-Mena and Scherf, 2016). Importantly, while adolescents may experience interest in sexual objects (receptivity), this does not necessarily equate with the urge to seek and initiate sexual activity (proceptivity) (Diamond and Savin-Williams, 2009; Tolman and McClelland, 2011).

Girls tend to enter puberty sooner than boys (Marshall and Tanner, 1969, 1970), which is characteristic of species in which males are more competitive for mates and require longer to attain large body size and other features necessary to compete successfully (Daly and Wilson, 1983; Shea, 1985). However, early life exposure to cues of extrinsic mortality risk (e.g. fluctuating resources, high mortality rates, and low parental investment) can lead to earlier pubertal timing and reproduction (Ellis, 2013; Ellis et al., 2011; Walker et al., 2006). For instance, low-quality parental investment may signal an environment in which parental investment is weakly linked to reproductive success. In this case, resources should theoretically be allocated toward reproducing early and often through accelerating pubertal development (Belsky, 2012; Belsky et al., 2015; Chisholm et al., 2005). Moreover, because high extrinsic mortality risk favors current reproduction over future reproduction, mortality risk may promote earlier puberty, sexual debut, and reproduction (Doll et al., 2015; Ellis, 2013; Walker et al., 2006). Importantly, girls who begin puberty earlier, especially those who are maltreated (Negriff and Trickett, 2010) and living in disadvantaged neighborhoods (Lynne et al., 2007; Obeidallah et al., 2004), are

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more likely to engage in delinquent and aggressive behavior, which may be related to increased expenditure of mating effort (Campbell, 2013).

In addition to environmental predictors of mortality risk, a host of other factors influence within-sex variability in pubertal timing, including genes (Kaprio et al., 1995), ethnicity, and nutrition (Chisholm et al., 2005; Ellis, 2004; Eveleth, 1978). Nutritional state facilitates growth and attainment of reproductive maturity (Walker et al., 2006), and differences in resource availability help explain the considerable variation that exists across populations in the timing of girls' pubertal development (Anderson et al., 2003; Worthman, 1993). For example, girls of the Kikuyu of Kenya reach menarche at 15.9 years on average (Worthman, 1993), whereas American girls reach menarche around 12.5 years (Styne, 2004).

Societal norms and attitudes concerning adolescent sexuality and premarital sex also vary widely across societies (Diamond and Savin-Williams, 2009; Oliver and Hyde, 1993), and these variables may not only independently influence sexual interests and behaviors (Short, 1976), but they may also interact with pubertal timing (Worthman, 1993). For instance, earlier puberty leads to earlier marriage and reproduction among the agropastoral Kipsigis of southwestern Kenya, in which girls have a mean age at marriage of 16.6 years (Borgerhoff Mulder, 1989). However, in industrialized societies where teenage sex is discouraged and the mean age at marriage is considerably higher, pubertal timing is likely to have less influence on the timing of marriage and reproduction.

4. Mating competition

Competition exists whenever the use of a resource, including a mate, makes the resource unavailable to others. Competition over mates can take multiple forms, including physical aggression or threats to exclude same-sex competitors from mating opportunities, as well as the expression of anatomical and behavioral traits to attract mates. Many benefits conferred by men cannot be shared among women, and thus variation in male quality likely engenders female mating competition. Perhaps because human males are unusual among primates in the degree to which they invest in their mates and offspring, women are unusual among primates in the intensity of their competition for male investment (Campbell, 2013). Women may also compete over males of high genetic quality because the availability of males with good genes is limited by male–male competition and female proprietariness over mates (Cashdan, 1996; Puts, 2016). Sex steroids play important roles in coordinating the adult expression of traits that function in women's mating competition, as we now discuss.

4.1. Sexual ornaments

Several traits that develop at puberty may function as sexual ornaments that signal women's residual reproductive value (Thornhill and Gangestad, 2015) and/or current fecundability (Wheatley et al., 2014) to potential mates. For example, the estrogen-driven pattern of fat distribution on the breasts, hips, and buttocks may constitute such an ornament. Fat around the midsection can be quantified with the waist-to-hip ratio (WHR), the ratio of the narrowest part of the waist to the widest part of the hips (Björntorp, 1991; Singh, 1993). From puberty through the reproductive years, the normal range of WHR is 0.67–0.80 (Lanska et al., 1984; Marti et al., 1991; O'Brien and Shelton, 1941). Before puberty and after menopause, fat is more evenly distributed across the hips and abdomen, resulting in a WHR closer to 1 (Singh, 1993). Evidence from 119 women ranging from 24 to 37 years of age suggests that large breasts and a narrow waist predict higher levels of both estradiol and progesterone, indicating higher fecundability (Jasienska et al., 2004). While Grillot et al. (2014) found no such association, this inability to replicate may be due to the smaller sample size (33 women) and narrower ranges of ages (18–20 years) and WHR. In another study of 500 women attending a fertility clinic, each 0.1 increase in WHR was associated with a 30% decrease in the probability of conception per cycle (Zaadstra et al., 1993).

Copious mammary glandular tissue and a wider pelvis in women may have correlated with greater milk production and probability of successful childbirth, respectively, in ancestral populations. This in turn may have selected for male preferences for larger breasts and a wider pelvis, and women's fat deposition on the breasts and hips may have subsequently evolved to take advantage of these preferences (Low, 1979; Low et al., 1987; Puts, 2010). Men prefer a gynoid pattern of body fat distribution across a wide variety of societies (Dixson et al., 2007a; Dixson et al., 2007b; Dixson et al., 2010a; Dixson et al., 2010b; Dixson et al., 2011a; Dixson et al., 2011b; Marlowe et al., 2005; Singh, 1993; Singh et al., 2010; Sorokowski et al., 2014; Sugiyama, 2004). Given cross-cultural and individual variability in men's preferences for overall body fat, it may be important to consider the possible moderating role of body mass index (BMI; Wheatley et al., 2014). For example, in the forager Tsimané of Ecuador, men preferred a low WHR only after BMI was statistically controlled (Sorokowski et al., 2014).

However, if breasts and hips enlarged through fat deposition were entirely deceptive cues to mate quality, then selection would have favored inattention to them. Instead, men's preferences may have been maintained because fat deposition on the breasts, hips, and buttocks is linked to higher levels of reproductive hormones and higher fertility, as noted above. Moreover, during gestation, the mother's hip fat supplies her fetus with omega-3 fatty acids, which are critical for human brain development (Lassek and Gaulin, 2008). Women's WHR may also reflect a tradeoff between mate attraction and fecundity associated with low testosterone, and the ability to provision offspring through physical acquisition of resources facilitated by high testosterone (Cashdan, 2008).

Like body fat distribution, women's faces and voices may initially have evolved as partly deceptive signals, with male preferences maintained because of associations with women's mate value. Women's faces (Cunningham, 1986; Jones and Hill, 1993; McArthur and Berry, 1983) and voices (Puts et al., 2012a) are conspicuously neotenous and may have been shaped by a male preference for youth (Buss, 1989), which is strongly tied to residual reproductive value and fecundability (Wood, 1992). Indeed, men are especially interested in viewing women's faces, as opposed to bodies, when evaluating attractiveness for a long-term relationship, in which residual reproductive value is more salient than in a short-term, purely sexual relationship (Confer et al., 2010). Men prefer the voices of women in their mid-twenties and the faces of women around puberty, suggesting that women's voices provide relatively more information about current fecundability, and their faces provide relatively more information about residual reproductive value (Röder et al., 2013; Wheatley et al., 2014).

Feminine voices (Feinberg et al., 2008; Puts et al., 2011) and faces (Rhodes, 2006; Rhodes et al., 2000) are generally perceived to be more attractive in women, and their expression is related to lower testosterone levels compared to males across puberty (Puts et al., 2012c). Testosterone has also been negatively linked to women's reproductive capacity and negatively predicted individual differences in facial attractiveness (Wheatley et al., 2014; but see Gonzalez-Santoyo et al., 2015). Moreover, within-participant diurnal declines in testosterone predicted increased facial and vocal attractiveness (Wheatley et al., 2014). Similarly, cortisol may lower fertility (Csemiczky et al., 2000; Nepomnaschy et al., 2004; Nepomnaschy et al., 2006) and has been negatively associated with women's facial attractiveness (Rantala et al., 2013; but see Gonzalez-Santoyo et al., 2015). In short, women's bodies, faces, and voices are linked with fecundability and reproductive value through a variety of steroid hormones. Although more data are needed, the above evidence suggests that gynoid body fat deposition and vocal characteristics provide relatively more information about current fecundability, while facial appearance provides relatively more information about residual reproductive value.

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4.2. Cues to ovulatory phase

Nearly all primates display cues of ovulation (Dixson, 1998; Thornhill and Gangestad, 2015), although most cues may represent incidental "leakage" of fertility information linked to changing hormone levels, rather than advertisements of fertility status (Thornhill and Gangestad, 2008; Thornhill and Gangestad, 2015). One of the most noteworthy features of human reproduction is the apparent concealment of fertility within the ovulatory cycle (Alexander and Noonan, 1979; Pawlowski, 1999; Strassmann, 1981; Thornhill and Gangestad, 2008; Thornhill and Gangestad, 2015; but see Pawlowski, 1999 for a counterargument). Despite its subtlety, however, ovulation may not be entirely concealed in women (Gangestad et al., 2014; Haselton and Gildersleeve, 2011; for brief review see Haselton and Gildersleeve, 2016).

In laboratory-based experiments, men have reported stronger preferences for images of women in the follicular-phase compared to the luteal phase (Bobst and Lobmaier, 2012; Roberts et al., 2004), and normally-cycling women have reported more male-initiated sexual activities during the fertile phase of their ovulatory cycles (Harvey, 1987). Similarly, romantically committed men judged a woman in the fertile phase of her cycle as less attractive than did single men, suggesting an interaction between men's relationship status and women's cycle phase (Miller and Maner, 2010). However, contrary to other literature on intrasexual competition in women (see Section 4.3), evaluations of attractiveness made by other women were not influenced by the female's fertility cues.

These changes in attractiveness appear to be driven by estradiol and progesterone (Law Smith et al., 2006; Puts et al., 2013) and may reflect changing facial shape (Bobst and Lobmaier, 2012), skin oiliness (Arora et al., 2011), skin color (Burriss et al., 2015), acne (Lucky, 2004; Steventon, 2011; Stoll et al., 2001), or subtle differences in facial expression, such as smiling (Reis et al., 1990). Though some evidence suggests that ovulatory changes in facial skin color alone are too small to be detected by the human visual system (Burriss et al., 2015), skin color may sum or interact with other changes in facial appearance to influence perceptions.

Like faces, voices are more attractive during the fertile phase of the ovulatory cycle (Pipitone and Gallup, 2011; Pipitone and Gallup, 2008), and these increases in attractiveness appear to be related to elevated estradiol and decreased progesterone (Puts et al., 2013). It is presently unclear which acoustic or paralinguistic features are responsible for ovulatory shifts in vocal attractiveness (Bryant and Haselton, 2009; Puts et al., 2013).

Similarly, some studies have found that men prefer women's body odors in the follicular phase compared to other times in the ovulatory cycle (Gildersleeve et al., 2012; Havlíček et al., 2006; Kuukasjärvi et al., 2004; Singh and Bronstad, 2001; but see Thornhill and Gangestad, 1999). However, Roney and Simmons (2012) found no effect of ovulatory odors on men's testosterone levels. Evidence of decreased WHR during the follicular phase suggests that women's bodies may be more attractive at this time as well (Kirchengast and Gartner, 2002).

Finally, some evidence suggests that women's behavior (e.g. clothing choice, Haselton et al., 2007) enhances attractiveness around ovulation. In another study of clothing choice among 351 women attending an Austrian discotheque, testosterone levels predicted more revealing clothing, and in women who had a partner who was not present, estradiol positively predicted skin display and clothing tightness (Grammer et al., 2004). Miller et al. (2007) also found that professional lap dancers earned more tips around ovulation than during menstruation or the luteal phase. Contrary to the pattern observed in the above studies, however, Provost et al. (2008) found that men rated the motion-captured gaits of women as more attractive in the luteal phase than in the follicular phase. Perhaps behavioral cues to fertility are adjusted contextually, so that attractiveness can be increased where mate attraction is relevant (e.g., at a discotheque or when providing lap dances), and decreased in contexts where attractiveness is potentially costly, such as in the presence of undesirable males or female allies, who might perceive attractiveness to be threatening (see, e.g., Puts et al., 2011, Krems et al., 2016, and Buss and Dedden, 1990 for evidence that women find other women's attractiveness threatening). Indeed, in the Provost et al. study, there is no suggestion that the participants were attempting to attract a mate, and they were furthermore recruited by a female researcher and recorded covertly in the laboratory.

In sum, ovulation is not entirely cryptic in women. At the same time, ovulatory cues often require carefully designed studies to detect, and their subtlety indicates that selection has not favored broadcast signals of ovulatory status. It remains possible that some ovulatory changes, perhaps especially behavioral ones, function as "narrowcast" signals of fertility that can be directed toward specific desirable mates, a possibility that invites further investigation. In any case, selection would have strongly favored the ability to detect cyclic changes in conception risk and attuned men to whatever cues were available. Indeed, some evidence indicates that women's primary partners are able to detect cycle phase from scent (Poran, 1994) and are more assertive toward their partners when their partners are fertile (Gangestad et al., 2014).

4.3. Intrasexual competition

Although women's primary mode of mating competition over human evolution was probably mate attraction (Puts, 2010; Puts, 2016), women also engage in intrasexual competition, including derogation of competitors (Fisher, 2004; Vaillancourt, 2013), physical fighting over mates (Campbell, 2013), and less overt competitive behaviors, such as vigilance and mate guarding (Krems et al., 2015).

Generally, high baseline testosterone and low cortisol are linked to intrasexual competitiveness, although evidence in women is sparse. Salivary testosterone has been positively linked to psychometric measures of aggression in women (Harris et al., 1996), and salivary cortisol (but not testosterone) was found to be lower in women with dominant-appearing faces (Gonzalez-Santoyo et al., 2015). Women with dominant-looking faces may receive greater deference, leading to reduced psychological and/or physical stress and reduced cortisol levels. Alternatively, developmental stress could influence both facial morphology and HPA axis activity, which includes cortisol production (Nepomnaschy and Flinn, 2009). Finally, some evidence suggests that baseline testosterone positively predicts status among female athletes with lower baseline cortisol levels (Edwards and Casto, 2013), as well as competitive behavior after a victory (Mehta et al., 2008).

In some organisms, testosterone rises during competition and remains elevated after winning, possibly to adaptively regulate dominance behavior (Mazur, 1985; Wingfield et al., 1990). Evidence supporting this theory in women is mixed. Some work has found that women's cortisol and testosterone rise prior to (Bateup et al., 2002) and during (Edwards and Casto, 2013; Edwards and Kurlander, 2010) athletic competition, but not when playing a sports video game (Carré et al., 2013). Perhaps the lack of testosterone change in the video game context reflected lower motivation to compete or intensity of competition, or perhaps women's testosterone increases as a function of exercise rather than competition per se. In light of evidence that testosterone produces analgesia (Bartley et al., 2015), the latter possibility may explain why men, whose testosterone levels rise across diverse competitive situations, experienced analgesia after competition against a same-sex competitor regardless of exercise, whereas women experienced analgesia only after exercise (Boka et al., 2001). Another study found that testosterone treatment increased the desire to compete again after winning (relative to losing) only in women who were high in trait dominance (Mehta et al., 2015). More work is required to clarify these complex relationships.

Although McClintock (1971) initially reported that social affiliations among women synchronized their ovulatory cycles, this finding has not replicated (Strassmann, 1999; Yang and Schank, 2006). Instead,

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evidence indicates that intrasexual competitiveness intensifies around ovulation (Durante et al., 2008; Fisher, 2004; Haselton et al., 2007). For instance, within-subject changes in self-reported intrasexual competitiveness increased with salivary testosterone, which peaks near mid-cycle, but not with estradiol, progesterone, or cortisol (Hahn et al., 2016). Mate guarding behaviors have also been positively associated with estradiol dosages, but not progesterone dosages, in women's hormonal contraceptives (Welling et al., 2012).

Given that attractive, fertile females pose a threat to women in pair-bonded relationships, one would expect women to be adept at detecting cues to other women's ovulatory status. Some evidence indicates that this may be the case. Women rate the odors (Doty et al., 1975; Kuukasjärvi et al., 2004; Woodward et al., 2015), faces (Puts et al., 2013; Roberts et al., 2004), and voices (Pipitone and Gallup, 2008; Puts et al., 2013) of women near ovulation as more attractive. In 202 normally-cycling women sampled twice in the cycle, within-subject changes in progesterone negatively predicted their apparent threat to other women (Puts et al., 2013). That is, when progesterone was lower (and conception risk higher), women's faces and voices were perceived by other women to be more attractive to men, and their faces were perceived to be more flirtatious.

To the extent that women are able to detect and respond to cues of fertility in other women, these responses may take several forms. Women's testosterone levels increased in response to olfactory cues from other women in the periovulatory phase compared to low fertility in one study (Maner and McNulty, 2013), but not in another (Woodward et al., 2015). In fact, Woodward et al. found that women responded less aggressively toward a hypothetical young woman after exposure to fertile olfactory cues. However, across four experiments in which partnered women were shown photographs of other women taken during either the fertile or non-fertile cycle phase, women reported intentions to socially avoid fertile (but not non-fertile) women—but only when their own partners were highly desirable (Krems et al., 2016). Exposure to ovulating women also increased women's sexual desires for their (highly desirable) partners. These findings suggest that women may be sensitive to cues of fertility in other women, and respond in ways that balance mate retention with maintenance of same-sex friendships.

Finally, women's own cycle phase may interact with that of their female competitors in influencing competitive behaviors. Women's testosterone levels were higher when smelling a fertile-phase stimulus (relative to luteal-phase), but only when the smellers' own estradiol levels were high and progesterone levels were low (Woodward et al., 2015). Lobmaier et al. (2016) report a similar interaction; women's estradiol levels positively predicted their tendency to choose late follicular phase facial images (as opposed to luteal phase images) as more likely to entice their date away. Likewise, Necka et al. (2016) found that women withheld more resources from another woman in a Dictator game, keeping more for themselves, when both women were in the late follicular (fertile) phase of their ovulatory cycles. However, we note an important caveat to the above studies: While women may have evolved specialized adaptations for detecting other women's ovulatory cycle phase, it is also possible that this ability reflects adaptations for discriminating attributes between individuals (e.g., trustworthiness) or across other timescales (e.g., pregnancy) or contexts.

Overall, these findings suggest diverse hormonal influences on women's intrasexual competition, including baseline testosterone and cortisol, ovulatory cycle variation in testosterone, estradiol, and progesterone, and contextual changes in testosterone.

5. Sex drive and sociosexuality

5.1. Intercourse frequency

In most mammals, including primates (e.g., Deschner et al., 2004; Nadler et al., 1983), female sexual activity is heightened around the fertile phase of the ovulatory cycle (Beach, 1976; Dixson, 1998; Nadler et al., 1983; Thornhill and Gangestad, 2015). In some other mammals, including rhesus monkeys and humans, females do not confine sexual activity to the periovulatory period (Czaja and Bielert, 1975; Grebe et al., 2013; Martin, 2007). In past research, women's intercourse frequency has varied modestly and inconsistently across the ovulatory cycle (Baker and Bellis, 1995; Clayton et al., 1999; Matteo and Rissman, 1984; Udry and Morris, 1968; Wilcox et al., 2004). There may be many proximate reasons for this. Men may desire and attempt copulation throughout women's cycles (Meston and Buss, 2007; Wallen, 2001). Women may also modify sexual behavior to promote or avoid pregnancy (Tsui et al., 1991), or according to cultural factors (Pawlowski, 1999), such as avoiding sex during menstruation, as in the Dogon of Mali (Strassmann, 1997), or around holidays or particular days of the week (Palmer et al., 1982; Roney and Simmons, 2013; Wilcox et al., 2004).

There may have been selection for women to distribute their sexual behavior more evenly across the ovulatory cycle. Perhaps doing so enabled ancestral women to obtain good genes for offspring by copulating contingently outside of the pair-bond while retaining non-genetic benefits (e.g., food provisioning) conferred by a pair-bond partner (Thornhill and Gangestad, 2015). Indeed, in one study, women were especially self-assertive toward their partners during the periovulatory phase, and reported engaging in more behaviors that resist male vigilance and mate guarding, especially if they reported greater attraction to men other than their partners (Gangestad et al., 2014).

In another study of 2708 normally-ovulating British women who claimed to have a main male sexual partner, rates of reported extra-pair copulations (EPCs) peaked during the late follicular phase, while intra-pair copulations remained constant across the cycle (Baker and Bellis, 1995; Bellis and Baker, 1990). However, there are several limitations to this work. For example, the authors “standardized” women's cycles to 28 days but neglected to mention whether any differences in variability of the follicular vs. luteal phase were accounted for. Sexual infidelity is also highly stigmatized and therefore likely to be under-reported, although underreporting alone would not explain a correlation with cycle phase. Moreover, the observed change in proportion of EPCs (out of the total of extra-pair and in-pair copulations) from menses (days 1–5) to mid-/late follicular (highest fertility, days 6–14) to luteal phase (days 15–28) was small: 6.6% to 7.3% to 5.0%, respectively. Finally, this study has yet to be replicated, and thus these findings should be treated as tentative. In sum, while some evidence suggests that women's copulatory patterns across the cycle reflect a mixed-mating strategy, we underscore that this idea requires further testing.

5.2. Sex drive

Compared to intercourse frequency, sexual desire (Dennerstein et al., 1994; Harvey, 1987; Pillsworth et al., 2004; Stanislaw and Rice, 1988; Van Goozen et al., 1997) and female-initiated sexual behavior (Adams et al., 1978; Bellis and Baker, 1990; Bullivant et al., 2004; Burleson et al., 2002; Guillermo et al., 2010; Harvey, 1987; Matteo and Rissman, 1984; Prasad et al., 2014; Worthman, 1978), more consistently increase during the fertile phase. In a French nightclub, 20-year-old attractive male confederates individually approached young women and asked them to dance during slow, romantic songs (Guéguen, 2009a). Of 161 women who were single, normally ovulating, and within 28 days of their last menstrual onset, those estimated to be in the fertile cycle phase were more likely to agree to dance (58.8%) than those in the menstrual (34.4%) or luteal (38.5%) phases. In a similar study, attractive male confederates individually approached young women at daytime on a street in Vannes, France and asked for the women's phone numbers for a later rendezvous (Guéguen, 2009b). Normally-cycling women ($N = 200$) were more likely to agree to the request if they were estimated to be in the fertile phase of their cycle than in the menstrual or luteal phases.

Such variation across the cycle is not observed in orally contracepting women (Adams et al., 1978; Guéguen, 2009b), presumably due to suppression of ovulatory changes in ovarian hormones. Moreover, both sexual desire and frequency of sexual fantasies decreased following oophorectomy (surgical removal of the ovaries), indicating that the relevant hormones are ovarian in origin (Sherwin et al., 1985). However, the relative roles of different ovarian steroids remain unclear; both estradiol and testosterone peak near ovulation (Abraham, 1974; Korenman and Sherman, 1973), and thus both represent good candidates for driving cyclic shifts in sexual desire.

Some evidence indicates that women's sexual desire is driven by changes in estradiol. In a study of 49 oophorectomized women randomly assigned to 1 of 4 medication groups, estradiol treatment increased sexual desire, enjoyment, and orgasm frequency, but not coital frequency (Dennerstein et al., 1980). Further evidence from hormone replacement therapy trials suggests that elevated periovulatory concentrations of estradiol may be necessary to increase sexual motivation in perimenopausal women (for review, see Cappelletti and Wallen, 2016). Likewise, declining estradiol rather than testosterone predicted decreased sexual responsiveness and desire over an 8-year longitudinal study of 226 perimenopausal women (Dennerstein et al., 2002). Finally, in diary reports of normally-ovulating women across 1–2 cycles, reported sexual motivation was positively related to salivary estradiol, negatively related to progesterone, and unrelated to testosterone (Roney and Simmons, 2013).

Other evidence implicates androgens. For instance, androgen treatment enhanced the intensity of sexual desire and arousal and the frequency of sexual fantasies in oophorectomized women that were randomly assigned to receive either an estrogen-androgen combined preparation, an estrogen-alone drug, an androgen-alone drug, or a placebo (Sherwin et al., 1985). Further, in another study, oophorectomized women who received both estradiol and androgen reported greater sexual desire, sexual arousal, and numbers of fantasies than those who received estradiol alone or were untreated (Sherwin and Gelfand, 1987). Moreover, these measures covaried with plasma testosterone but not estradiol. Guay (2001) found low testosterone in 8 of 12 premenopausal women reporting decreased libido, and found improved sexual desire following androgen treatment in 6 of these 8 women, although this study was not placebo-controlled or blinded. However, in a double-blind, placebo-controlled 24-week trial involving 533 women (ages 20 to over 65) with oophorectomy and hypoactive sexual desire disorder, testosterone improved both sexual desire and satisfying sexual activity (Buster et al., 2005).

On the one hand, these data suggest a clear positive effect of testosterone on sexual desire in women with low or absent ovarian androgen production. On the other hand, treatment studies have utilized supraphysiological testosterone dosages, and endogenous estradiol has been more strongly linked to libido in both normally-cycling and perimenopausal women (Cappelletti and Wallen, 2016). Indeed, in a representative sample of 1021 Australian women aged 18–75, low androgens predicted low sexual desire, arousal, and responsiveness, but these relationships were modest and varied across androgens and measures (Davis et al., 2005). Most studies in which postmenopausal women were treated with both estradiol and supraphysiological doses of testosterone have found that testosterone enhances the effect of estradiol on libido, perhaps due to aromatization of testosterone to estradiol in the brain (Cappelletti and Wallen, 2016). Androgen levels also increase following sexual activity in women (Dabbs and Mohammed, 1992; van Anders et al., 2007), which could partly explain correlations between androgens and sexual desire, if desire leads to sexual behavior which in turn leads to high androgen levels. However, testosterone does not appear to remain elevated the day after copulation (van Anders et al., 2007).

Certainly, it would make adaptive sense if sexual desire were tied to both of these hormones, as both track key factors related to women's reproduction. Because both estradiol and testosterone increase near ovulation (Abraham, 1974; Korenman and Sherman, 1973), these hormones might drive women to engage in more sex during the periovulatory phase. However, both estradiol and testosterone are also elevated at non-fertile points in the cycle: estradiol exhibits a mid-luteal secondary peak, and testosterone is elevated in the early luteal phase (Abraham, 1974; Korenman and Sherman, 1973). Given this, one could speculate that estradiol- and/or testosterone-mediated changes in libido would especially promote sex with good-genes extra-pair males during the late follicular phase, and especially if women's primary partner is low in genetic quality (see also Section 6.1). Estradiol and testosterone also decrease throughout the transition to menopause (Lasley et al., 2002), and estradiol levels decline during caloric shortage (Fisher et al., 1986; Wade and Schneider, 1992) when reproductive conditions are unfavorable. Testosterone is elevated in single women compared to partnered women (Kuzawa et al., 2010; van Anders and Watson, 2007), and in polyamorous women compared to both single women and women with only one partner (van Anders and Watson, 2006). If being single and being polyamorous reflect greater competitiveness over mates, then these findings are consistent with the evidence reviewed above that women's testosterone rises in more intense competitive contexts and in response to a female rival. That is, testosterone may increase competitiveness for mates in part by increasing libido. Additional work is needed to disentangle the relative influences of estradiol and testosterone on sexual desire in women, which may vary across contexts and life history stages.

5.3. Sociosexuality

Testosterone has also been investigated in relation to women's sociosexuality, or interest in uncommitted sex. Although testosterone predicts sociosexuality in men and has been found to mediate the sex difference (males > females), no study to date has found relationships between testosterone and women's sociosexual desires or attitudes (Charles and Alexander, 2011; Edelstein et al., 2011; Puts et al., 2015). Some work, however, has shown positive correlations between testosterone and measures of women's sociosexual behavior (van Anders et al., 2007), particularly among partnered women (Edelstein et al., 2011). Taken together, the above results suggest that testosterone may be unrelated to women's desires for and attitudes toward uncommitted sex, although it may positively predict their uncommitted sociosexual behavior, perhaps by increasing libido.

6. Mate preferences

6.1. Ovulatory cycle shifts

A growing literature indicates that women's preferences for men's traits fluctuate across the ovulatory cycle (Gangestad and Haselton, 2015; Gangestad and Thornhill, 2008; Welling and Puts, 2014). In the late follicular phase, women appear to shift their preferences toward putative indicators of men's genetic quality, such as the odors of men whose bodies are more symmetrical (Gangestad and Thornhill, 1998), and masculine, dominant-appearing faces (Penton-Voak et al., 1999), voices (Puts, 2005), bodies (Little et al., 2007), and behaviors (Gangestad et al., 2004). In one study, women in the fertile phase exhibited more flirtatious behavior toward men displaying social dominance (Cantú et al., 2013). These cycle shifts were initially predicted because, ancestrally, mating with males bearing phenotypic markers of "good" genes would have been most beneficial during the fertile phase of the cycle (Gangestad and Thornhill, 1998; Penton-Voak et al., 1999; see Roney, 2009 for review). Ovulatory cycle effects are also generally stronger when women evaluate men for a purely sexual relationship, as opposed to a committed one (e.g., Gangestad et al., 2004; Puts, 2005), which accords with a putative function in recruiting genetic benefits for offspring.

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Surprisingly, two recent meta-analyses came to opposite conclusions regarding the existence of ovulatory cycle shifts in women's mate preferences. Wood et al. (2014) reported little support; however, several elements of their analytical approach have been criticized (Gildersleeve et al., 2014b). For example, Wood et al. coded multiple studies for which effect sizes were unknown as "0.00" rather than as missing data, which would bias the estimated overall effect toward zero. The other meta-analysis employed multilevel models to account for the nested nature of effects and aggregated across male traits in overall analyses (Gildersleeve et al., 2014a). This analysis concluded that ovulatory cycle effects are robust, not due to publication bias alone (as indicated by *p*-curve analysis; see Simonsohn et al., 2014), and are confined to women's preferences for men in a purely sexual mating context. However, analyses of women's preferences for specific male characteristics revealed that some cycle shifts were not robust or require additional research before these shifts can be established with confidence.

An examination of 22 heterosexual women's subjective and genital arousal to male and female sexual stimuli during both the follicular and luteal phases revealed no evidence of increased arousal to male stimuli during the follicular phase (Bosio et al., 2014). This study utilized a within-subjects design, which greatly reduces the sample size needed to observe ovulatory cycle effects (Gangestad et al., 2015), and cycle phase was hormonally validated. These results thus provide evidence (contra Buller, 2005) that sexual interest in specific male traits, rather than attraction to males generally, shifts over the ovulatory cycle.

As methods are refined, it will become clearer how and to what degree women's preferences shift over the cycle. Within-subjects designs and hormonal validation of cycle phase are particularly likely to advance knowledge (Gangestad et al., 2015). Hormone assays may be especially useful because the mechanisms underlying these shifts are almost certainly endocrine. Initial attempts to estimate hormonal effects assigned hormone levels using participants' self-reported cycle information and published data on daily hormonal averages. These reports suggested that women's preferences for masculine traits might correlate negatively with progesterone, and positively with estradiol and prolactin (Garver-Apgar et al., 2008; Jones et al., 2005; Puts, 2006).

A few studies have assayed hormones to explore relationships with women's preferences. Welling et al. (2007) compared women's preferences for masculine faces at two points in the ovulatory cycle and found stronger preferences during the session when testosterone levels were higher, but did not relate preferences to measured hormone levels directly. Using within-subjects designs, Roney and colleagues (Roney and Simmons, 2008; Roney et al., 2011) found that estradiol, but not testosterone or progesterone, predicted increased preferences for the faces of men with high testosterone levels. Marcinkowska et al. (2016) found no relationship between women's estradiol levels and preferences for men's facial masculinity. However, they used a between-subjects design and a sample less than half the size needed to detect an effect of $d = 0.5$ with 80% power (Gangestad et al., 2015). Using a within-subjects design, Pisanski et al. (2014) found that changes in estradiol, but not progesterone, trended toward ($p < 0.06$) predicting increased preferences for masculine voices. These mixed results point to the need for further research to determine the hormonal correlates of any cycle shifts in women's mate preferences.

Near ovulation, women have also reported higher rates of extra-pair copulation (Baker and Bellis, 1995; see Section 5.1) and greater extra-pair sexual attractions (Gangestad et al., 2002, 2005; Pillsworth and Haselton, 2006; Larson et al., 2012) and flirtation (Haselton and Gangestad, 2006), as well as feeling less close to and more critical of their primary partner, particularly if he was less sexually attractive (Larson et al., 2013). One study explored hormonal predictors of these cycle shifts. In 33 women, each sampled twice, estradiol positively predicted extra-pair interest and negatively predicted in-pair interest, and progesterone positively predicted in-pair interest (Grebe et al., 2016). However, another study of 15 partnered women, each sampled daily across 1–2 menstrual cycles (Roney and Simmons, 2016) reported a dip in in-pair attraction during the luteal phase (contra Grebe et al., 2016). Besides the differences in sample size and numbers of repeated observations per women, these studies also differed in that Grebe et al.'s sample was generally very committed, whereas at least one-third of Roney & Simmons's sample were not paired with their partner for the full two months of the study.

6.2. Female orgasm

Although the endocrine surges in prolactin, luteinizing hormone, and oxytocin that accompany women's orgasm may have originally evolved in mammals in the context of copulation-induced ovulation (Pavličev and Wagner, 2016), these and other components of women's orgasm may subsequently have been shaped to function in mate choice (Wheatley and Puts, 2015). Some evidence suggests that women's orgasm functions to promote pair-bonds and male investment (for review, see Wheatley and Puts, 2015). Oxytocin levels peak during orgasm (Blaicher et al., 1999; Carmichael et al., 1987, 1994) and are elevated among women in romantic relationships (Schneiderman et al., 2012; Taylor et al., 2006; Turner et al., 1999), suggesting an influence on affiliation, emotional closeness, and pair-bonding.

Arguably more compelling evidence suggests that female orgasm promotes conception, perhaps especially with males of high genetic quality. For example, women have been found to report more frequent and earlier-timed orgasms with male sexual partners who are putatively higher in genetic quality (Puts et al., 2012d). Orgasm may facilitate fertilization by reinforcing copulation with such males and motivating continued copulation until ejaculation occurs (Puts and Dawood, 2006, 2012; Puts et al., 2012b). Oxytocin also induces peristaltic contractions of the uterus and oviducts (Knaus, 1950; Wildt et al., 1998), which help transport sperm toward the ovum (Kunz et al., 2007; Wildt et al., 1998; Zervomanolakis et al., 2007), and orgasmic prolactin surges may help capacitate sperm (make them capable of fertilizing the ovum; Meston et al., 2004).

Moreover, orgasm appears to be more common during the fertile phase of the ovulatory cycle (Matteo and Rissman, 1984; Udry and Morris, 1968), which is compatible with a function in promoting conception with males who are able to induce it. In a study of romantically involved heterosexual couples, normally-cycling women reported more orgasms if their partner had immune system genes that were compatible with theirs, but only during the fertile phase of the ovulatory cycle (Garver-Apgar et al., 2006). Although no studies of which we are aware have explored which hormones drive any cyclic changes in orgasm, treatment studies indicate that testosterone (Buster et al., 2005; Sherwin and Gelfand, 1987) and estradiol (Dennerstein et al., 1980) increase women's frequency of experiencing orgasm. As these hormones peak during the late follicular phase and may increase women's libidos, they may also promote conception with good-genes males via orgasm.

7. Motherhood

Conception initiates the next major life history stage, motherhood. However, the transition to motherhood first depends on a successful pregnancy that carries to term, and this appears to track the propitiousness of the reproductive conditions. Because reproduction is extremely costly, selection would tend to favor mechanisms to terminate pregnancy if the offspring is likely to be low in quality, or if circumstances are poor for the mother—for example, if she has poor access to resources, is ill, or is experiencing intense psychosocial stress. Indeed, early pregnancy loss approaches 75% for reproductive-age women, primarily due to chromosomal or other defects (Holman and Wood, 2001). Very early pregnancy loss is also associated with high levels of the stress hormone cortisol (Nepomnaschy et al., 2006), perhaps because high cortisol is associated with increased progesterone and gonadotropin levels during the follicular phase and decreased progesterone levels during

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the mid-luteal phase (Nepomnaschy et al., 2004). Such excessive or poorly timed LH surges have been hypothesized to impair follicular development (Ferin, 1999), but it is yet unclear whether elevated follicular-phase progesterone or LH is associated with pregnancy loss in humans. Some work suggests that early pregnancy loss is associated with inadequate luteal progesterone and/or elevated follicular progesterone (Vitzthum et al., 2006). However, the robustness of the link between stress and reduced fecundability remains debated and merits further investigation.

A successful pregnancy stimulates a cascade of physiological and psychological changes to the female body (Jones and Lopez, 2013; Uvnäs-Moberg, 1996). In many species, hormonal and neurogenic mechanisms such as oxytocin, vasopressin, and prolactin trigger maternal behavior, such as caring for and protecting the young (as in prairie voles, Bales et al., 2007; and humans, Carter, 2014; Feldman et al., 2010). Specifically, the neuropeptide oxytocin has been implicated in affiliative social behavior in female mammals across a variety of species (in rats, Champagne et al., 2001; and in women, Preckel et al., 2014; Scheele et al., 2013). Some work suggests that approach behaviors may be facilitated with doses of oxytocin in new mothers in humans (Mah et al., 2015; Preckel et al., 2014; Taylor, 2006), but the lasting effects are yet unclear.

Evidence from human studies suggests that, following parturition, a mother's attachment to her infant provides the foundation for the infant's later mental health and adaptation through maternal sensitivity (Feldman, 2016; Schoenmaker et al., 2015; van Ijzendoorn et al., 1999; Wolff and Ijzendoorn, 1997). Maternal sensitivity depends on interactions between the mother's brain and endocrine system (for review of maternal behavior in mammals generally, see Bridges, 2015; Numan and Sheehan, 1997; Pedersen, 1997; social attachment in rodents, Carter, 1998). Pituitary hormones, as well as peripheral endocrine tissues (e.g. ovaries, adrenal glands, and placenta), act on the hypothalamus and other regions of the central nervous system to stimulate and modulate the expression of maternal behavior (for review, see Bridges, 2015). The link between the hypothalamus and the pituitary gland works to mediate the release and subsequent actions of neuroactive hormones as part of a feedback system (Fleming et al., 1997), allowing the mother to regulate her behavior in response to her young (Numan and Sheehan, 1997; Pedersen, 1997).

At parturition, there is a sharp increase in prolactin, which is involved in milk production and accelerated growth of mammary tissue during pregnancy in humans (Freeman et al., 2000; Hinde and Milligan, 2011; Neville et al., 2002), as well as promoting maternal behavior, such as licking and grooming in rodents (Bridges et al., 1985; Rosenblatt, 1994). These hormonal events of late pregnancy (rising estrogen and prolactin, and declining progesterone) are further necessary for stimulating the onset of maternal behavior (Carter, 1998; Numan et al., 1994; Numan and Sheehan, 1997).

Breastfeeding itself integrates multiple bodily systems, for instance increasing the mother's food intake while suppressing her fertility to allow her child to grow before she produces another. Lactation suppresses the metabolic hormones, insulin and leptin, and induces neuropeptide Y expression, contributing to increased appetite in order to meet its own energetic demands (Smith and Grove, 2002; Smith et al., 2010). At the same time, breast stimulation via nursing suppresses GnRH secretion (Smith et al., 2010), so that the LH surge needed to induce ovulation is also suppressed (McNeilly et al., 1994). The result is lactational amenorrhea, which acts as a natural birth spacer across populations. In both American mothers and !Kung hunter-gatherers of Botswana, more intense nursing behavior leads to longer amenorrhea and hence longer inter-birth intervals (Konner and Worthman, 1980; Stern et al., 1986), perhaps adaptively adjusting the length of investment in an infant in proportion to its vigor and caloric needs.

Some research also indicates a relationship between motherhood and testosterone. At least two studies have reported lower testosterone among human mothers, particularly young mothers (Barrett et al., 2013; Kuzawa et al., 2010). In a sample of 67 Filipino women, mothers had lower testosterone than non-mothers, and in both this sample and a sample of 195 Norwegian women, mothers of younger children had lower testosterone than mothers of older children. Among heterosexual women, being in a committed, monogamous relationship is also associated with lower testosterone (Barrett et al., 2013; Edelstein et al., 2011; Kuzawa et al., 2010; van Anders and Watson, 2006; but see Hooper et al., 2011). Thus, it is possible that motherhood lowers testosterone levels as a means of channeling reproductive effort toward parenting rather than mating, as appears to be the case in men (Kuzawa et al., 2009; Puts et al., 2015). However, the direction of any relationship remains unclear; lower testosterone may also contribute to being in a relationship and having young children, perhaps because testosterone influences attractiveness (Puts et al., 2012c; Wheatley et al., 2014), fertility (reviewed in Wheatley et al., 2014), and thus perhaps birth spacing.

Critically, while extensive animal work has elucidated the role of various endocrine mechanisms in non-human parent-infant bonding, empirical data in humans remains sparse. Understanding the neurobiology of normal human parental attachment and parenting behaviors is also likely to shed light on clinical cases such as postpartum depression (Kim et al., 2015).

8. Menopause

Menopause is a life history transition in which fertility declines more rapidly than other aging processes (Kirkwood and Shanley, 2010), resulting in follicular depletion and permanent cessation of menstrual periods (Burger et al., 1995; Burger et al., 2008; Hulka and Meirik, 1996; Soules et al., 2001). Although an extended post-reproductive life has been observed occasionally in at least 35 different mammalian species (for review, see Cohen, 2004), its ubiquity in humans appears to distinguish us from other primates (Levitis et al., 2013). In a sample of nonhuman primate species, only a small minority of individuals experienced reproductive senescence in species in which it occurred (Alberts et al., 2013).

The function of menopause in humans may relate to the long period of offspring dependency. In forager societies, each child that survives to adulthood represents approximately 18 years of parental investment (Lancaster and Kaplan, 2009). This pattern is strikingly different from that of our closest living relatives, chimpanzees, in which offspring begin to provide for themselves early in development and are calorically independent from their mothers in the first decade of life (Kaplan et al., 2000).

Although men provide the majority of calories for offspring in forager societies, women are the primary caregivers (Kaplan et al., 2000). If women continued to reproduce throughout their entire lives, then upon their deaths, they would likely leave some children who would not survive. Some reproductive effort, then, might be more profitably directed toward existing offspring and grand-offspring. One perspective regarding the functional role of menopause is the “stopping early” hypothesis. Williams (1957) proposed menopause as an adaptation to the long period of human juvenile dependency. According to this hypothesis, early termination of fertility would evolve when extended maternal care became crucial to offspring survival. Thus, post-reproductive female investment decreased the age of female fertility cessation in our lineage without altering longevity (Williams, 1957). Menopause may thus represent a shift from mating effort to investing in current offspring.

Alternatively, Hawkes et al. (1997, 1998) proposed that women do not reach reproductive senescence early relative to other primates; rather, they continue to live long after reproductive senescence – which is what is unique and interesting about women (Hawkes et al., 1998; Hawkes, 2003, 2010). Further, Hawkes proposed that women's post-reproductive lives have been extended because grandmothering has slowed aging (senescence of other physiological systems) by increasing selection against late-acting mutations and/or by other means (Hawkes et al., 1998; Hawkes, 2003, 2010).

Consequently, menopause brings with it reduced libido, sexual thoughts and fantasies, vaginal lubrication, coital frequency, and satisfaction with sexual partners (McCoy and Davidson, 1985). In addition, women's mate preferences may shift away from mates putatively high in genetic quality and toward investing mates (Jones et al., 2011).

As noted in Section 5.2, these changes are likely to reflect declining estradiol and testosterone levels (Lasley et al., 2002). During the perimenopausal period, FSH and LH levels increase, and progesterone levels drop as ovulation ceases – with high variability in each of these changes (Soules et al., 2001). Endocrine changes associated with menopause begin around age 40 when FSH levels begin to rise and the loss of ovarian follicles markedly accelerates (Burger et al., 1995), initiating a change in menstrual cycle frequency. Within one year of the last menstrual cycle, FSH spikes, and estrogen levels drop significantly (Derry, 2002; Hawkes, 2010; Kim et al., 2014; Pavelka and Fedigan, 1991).

9. Discussion

Beginning with early development, human female sexuality and reproduction respond to hormonal changes as a way of adjusting reproductive phenotypes to life history transitions, context, and time of day or ovulatory phase. Evidence from multiple sources, including gender reassignment, CAH, and CAIS, supports the notion that prenatal androgens are fundamental to early neurobehavioral sexual differentiation. Puberty represents another life history transition in which neural development works in concert with endocrine changes, initiating a cascade of physical, psychological, and social changes. The timing of this transition is crucial for providing the foundation for one's life history strategy, including the timing of maturation and first reproduction, and the degree of investment in offspring.

Through puberty and beyond, women compete for mates and possess hormone-dependent sexual ornaments that appear to advertise reproductive potential to prospective mates. Testosterone may serve a competitive function in women, but the contexts under which testosterone alters women's behaviors remains elusive and appears complex. Women also exhibit relatively cryptic fertile windows in their ovulatory cycles (Nunn, 1999), meaning that compared to most female primates, women's observable phenotypes are less tethered to cyclic fluctuations in ovarian hormones. Women's sexuality extends across the cycle, likewise implying that their libidos are emancipated from ovarian hormones. Yet, this decoupling is only partial. Women's attractiveness and libido in fact shift across the cycle with ovarian hormones, raising intriguing questions about evolutionary causes and hinting at roles of pair-bonding and extra-pair mating. If ovulation is concealed and copulation occurs throughout the cycle, then a mid-cycle rise in libido could promote extra-pair copulation in order to recruit good genes, while retaining non-genetic benefits conferred by the pair-bond partner (Thornhill and Gangestad, 2015). Indeed, women have been found to exhibit greater sexual preferences for putative cues to male genetic quality at mid-cycle, and this shift appears to be driven by ovarian hormones. Similarly, although women experience increased libido at mid-cycle, they generally do not have more sex with their long-term partners. Instead, they have more extra-pair sex and fantasies at mid-cycle, particularly if the long-term mate is low in putative indicators of genetic quality.

A constellation of hormonal changes coordinates pregnancy, lactation, and maternal behavior, as well. Cortisol appears to mediate stress-related early pregnancy loss, for example, while breastfeeding prevents ovulation by suppressing GnRH levels as a means of natural birth spacing. Oxytocin, vasopressin, and prolactin trigger maternal behavior, while prolactin stimulates milk production. To meet the metabolic demands of nursing, breastfeeding increases appetite by suppressing insulin and leptin levels. As women approach mid-life reproductive senescence, ovarian steroid levels decrease—with high variability among women (Soules et al., 2001). These endocrine changes may serve to reduce mating effort in women in order to intensify investment in their existing offspring and grand-offspring (Hawkes and Smith, 2010).

Although a coherent picture is emerging, many important questions remain unanswered about how hormones coordinate women's reproduction and reproductive behaviors. For example, much research has been correlational, leaving causal relationships unclear. Placebo-controlled treatment studies are needed, but longitudinal correlational studies can also help shed light on causality where true experiments are unethical or infeasible. Measuring or manipulating hormones and phenotypic correlates repeatedly within subjects can also clarify the timescale of any relationships. In most cases, the underlying mechanisms are incompletely understood. What are the physiological pathways that regulate hormone secretion, and how do hormones regulate the expression of specific genes in different target tissues? How does this affect the development of the nervous system and its activity on more acute timescales? At the present state of technology, animal models may be required, particularly anthropoid primates, due to apparent differences in the hormonal mechanisms underlying human and rodent brain sexual differentiation. Imaging studies, including MRI and fMRI, would illuminate how the brain is differentially organized and activated by hormones. Finally, as the forgoing review makes apparent, more fieldwork is needed to elucidate the magnitude of effects outside of the laboratory in more naturalistic settings.

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Appendix A. Supplementary data

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