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C29

CHAPTER

29

Hormones and Human Mating

James R. Roney

Abstract

Hormones are integral to the regulation of mating behavior in most sexually reproducing species and are likely to have similar importance for human mating. This chapter reviews major research themes regarding the role of endocrine variables in the adaptations that implement human mating psychology and behavior, including the roles of hormones in the development of sexual orientation, the regulation of sexual motivation and its trade-offs with competing motivational priorities, the relationship between hormones and attractiveness, and the role of hormones in the regulation of mate preferences. Investigation of the endocrine predictors of specific variables can help to arbitrate between competing theoretical arguments regarding human mating, and the chapter systematically reviews the relevant data on hormone variables within the context of these theoretical debates. As a broad generalization, accumulating evidence in humans supports roles for gonadal hormones in regulating shifts in the allocation of behavioral and somatic effort toward mating versus alternative adaptive problems. In women, evidence supports the ovarian hormones estradiol and progesterone acting as a two-signal endocrine code that indexes temporal fluctuations in fecundity and increases the prioritization of sexual motivation when fecundity is elevated. In men, accumulating evidence supports testosterone as a signal that regulates trade-offs between effort invested in mate-seeking and mate competition versus in survival effort and investment in pair- bonds and paternal care. Similar patterns in many nonhuman species suggest that phylogenetically ancient roles for hormones have been partially conserved in humans and continue to exert important effects on human mating psychology and behavior.

Key Words: estradiol, progesterone, testosterone, sexuality, menstrual cycle

C29.S1

Introduction: The Theoretical Framework Approach to Behavioral Endocrinology

C29.P1

Endocrine variables play major roles in the regulation of mating behaviors across sexually reproducing species. Hormonal signals both regulate and respond to gamete (i.e., sperm and egg) production and maturation, which makes these signals well-positioned to coordinate sexual psychology and behavior with the physiological conditions necessary for reproduction (Adkins-Regan, 2005). These statements are as true for humans as for

other sexually reproducing species. This chapter reviews broad themes in the extant literature regarding the endocrine regulation of human mating psychology and behavior. The chapter takes a functional approach throughout in which hormones are viewed as signals that evolved to coordinate multiple, adaptive responses to the input conditions that trigger changes in hormone concentrations. I introduce that approach in what follows, before turning specifically to empirical research programs that investigate the endocrinology of human mating.

C29.S2 ### *Theoretical Frameworks for Behavioral Endocrinology*

C29.P2 Elsewhere, I have recently argued for a specific approach to building theories regarding the functions of hormones (Roney, 2016a). This approach is predicated on the well-supported observation that hormones are typically released into the general circulation, whereby they can affect multiple, diverse outcomes simultaneously. In many cases, these diverse outcomes can be seen as coordinated, adaptive responses to the input conditions that triggered changes in hormones. Given these premises, a logical way to build functional theories of endocrine signals is to catalog how input conditions that affect hormone production are mapped into coordinated output responses caused by the changes in hormones. I have called these listings of input–output mappings "theoretical frameworks" for specific hormones. The explicit construction of theoretical frameworks provides an efficient means of discovering the functions of endocrine signals (Roney, 2016a; see also Gangestad & Grebe, 2017).

C29.P3 A concrete example of a partial theoretical framework concerns seasonal shifts in male testosterone production in seasonally breeding species. During the breeding season, males of many species increase their testosterone production in response to input cues such as photoperiod or the presence of fertile females; conversely, during the nonbreeding season, testosterone often falls to castrate levels (for reviews, see Daly & Wilson, 1983; Ketterson & Nolan, 1992; Muller, 2017; Wingfield et al., 1990). On the output side of the equation, androgens are well known to promote the growth of ornaments and armaments such as antlers, horns, or bright coloration; to support investment in skeletal muscle mass; but also to produce psychological and behavioral changes such as increased sexual motivation and intrasexual aggressiveness. Androgens appear to obtain energy for these output effects by suppressing energetic investments in survival-related functions such as immune responses and fat storage, and as a result, illness and food shortage are additional input conditions that reduce testosterone production in order to avoid these output effects when they would be especially harmful to survival prospects (see Bribiescas, 2001; Folstad & Karter, 1992; Ketterson & Nolan, 1992). Figure 29.1 summarizes this list of input conditions and output responses associated with seasonal changes in testosterone production in a way that provides a simple visual depiction of a partial theoretical framework.

C29.P4 Importantly, the theoretical framework depicted in figure 29.1 strongly suggests a core functional logic that *explains* the input–output mappings associated with testosterone

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rather than merely describing them. The output effects of elevated testosterone are multiple and diverse but are unified in promoting successful mate competition at precisely the time when such competition can facilitate reproductive success (i.e., when females are fecund during the breeding season). During the nonbreeding season when conception opportunities are absent, conversely, the drop in testosterone reduces the display of risky behaviors and reallocates energy into survival functions such as fat storage and immune responses, all of which should promote survival to the next breeding season in better physical condition. Natural selection may have used testosterone as the signal that mediates these input–output relationships because of its phylogenetically conserved role in the regulation of sperm production, since reproductively relevant inputs and outputs that were added over evolutionary time would all be efficiently coordinated with male fertility.

C29.P5 The theoretical framework approach becomes more complex when one considers that different aspects of input contexts can affect multiple hormonal signals simultaneously, all of which may interact to influence specific patterns of output responses. As explained more fully in Roney (2016a), the simultaneous influence of multiple endocrine signals can greatly expand the specificity and nuance of responses to specific variations in input conditions. Indeed, one can conceive of different combinations of baseline and reactive hormone values as endocrine codes that respond to adaptively relevant constellations of eliciting conditions, and that in turn prime coordinated downstream effects that are functional responses to those circumstances. Looked at in this way, behavioral endocrinology is an exercise in code-breaking. The codes being cracked, furthermore, describe the functional properties of psychological adaptations that map adaptively significant input circumstances to the evolved responses to the inputs in question.

C29.S3 ### *Theoretical Frameworks Related to the Endocrinology of Human Mating*

C29.P6 The theoretical framework approach can also provide an integrated, functional perspective on the role of hormones in human mating psychology and behavior. At times in the extant literature, hormones are treated as somewhat arbitrary variables that are associated with certain mating-relevant outcomes, or as signaling devices that indicate attractiveness or other externally observable properties. Viewing hormones as internal signals that jointly mediate functional input–output mappings can help to explain why hormone concentrations might in some cases predict outcomes such as perceived physical attractiveness, while also potentially explaining circumstances under which such correlations will be absent.

C29.P7 The partial theoretical framework depicted in figure 29.1 provides a prototypical example of the way that hormones affect mating psychology and behavior. Hormones often act as signals that coordinate shifts in the investment of resources in mating effort versus in efforts to address alternative adaptive problems. This general principle can organize many findings regarding the roles of hormones in human mating psychology at a range of different timescales, as explained in the sections that follow. Much of this chapter focuses on

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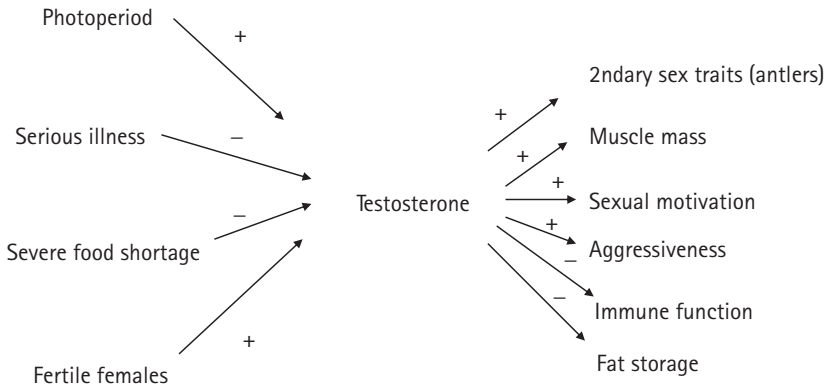

C29.F1 **Fig. 29.1** An example theoretical framework depicting common input–output relationships for testosterone among males of seasonally breeding species.

activational (i.e., reversible, relatively short term) effects of hormones, but organizational (i.e., relatively irreversible, developmental) effects are also important for understanding human mating psychology and are reviewed first in the next section.

C29.S4 ## Organizational Influences of Hormones on Human Mating Psychology and Behavior

C29.P8 It is well established that hormones exert organizational effects on the sexual differentiation of vertebrate phenotypes, including brain mechanisms that regulate mating behaviors. In mammals, genes on the Y chromosome promote prenatal development of testes that in turn lead to greater androgen production in males than in females; androgens like testosterone, in turn, alter gene expression governing development, providing a mechanism for the emergence of phenotypic sex differences (reviewed in Breedlove & Hampson, 2002). Organizational effects of hormones provide clear examples of the coordinating functions of endocrine signals, as they provide a broad means of coordinating sex-specific morphologies (including genitalia, reproductive tracts, and other sex-differentiated components of the body) with sexually selected behavioral strategies implemented by the brain. Given these organizational effects, it is likely that many sexually differentiated aspects of mating behaviors are influenced by hormones, making endocrine signals indispensable to comprehensive accounts of mating psychology and behavior.

C29.P9 In principle, variation in early hormone exposure may also explain within-sex variability in mating psychology and behavior. One prominent topic to which this idea has been applied is sexual orientation. In many nonhuman species, experimental manipulations of pre- or early postnatal androgen exposure can produce sex-atypical sexual behaviors and partner preferences (e.g., Phoenix et al., 1959; reviewed in Adkins-Regan, 1988). In humans, more indirect evidence supports early androgen exposure as a cause of sexual orientation. First, individuals with an XY karyotype who do not respond to androgens

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due to complete androgen insensitivity syndrome (CAIS) present a female-typical external phenotype and report sexual attraction to men (e.g., Wisniewski et al., 2000; reviewed in Motta-Mena & Puts, 2017). This supports the necessity of androgen signaling for male-typical development and gynephilia (i.e., attraction to women) in humans. Second, the possible attribution of androphilia (i.e., attraction to men) in CAIS individuals to socialization as females and not to androgen deprivation is refuted by cases in which XY individuals with male-typical prenatal androgen exposure were reared as females. These cases involved either surgical accidents that damaged the penis in infancy or cloacal exstrophy (an abdominal abnormality that causes malformation of the penis), and entailed both early surgical reassignment and social rearing as females. Despite these interventions, in all seven cases in which published studies surveyed sexual attraction after puberty, the individuals in question reported predominant or exclusive ~~to~~ attraction to women (reviewed in Bailey et al., 2016). Third, XX karyotype individuals with congenital adrenal hyperplasia (CAH)—a condition in which prenatal androgens can be highly elevated—often experience partial masculinization of genitalia and higher rates of gynephilia than do women without CAH, although the majority of such women do in fact report predominant attraction to men (Bailey et al., 2016). Thus, all of these cases demonstrate associations between prenatal androgen exposure and human sexual orientation, and indeed these and other lines of evidence support a dose-related relationship between amount of prenatal androgen exposure and the likelihood of exhibiting androphilia versus gynephilia (Motta-Mena & Puts, 2017).

C29.P10 Although the above lines of evidence strongly support a role for prenatal androgens in the determination of human sexual orientation, it is nonetheless the case that hormone exposure alone does not appear fully explanatory. For instance, women with CAH in some cases have prenatal androgen exposure comparable to males and yet the majority of such women report sexual attraction to men. This and other evidence led Bailey et al. (2016) to suggest that something other than androgen exposure that is associated with the Y chromosome may predict gynephilia, although whatever that might be cannot be completely necessary or there would be no cases of XX karyotype individuals experiencing attraction to women.

C29.P11 Rice et al. (2012) presented a theory of epigenetic influences on human sexual orientation that can potentially resolve ambiguities associated with hormonal influences. They reviewed evidence that in both rats and humans, the degree of prenatal androgen exposure shows more overlap between the sexes than is commonly appreciated. This in turn should exert selection pressures to canalize degree of androgen signaling to avoid discordances between genital and brain development. Epi-marks (such as DNA methylation) that are added during early embryogenesis are capable of amplifying or blunting androgen signaling. Rice et al. proposed that such epi-marks are the canalizing mechanism that prevents fluctuations in prenatal androgen exposure from producing development that is discordant with genital sex. Homosexuality then results when an epi-mark inherited on

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a gamete from an opposite-sex parent fails to be erased during early development and is stronger in its effects than the new epi-mark that is added during embryogenesis. They also presented a mathematical model of selection pressures demonstrating that mutations for such canalizing epi-marks can invade a population under a range of plausible parameter values when the fitness costs of same-sex attraction are limited by such attraction being expressed in only a relatively small percentage of opposite-sex offspring. Eventually, over time, modifier loci that limit carryover of parental epi-marks that affect androgen signaling related to sexual attraction would be expected to evolve, but time lags may be common for this variable given that the stimuli that determine sexual attraction change frequently with speciation events.

C29.P12 The theory presented by Rice et al. (2012) has not been definitively tested via identification of the relevant epi-marks, to my knowledge, but its logic can account for many known patterns. Relatively low rates of gynephilia in XX karyotype women with CAH make sense, for instance, if such women have female-typical epi-marks that blunt the effects of their elevated prenatal androgens. Likewise, since epi-mark erasure and addition are somewhat stochastic during development, the theory can account for discordances between monozygotic twins in sexual orientation (reviewed in Bailey et al., 2016). Importantly, epi-marks can be specific to different targets of androgen signaling, which can help account for the mosaic nature of same-sex sexual orientations in that, for example, somatic development is usually sex typical even as the target of sexual attraction is sex atypical. Finally, the theory is consistent with all of the positive evidence for the organizing effects of hormones on sexual orientation, while resolving some empirical anomalies associated with the prenatal hormone hypothesis.

C29.P13 Epigenetic influences add considerable complexity to the study of organizational effects of hormones in humans since variables like epi-marks are very difficult to measure and can vary in their influences across different outcomes. Nonetheless, research has attempted to examine putative markers of early androgen exposure in order to explain within-sex variability in additional mating-relevant variables other than sexual orientation. For example, the ratio of the lengths of the second to fourth digits on human hands (2d4d ratio) has been argued to reflect levels of prenatal androgen exposure during digit development (reviewed in Manning, 2002). Because androgens often organize the development of sexually selected traits in mammals, higher prenatal androgens indexed by 2d4d ratio could in principle explain trait-like, within-sex individual differences that persist into adulthood. Some research consistent with this has shown correlations between digit ratio and putatively androgen-dependent outcomes such as athletic ability, performance on spatial cognition tests, sperm production in men, levels of facial masculinity, and more dominant or aggressive behaviors (reviewed in Manning, 2002). However, some comparably powered attempts to test correlations between 2d4d and a suite of potentially androgen-dependent variables (including number of sex partners) have produced largely null results (e.g., Putz et al., 2004), and meta-analyses have reported either null or very

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small magnitude overall correlations between digit ratios and androgen-related behavioral variables (e.g., Hönekopp & Watson, 2011; Turanovic et al., 2017; Voracek et al., 2010; cf. Hönekopp & Schuster, 2010, for evidence of a reliable meta-analytic effect for measures of athletic ability).

C29.P14 Polymorphisms in the androgen receptor (AR) gene have also been investigated as possible influences on the organizational effects of hormones that may impact mating psychology and behavior. The number of cytosine-adenine-guanine (CAG) repeats in the AR gene varies continuously in humans, and evidence supports shorter repeat lengths predicting greater gene transcriptional activity mediated by the AR when the AR is bound by hormones like testosterone (Chamberlain et al., 1994). Because androgens regulate the expression of many different genes, polymorphisms in the AR gene could act as a type of dial that calibrates the magnitude of responses to circulating androgens in a coordinated way across the entire organism (see Simmons & Roney, 2011). This calibration should apply to both organizational and activational effects of hormones, with the expectation that individuals with shorter CAG repeat lengths will have more androgenized phenotypes per unit of androgen that they produce. Some studies have reported that men with shorter CAG repeat lengths exhibit stronger androgen-related outcomes related to intrasexual competition, such as greater muscle mass (Nielsen, 2010), physical strength (Simmons & Roney, 2011), and violent and aggressive behavior (e.g., Butovskaya et al., 2015; Rajender et al., 2008), although findings for these variables have been mixed and appear to vary across different ecological environments (Campbell et al., 2009; Ryan et al., 2017). Because androgen-dependent outcomes jointly depend on both androgen production and AR sensitivity, polymorphisms in the AR gene alone may not consistently predict phenotypic outcomes due to both developmental and contextual variability in hormone production. Rather than strongly predicting trait-like individual differences in mating-relevant traits, then, AR gene polymorphisms may have more explanatory power as moderators of the effects of context-specific shifts in hormone production (e.g., Roney et al., 2010).

C29.P15 In summary, converging lines of evidence support an important role for prenatal hormones in causing the development of human sexual orientation, and there is every reason to believe that similar organizational effects of hormones cause the sexual differentiation of brain mechanisms involved in other aspects of human mating psychology. The study of organizational effects of hormones in humans is especially challenging, however, given the inability to experimentally manipulate early hormone exposure. Attempts to use measurable markers of the magnitude of early hormone exposure have met with mixed success in predicting phenotypic outcomes in adulthood, perhaps in part because there are many complex modifiers of androgen signaling, some of which, like epi-marks, are difficult to measure. Furthermore, if hormones do have as a basic function the coordination of adaptive responses to input circumstances that change over time, then we might expect a priori that activational effects of hormones that respond to such circumstances will not be overly

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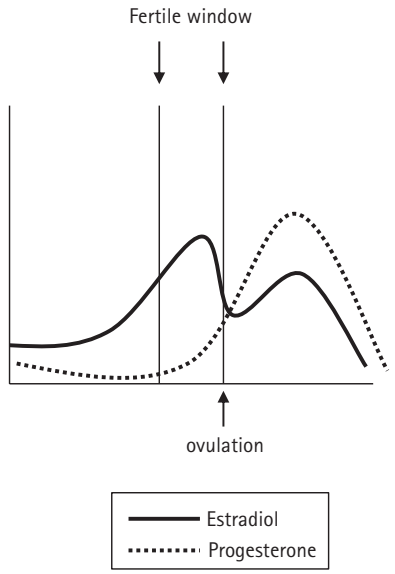
constrained by quantitative differences in within-sex early hormone exposure. The functional logic of such activational effects of hormones is the focus of the rest of this chapter.

C29.S5 **Ovarian Hormones and Human Mating**

C29.P16 An interesting aspect of the theoretical framework approach is the possibility that multiple hormones can combine in their effects to jointly coordinate functional responses to the eliciting conditions that triggered the changes in hormone concentrations. Here, I argue for a simple, two-signal endocrine code involving ovarian hormones that follows a straightforward functional logic. This two-signal system appears to be expressed in some form in most mammalian females that have been investigated, and I review evidence that it is also conserved in humans. The argument here surely entails simplifications of the relevant physiological processes, but it is also heuristically useful in providing a functional framework for organizing research findings on ovarian hormones.

C29.S6 *Estradiol and Progesterone as a Two-Signal Endocrine Code*

C29.P17 Figure 29.2 depicts the prototypical patterns of estradiol and progesterone production in an ovulatory human menstrual cycle. The increase in estradiol that occurs in the approach to ovulation is produced by the dominant follicle (the ovum and its surrounding support cells, with the latter producing estradiol) and is itself part of the mechanism that triggers the luteinizing hormone (LH) surge that causes ovulation, such that, as in other species, the estradiol surge is a reliable signal of impending ovulation. After ovulation,



C29.F2 **Fig. 29.2** Prototypical patterns of estradiol and progesterone secretion in ovulatory human menstrual cycles. From left to right, the "follicular phase" runs from the first day of menstruation until the day of ovulation; the "luteal phase" is all days after ovulation. The fertile window represents days when conception is possible.

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the follicle becomes a new structure called the corpus luteum, which continues to secrete estradiol but also secretes progesterone in high concentrations. The fertile window denotes the days of the cycle in which conception is possible, which in humans runs from approximately five days before ovulation through the day of ovulation itself (Wilcox et al., 1998). Estradiol and progesterone have local functions in the reproductive tract where they prepare the endometrium for possible attachment of a zygote and development of a subsequent embryo and fetus (reviewed in Hall, 2019; Lessey & Young, 2019), but they are also released into the general circulation whereby they can reach brain mechanisms that regulate psychology and behavior.

C29.P18 My proposal is that brain mechanisms largely read changing estradiol and progesterone concentrations as signals of *fecundity* (i.e., the likelihood of successful conception and subsequent gestation given unprotected copulation) (see Roney, 2015). It can be seen from figure 29.2 that the combination of high estradiol and low progesterone can be read as a code denoting high fecundity, whereas high progesterone itself can indicate low fecundity (at least at the within-cycle timescale). Thus, a simple way to increase the expression of a given behavior during high fecundity is to have brain mechanisms that promote the behavior be primed by estradiol but inhibited by progesterone, which should tend to couple the behavior to the fertile window. Conversely, specific behaviors can be reduced during the fertile window by reversing the direction of these effects, such that estradiol is inhibitory and progesterone excitatory. In this way, estradiol and progesterone can act as a simple two-signal endocrine code that coordinates behaviors with fecundity-relevant events in the reproductive tract.

C29.P19 There are clear functional reasons to increase the expression of sexual behaviors during fecund cycle days among females of most mammalian species. As an example, consider a rodent species in which males invest nothing in offspring other than genes. Females who engaged in sexual behavior when conception was not possible in this species would risk predation, injury, or infection and also incur opportunity costs of invested time and energy in order to exhibit a behavior that had no current fitness benefits. When conception was possible, however, promoting its occurrence would bring large fitness benefits, especially since in a short-lifespan species with high mortality rates, missed conception opportunities in fecund cycles could have significant effects on rates of reproduction. Based on this simple functional analysis, one expects motivation to shift between sexuality and alternative priorities based on current fecundity.

C29.P20 Consistent with this expectation, in most mammalian females, sexual and feeding motivation exhibit opposite cycle phase shifts, with sexual receptivity either restricted to or greatly enhanced on days when conception is possible (reviewed in Adkins-Regan, 2005; Beach, 1976; Roney, 2015), but with feeding and foraging at their nadirs within the same species-specific fertile windows (reviewed in Fessler, 2003; Schneider et al., 2013). Estradiol and progesterone cause these shifts via the exertion of opposite effects on the two motivational priorities. Estradiol increases female sexual motivation in basically all

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nonhuman mammalian species that have been directly investigated (reviewed in Blaustein, 2008; Roney, 2015; Thornhill & Gangestad, 2008), whereas progesterone at luteal phase concentrations is inhibitory (reviewed in Roney et al., ~~in press~~). Conversely, estradiol administration reduces food intake in ovariectomized females, whereas subsequent progesterone injections in the same animals reverse the effects of estradiol and return eating to the ovariectomized baseline levels (e.g., Bielert & Busse, 1983; Kemnitz et al., 1989; reviewed in Asarian & Geary, 2006). This overall pattern of findings suggests that multiple brain mechanisms read estradiol and progesterone fluctuations as a two-signal code for fecundity, but by responding to this code in opposite ways, an increase in sexual motivation is coordinated with a decrease in feeding motivation during the fertile window when the relative fitness benefits of sexual behavior are at their highest.[1]

C29.P21 Is this two-signal endocrine code conserved in humans? Many studies have provided evidence that measures of women's sexual motivation are higher during the fertile window than at other times of the menstrual cycle (reviewed in Motta-Mena & Puts, 2017; Roney, 2015; Wallen, 2001). This pattern is consistent with effects of estradiol and progesterone given their secretion patterns across the cycle, but until recently, no studies had provided direct evidence for hormonal regulation of these shifts. In a daily diary study in which women were sampled across one to two menstrual cycles, my lab reported positive, within-cycle correlations between fluctuations in estradiol and self-reports of sexual desire, and even larger negative correlations between progesterone and desire (Roney & Simmons, 2013). Jones et al. (2018a) also found negative within-women correlations between progesterone and self-reported desire in a sample of more than three hundred women sampled weekly for at least five weeks, as well some evidence for positive associations between estradiol and desire. More recently, Righetti et al. (2020) reported null within-cycle correlations between general sexual desire and changes in either estradiol or progesterone, although hormones were measured from urine samples that reflect broader and more variable temporal windows of hormone production than do the salivary measures that were collected in the prior studies. Thus, although further research on this question is warranted in humans, evidence supports estradiol and progesterone as opposing signals that regulate sexual motivation and that may causally generate fertile window shifts in women's sexual desire.

C29.P22 As in nonhuman mammals, evidence supports estradiol and progesterone having associations with women's feeding motivation that are opposite in sign to the hormones' associations with sexual desire. First, many studies have reported evidence for drops in women's food intake near ovulation when estradiol is high and progesterone low (Asarian & Geary, 2006; Fessler, 2003). Second, women in the Roney and Simmons (2013) study in which we assessed hormonal predictors of sexual desire were also surveyed about their daily food intake. For this dependent variable, we found that within-cycle changes in estradiol negatively predicted day-to-day changes in amount eaten, progesterone fluctuations positively predicted them, and the two hormones together statistically mediated a

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drop in food intake during the fertile window (Roney & Simmons, 2017). These findings support a phylogenetically conserved role for ovarian hormones in shifting women's motivational priorities between sexuality and alternative adaptive problems based on whether conception is currently possible.

C29.P23 The idea that an important function of hormones is to regulate shifts in the prioritization of alternative adaptive problems is a position that I have labeled "motivational priorities theory" (Roney, 2018).[2] Motivational priorities theory can be extended beyond the timescale of individual menstrual cycles in addressing the functions of ovarian hormones. For example, shifts in sexual motivation associated with lactation (during which sexual desire generally declines), menopause, and hormone replacement therapy all provide further evidence for this position in humans (reviewed in Roney, 2015, 2016a, 2018). Ovarian hormones have phylogenetically ancient roles in calibrating mating motivation, and such effects are likely to be foundational for understanding endocrine influences on mating dynamics in humans. Nonetheless, human mating systems have some relatively unique properties that may have changed the roles of ovarian hormones relative to other mammalian species. Some of those properties are addressed in the next section.

C29.S7 ### *Extended Sexuality, Pair-Bonding, and Endocrine Predictors of Female Attractiveness*

C29.P24 Contrary to most mammals in which sexual behavior is often largely confined to the fertile window, humans engage in high rates of nonconceptive sex, referred to as "extended sexuality." Extended sexuality is argued to evolve when females obtain material, nongenetic fitness benefits from nonconceptive sex (see Thornhill & Gangestad, 2008). In humans, those benefits were likely related to pair-bonding and its associated male investments in the welfare of their mates and offspring. Most major theories of the evolution of human pair-bonding posit that concealed ovulatory timing was a necessary step for the emergence of male investments in long-term mating (e.g., Lovejoy, 2009; Strassmann, 1981; Symons, 1979). Since sexual behavior confined to the fertile window would reliably reveal ovulatory timing, these arguments posit an extension of sexual receptivity beyond conceptive cycle days as part of the evolution of human pair-bonding. Based on these ideas, the basic biological function of women's extended sexuality is the formation and maintenance of long-term pair-bonds.

C29.P25 Elsewhere, I have argued that nonhormonal, social inputs to brain mechanisms regulating women's sexuality have effects that are additive to hormonal influences and that largely explain human extended sexuality (Roney, 2018). For example, research supports new relationship status as a positive predictor of women's sexual desire, and dyadic variables such as relative commitment to the relationship across the two partners may also moderate women's desire and rates of sexual initiation (reviewed in Roney, 2018, 2019). Such social inputs are proposed to promote the initiation and maintenance of pair-bonds, and by responding to social variables in a hormone-independent way, can maintain sexual receptivity even during anovulatory time periods. Thus, women's sexual motivation is

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proposed to be regulated by two broad input pathways: (1) a hormone input pathway that shifts motivation toward sexuality during the fertile window when the net ancestral fitness benefits of sex were likely to have been elevated, on average, and (2) a social input pathway that responds to mating opportunities and relationship dynamics to promote successful romantic relationships. Consideration of how these two pathways combine in their effects can be used to explain contexts in which women's sexual desire is elevated and conversely to explain cases of hypoactive sexual desire (Roney, 2019). The two-input pathway position is also important for understanding the limits of endocrine influences on women's sexuality, since in many contexts social variables may have stronger effects than do hormonal inputs.[3]

C29.P26 These arguments for the evolution of pair-bonding and extended sexuality carry implications for the possible effects of ovarian hormones on women's attractiveness. In many nonhuman species for which sexuality is largely confined to fecund cycle days, females often emit diagnostic cues of ovulatory timing, such as genital swellings or changes in odor (reviewed in Coombes et al., 2018; Dixson, 1998). Furthermore, as one would expect from the hormone secretion patterns depicted in figure 29.2, the same two-signal endocrine code implements these effects, with evidence supporting positive effects of estradiol and negative effects of progesterone on cues such as odor attractiveness across a range of different mammalian species (e.g., Baum et al., 1977; Ferkin & Johnston, 1993; Lucas et al., 1982; Michael et al., 1976). Concealment of ovulatory timing is a major component of theories for the evolution of human pair-bonding, however, which raises questions regarding the conservation of such hormone effects in humans.

C29.P27 Studies have reported that women's voices, odors, and faces are rated more attractive, on average, during the fertile window than at other times of the menstrual cycle (reviewed in Haselton & Gildersleeve, 2011, 2016). Some authors have suggested from such findings that human ovulation is not actually concealed (e.g., Kuukasjärvi et al., 2004; Singh & Bronstad, 2001). There is a clear tension between such statements and theories about the evolution of human pair-bonding. Data regarding the endocrine predictors of cycle phase shifts in stimulus attractiveness can contribute to this debate.

C29.P28 First, a statistically significant change in stimulus attractiveness does not necessarily mean that a cycle phase shift is large enough to be diagnostic of ovulatory timing. As an example of this, Havliček et al. (2006) showed that although women's odors were on average rated more attractive when collected at midcycle than when collected during menstruation or in the estimated luteal phase, it was nonetheless the case that between-women variability in odor attractiveness was much greater than within-cycle variability. This means that some women smelled consistently better outside the fertile window than did other women inside, which essentially leaves odor perceivers without clearly diagnostic information regarding ovulatory timing (see Roney, 2009). This is relevant to hormone effects, as well, since research designs may be able to detect statistically significant

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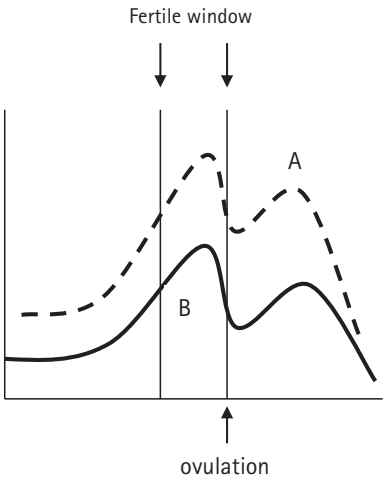
hormonal predictors of stimulus attractiveness that are nonetheless too subtle to be diagnostic of fertile window timing.

C29.P29 Second, different hormonal predictors of stimulus attractiveness carry different implications regarding the detectability of ovulatory timing. A positive effect of estradiol alone, for example, would not necessarily provide much information regarding ovulatory timing given between-women and between-cycle variability in production of this hormone. Estradiol tends to be elevated in cycles with greater conception probability (Lipson & Ellison, 1996). Figure 29.3 depicts estradiol production across two different ovulatory cycles, which could represent cycles from different women or from the same woman at different times. It can be seen from the figure that estradiol can be higher during the luteal phase of a higher fecundity cycle (point A) than it is inside the fertile window of a lower fecundity cycle (point B). Positive regulation of odor attractiveness by estradiol alone, then, would lead to cases in which nonfecund samples (point A) are rated more attractive than fertile window samples (point B), thus making odor an unreliable indicator of ovulatory timing (notice that even a woman's own partner could mistake point A as a fertile window day if their partner smells more attractive than usual on that day). Negative effects of progesterone on attractiveness, if large enough, by contrast, would more consistently reduce stimulus attractiveness during the luteal phase, after the fertile window had ended (see fig. 29.2).

C29.P30 These considerations suggest that one evolutionary pathway for concealing ovulatory timing might involve suppression of effects of progesterone on perceivable stimuli. If estradiol continued to affect stimuli, however, selection may have maintained men's preferences for cues associated with higher estradiol because those cues predicted higher



C29.F3 **Fig. 29.3** A depiction of estradiol secretion across cycle days of two different menstrual cycles that differ in their overall estradiol production.

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fecundity between cycles or across different women. In that case, within-cycle shifts in stimulus attractiveness would be by-products of mechanisms that track overall concentrations of estradiol (see Havlíček et al., 2015; Roney, 2009). In sum, positive effects of estradiol combined with weakened effects of progesterone on women's stimuli could generate shifts in women's attractiveness that follow the same patterns as the estradiol curves depicted in figure 29.3. Those patterns can generate subtle within-cycle shifts in attractiveness that nonetheless leave ovulatory timing effectively concealed.

C29.P31 Does existing evidence support primary regulation of cycle phase shifts in attractiveness via positive effects of estradiol? Puts et al. (2013) did not find that change in estradiol across two cycle days predicted change in women's face or voice attractiveness. However, the two days compared—near ovulation and in the estimated midluteal phase—do not typically differ much in mean estradiol. Their study did find a negative correlation between change in progesterone and change in both types of attractiveness, although there was such large variability between women in whether their high or low progesterone days were rated more attractive that it is unlikely that perceivers could extract reliable information about ovulatory timing. Furthermore, Jones et al. (~~Jones et al., ~~2018c) failed to replicate a negative within-women relationship between changes in progesterone and changes in face attractiveness when photos and hormones were sampled more evenly across the cycle at five weekly intervals (within-women associations between estradiol and face attractiveness were also null). Other research has shown that face morphs constructed from photos taken on cycle days when measured estradiol was higher were ranked more attractive than morphs of the same women created from photos taken was estradiol was lower (Catena et al., 2019; cf. Bobst & Lobmaier, 2012). More indirectly supporting hormone effects, Miller et al. (2007) showed that tips received by lap dancers were distributed across the cycle in a way that closely mimicked the prototypical estradiol curve (see their Miller et al., 2007, fig. 1), which is consistent with attractiveness changes tracking estradiol but not progesterone.

C29.P32 The above evidence is inconclusive regarding hormonal predictors of within-cycle shifts in the attractiveness of women's stimuli, and further research is necessary. Notably, no published studies have tested hormonal predictors of within-women shifts in odor attractiveness, despite the important role of odors in signaling ovulatory timing in many nonhuman species. A study similar to Jones et al. (2018c) but assessing hormonal correlates of odor attractiveness repeatedly across the full cycle would be especially valuable for adjudicating how endocrine influences on cycle-associated stimuli may have changed in humans relative to many nonhuman mammals.

C29.P33 Other research has assessed between-women relationships between hormones and attractiveness. These studies assess whether, for instance, a woman represented by the top estradiol curve in figure 29.3 would tend to be rated more attractive than one represented by the bottom curve. Since conception cycles are associated with higher estradiol production (Lipson & Ellison, 1996), evidence for such a correlation would support the idea

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that human attractiveness judgments track fitness-relevant properties, such as conception probability. This in turn would corroborate other evidence (e.g., Gangestad & Scheyd, 2005) that argues against the idea that attractiveness judgments are arbitrary social constructions, since on the social construction account the hormone correlations would be unexplained coincidences.

C29.P34 Initial evidence for such hormone correlations was promising. In a study of more than one hundred women with daily hormone values across a full menstrual cycle, Jasienska et al. (2004) reported that women with lower waist-to-hip ratio (WHR) and larger breasts had higher estradiol and progesterone concentrations than did other women. Features like low WHR are rated attractive in women (e.g., Singh, 1993), though Jasienska et al. did not collect attractiveness ratings of the women in their sample. Law-Smith et al. (2006) reported that women with higher estradiol (measured from one or two urine samples in the estimated late follicular phase) had face photographs that were rated more attractive, though their estimation of cycle region was imprecise and their finding based on a small sample of women who were not wearing makeup (n = 30). Finally, Durante and Li (2009) averaged two estradiol values per woman (collected from near ovulation and in the luteal phase) in a sample of forty-five women, and found a positive correlation between women's mean estradiol concentrations and attractiveness ratings of their photos in which both bodies and faces were visible.

C29.P35 More recent studies have not consistently replicated between-women relationships between hormones and determinants of women's attractiveness. Grillot et al. (2014), in a study with daily hormone values, found no evidence that women with lower WHR or larger breasts had higher estradiol or progesterone, though the sample size (n = 33) was smaller than in Jasienska et al. (2004). The Grillot et al. study did report a positive partial correlation between ratings of women's body attractiveness and their mean estradiol concentrations when body mass index (BMI) was held constant, though replication of that unpredicted finding has not been assessed. In a large sample of nearly 250 women, Jones et al. (2018c) found that mean estradiol computed over five weekly samples per woman was *positively* correlated with measurements of women's WHR, opposite to the finding from Jasienska et al. (2004). Furthermore, Jones et al. reported null associations between mean estradiol and progesterone and ratings of women's face attractiveness, thus failing to replicate findings that were reported by Law-Smith et al. (2006) with a much smaller sample size.

C29.P36 The overall evidence for between-women relationships between ovarian hormones and physical attractiveness is thus mixed and inconclusive. It is not entirely clear that consistent effects should be expected, however. Ovarian hormones fluctuate across time within-women based on energetic variables (reviewed in Ellison, 2001), which in turn can be seen as input conditions for the initiation of ovulatory cycles in theoretical frameworks for ovarian hormones (Roney, 2016a). Studies that have measured ovarian hormones have obtained snapshots of their production within a given cycle, but hormones

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can vary considerably across cycles within women even in well-nourished populations (see Lipson & Ellison, 1996), whereas variables like facial attractiveness or WHR may be much more stable over similar time-periods. This should add considerable noise to hormone-attractiveness correlations. Finally, within-women, between-cycle effects of hormones on women's attractiveness (e.g., in fig. 29.3, is the same woman more attractive when in a cycle characterized by the top vs. the bottom estradiol curve?) have never been tested. Although challenging, such tests—especially for more state-like traits like odor or voice attractiveness—could provide important evidence regarding whether men's preferences mechanisms are primarily tracking between- rather than within-cycle indicators of fecundity.

C29.P37 In summary, human pair-bonding may have altered some aspects of the two-signal endocrine code that can be used to understand ovarian hormones in many nonhuman species. Endocrine influences on sexuality have weakened relative to social influences in humans, facilitating an increase in extended sexuality that may have promoted investment by long-term pair-bond partners over the course of human evolution. Suppression of some hormone effects on women's observable stimuli may have been important for sufficient concealment of ovulatory timing to promote pair-bonding, although more detailed research on the hormonal predictors of within-cycle attractiveness shifts is necessary to test precisely how this may have occurred. Finally, existing evidence is insufficient to support the conclusion that more attractive women tend to have higher ovarian hormone production, although such effects might be detectable if it were possible to account for between-cycle variability in hormone production by measuring hormones over longer stretches of time.

C29.S8 ### *Dual Sexuality, Hormones, and Women's Mate Preferences*

C29.P38 The argument that estradiol and progesterone act as a two-signal endocrine code that calibrates motivational priorities to fluctuations in fecundity is well supported across many nonhuman species and, as reviewed above, is also supported by evidence in humans. Nonetheless, the human cycle phase literature has been dominated by an alternative theoretical perspective known as "dual sexuality theory." Prominent versions of this perspective have posited that women's sexual psychology is qualitatively different inside the fertile window than at other times of the cycle: attraction to and desire for men with markers of high genetic quality are elevated in the fertile window, but attraction to and desire for high investing pair-bond partners are elevated outside the fertile window, and especially in the luteal phase (reviewed in Thornhill & Gangestad, 2008). One functional explanation for this shift is that it implements a mixed-mating strategy in which ancestral women could obtain direct benefits from high investing pair-bond partners at most times but could obtain higher-quality genes from extra-pair men by committing infidelities with them during the fertile window when conception was possible (e.g., Gangestad et al., 2002; Penton-Voak et al., 1999).

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C29.P39 A version of dual sexuality theory could be compatible with motivational priorities theory if it were the case that there is a general increase in sexual motivation during the fertile window but that women also exhibit stronger attraction to markers of good genes at that time. Proponents of dual sexuality theory have argued, however, that sexual motivation in general does not increase near ovulation (Gangestad et al., 2002; Haselton & Gangestad, 2006) (instead, only desire for men with markers of high genetic quality increases), that most women do not experience increased desire for their long-term partners in the fertile window (Gangestad et al., 2002; Pillsworth & Haselton, 2006), and that, if anything, desire for own partners is higher during the luteal phase when progesterone is elevated (Grebe et al., 2016). These conclusions—based on results from studies that generally collected only two data points per cycle—if true, would refute motivational priorities theory, which posits that sexual motivation in general trades off against alternative motivational priorities under the influence of fecundity-signaling ovarian hormones. However, daily diary studies with much larger numbers of sample days within-women have shown that all measures of sexual motivation, including desire for and sex with women's own long-term partners, tend to increase near ovulation and to decline during the luteal phase when progesterone is elevated (Arslan et al., 2021; Roney & Simmons, 2016; Shimoda et al., 2018; Wilcox et al., 2004). There is ongoing debate about whether the size of cycle phase shifts in desire is moderated by the attractiveness of women's partners (e.g., Larson et al., 2012), but as a main effect, evidence is converging on the conclusion that in-pair desire and sexual activity increase during the fertile window, consistent with predictions from motivational priorities theory (reviewed in Roney, 2018).

C29.P40 Most research on dual sexuality has focused on mate preferences, however, rather than sexual desire. The "ovulatory shift hypothesis" predicts that preferences for putative markers of genetic quality—including facial and body masculinity, deeper voice pitch, and more dominant behaviors—increases during the fertile window specifically when women are rating stimuli for short-term, sexual attractiveness (Gildersleeve et al., 2014). Although many studies initially supported this hypothesis, a number of more recent investigations with precise determination of ovulatory timing have failed to replicate these findings (reviewed in Jones et al., 2019). Because there is a separate chapter on cycle phase effects, I will not specifically review these studies (see Stern & Penke, this volume). Rather, in what follows, I suggest how knowledge of the hormonal predictors of cycle phase shifts may inform this debate.

C29.P41 From inspection of figure 29.2, a straightforward proximate means of implementing the effects postulated by the ovulatory shift hypothesis would entail positive effects of estradiol combined with negative effects of progesterone on preferences for masculine features. The mixed-mating explanation for cycle phase shifts should predict very strong inhibitory effects of progesterone on preferences for masculine traits, since the genetic benefits of stealth infidelity are impossible to obtain during the nonfecund luteal phase, but the costs of being caught in an infidelity remain at that time. Thus, on the infidelity-based model,

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empirical studies should detect strong negative correlations between progesterone and attraction to putative fitness indicators.

C29.P42 Elsewhere, my collaborators and I have proposed an alternative to the infidelity-based model of cycle phase shifts that we called "between-cycle theory" (Lukaszewski & Roney, 2009; Roney, 2009; Roney & Simmons, 2008). This theory proposes that women upregulate attention to markers of genetic quality during broad time periods when fecundity is elevated, rather than doing so only during the fertile windows of ovulatory cycles. In figure 29.3, for instance, the theory proposes a mechanism to increase attraction to fitness indicators when moving from the lower to the higher fecundity cycle represented by the two estradiol curves. The lower curve could occur during events such as lactation when hormones and fecundity are suppressed, and when partner evaluation may be focused on crucially important direct benefit provisioning at that time. But with a return to more fecund cycles (represented by the higher curve), the weighting placed on potential mates' genetic quality may increase at a time when partner switching could occur before the next conception. On this position, the mechanism in question is responding to overall cycle fecundity and not to fertile window timing, and thus there is no reason to expect inhibitory effects of progesterone on attraction to putative cues of genetic quality. Instead, between-cycle theory predicts that attraction to fitness indicators will correlate positively with estradiol concentrations. Between-cycle theory and the mixed-mating hypothesis thus generate similar predictions regarding effects of estradiol on women's preferences for cues of men's genetic quality, but mixed-mating theory uniquely predicts inhibitory effects of progesterone on such preferences.

C29.P43 What does the extant literature show regarding hormonal predictors of women's attraction to masculine features in men? Recent studies have consistently reported null associations between within-cycle shifts in measured progesterone concentrations and within-cycle shifts in women's preferences for masculine behaviors, voices, bodies, and faces (Ditzen et al., 2017; Jones et al., 2018b; Jones et al., 2018d; Jünger et al., 2018b; Marcinkowska et al., 2018; Pisanski et al., 2014; Stern et al., 2020). Gangestad et al. (2019) argued for a negative association between progesterone and attraction to measures of men's body masculinity in partnered women only in a reanalysis of data from Junger et al. (2018a), but their reanalysis was challenged by the original authors (Stern et al., 2019); furthermore, that same association in partnered women was not found in Marcinkowska et al. (2018). Thus, a striking finding from recent hormone studies of mate preferences—some of which, like Jones et al. (2018b), were very highly powered—is an overall lack of evidence for inhibitory effects of progesterone on preferences for putative good genes indicators in men. Because the infidelity-based mixed-mating hypothesis should predict strong inhibitory effects of progesterone, as explained above, these results provide direct evidence against the mixed-mating model.

C29.P44 Evidence for the between-cycle theory has been more mixed. Two initial studies reported that women's estradiol concentrations positively predicted their attraction to faces of men with higher measured testosterone concentrations (Roney et al., 2011; Roney

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& Simmons, 2008); combined with null results for progesterone, these findings were consistent with predictions from between-cycle theory. In Roney et al. (2011), however, this effect was not found for women's ratings of artificially masculinized faces, suggesting a possible dissociation between preferences for cues of testosterone and preferences for some measures of facial masculinity. Jones et al. (2018b), in the highest-powered investigation of women's preferences for facial masculinity yet conducted (at least five weekly measurements in more than three hundred women), also reported null within-women associations between changes in estradiol and changes in attraction to artificially masculinized faces. Some evidence for positive associations between estradiol and preferences for face masculinity was reported in Ditzen et al. (2017), albeit in a smaller sample than in Jones et al. A series of studies by Junger and colleagues reported null within-women associations between estradiol and preferences for various masculine traits (Jünger et al., 2018a; Jünger et al., 2018b; Stern et al., 2020), but these studies all compared the late fertile window to the midluteal phase, which are time periods across which estradiol does not vary much. Finally, Pisanski et al. (2014) reported marginally significant within-women correlations between estradiol and preferences for deeper voice pitch in men among a sample of sixty-two women tested across five weekly sessions; when this sample was expanded to more than three hundred women, however, a robust positive effect of estradiol on attraction to deeper voices was found (Jones et al., 2018d). Thus, although findings are mixed and further research appears necessary, evidence supports stronger attraction to facial cues of high testosterone and to lower voice pitch when women's estradiol is elevated. These positive findings—in conjunction with null effects for progesterone in the same studies—provide some evidence consistent with between-cycle theory.

C29.P45 In summary, a series of recent studies have provided new evidence regarding hormonal predictors of women's mate preferences. These studies are generally consistent in finding null effects of progesterone on preferences for masculine traits in men, which argues against the mixed-mating hypothesis. Some but not all findings have supported positive correlations between estradiol and preferences for masculine traits. Although within-cycle correlations between estradiol and preferences for putative fitness indicators are consistent with predictions from between-cycle theory, a more direct test of the theory would entail comparing the same women's preferences across cycles with higher versus lower production of estradiol (as in fig. 29.3). It is possible, however, that the few positive findings for effects of estradiol on women's mate preferences are actually false positives. In that case, rather than regulating mate preferences, ovarian hormones may primarily regulate shifts in women's sexual motivation, which is a phylogenetically conserved role for estradiol and progesterone across females of most mammalian species.

C29.S9 ## Testosterone and Human Mating

C29.P46 The partial theoretical framework presented for males of seasonally breeding species in figure 29.1 summarizes broad input–output patterns associated with testosterone across

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many vertebrate species. These input–output relationships support an abstract characterization of testosterone as regulating trade-offs between investment in mating competition and investment in alternative adaptive problems. Functionally, because different adaptive problems vary in immediate importance across different contexts and time periods, having signals that can coordinate shifts in investments across the whole organism facilitates adaptive allocations of effort to those problems that are currently most pressing. Testosterone can be understood as one such signal.

C29.P47 The "challenge hypothesis" is an influential model of how testosterone shifts across time periods and contexts (Wingfield et al., 1990). The model was originally developed for understanding hormone effects in seasonally breeding birds, including among those that form pair-bonds. It suggests some refinements to figure 29.1 in the sense that testosterone production is posited to vary across three broad levels: very low production during the nonbreeding season; intermediate production in response to seasonal cues that serves as a breeding season "baseline," which increases expression of plumage ornaments, upregulates spermatogenesis, and produces sexual motivation sufficient for sexual behavior; and a maximal "challenge"-induced level that responds to competition with other males for territory establishment and access to and mate guarding of fertile females. In addition to the types of physiological effects summarized in figure 29.1, testosterone also clearly regulates shifts in male birds' motivational priorities between mate competition and paternal effort: exogenous administration of testosterone to fathers (at a time when their natural testosterone has typically fallen from challenge-induced concentrations) increases their courtship and competitive behaviors at the cost of reduced paternal provisioning of offspring, leading to substantial increases in juvenile mortality (e.g., Hegner & Wingfield, 1987). The general pattern described by the challenge hypothesis can be used to organize findings about how testosterone production varies across time in human males and the role of such variability in regulating shifts in motivational priorities between mating effort and investment in alternative adaptive problems.

C29.S10 ### *Testosterone and Men's Relationship Dynamics*

C29.P48 Humans are not seasonal breeders, but they clearly move through life history stages that vary in degree of mate-seeking versus investment in alternative priorities, such as parenting. If effects of testosterone in allocating effort to mate competition are conserved in humans, then one would expect men's testosterone to be elevated when single and mate-seeking but to decline when pair-bonded and investing in offspring. Relatively higher testosterone concentrations in single men may be loosely analogous to the intermediate, breeding season elevation of testosterone posited by the challenge hypothesis. If men's testosterone also responds to more immediate social events—interactions with potential mates or competitive challenges from same-sex rivals—then these further increases in testosterone could be seen as analogous to the challenge-induced maximal testosterone

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production posited by the challenge hypothesis. In what follows, I review evidence for both of these patterns in human males.

C29.P49 First, it is important to point out that the broader coordinating functions of testosterone seen in many nonhuman species do appear to be largely conserved in humans. Elsewhere, in developing a fuller theoretical framework for men's testosterone, I reviewed evidence that many of the inputs and outputs listed in figure 29.1 (minus the antlers, of course) also characterize human males (Roney, 2016a; see also Bribiescas, 2001). This helps make functional sense of a possible drop in men's testosterone when partnered or fathering, since some of the somatic effects of this hormone on outcomes such as immune function, elevated metabolic rate, and fat storage would have imposed ancestral survival costs that should have been avoided when diversion of energy was not needed for mate competition. Here, however, I focus more directly on psychological and behavioral variables related to mating, and the hypothesized role of testosterone in mediating shifts in motivational priorities.

C29.P50 A large number of cross-sectional (reviewed in Gray & Campbell, 2009; Roney & Gettler, 2015) and a few longitudinal (Gettler et al., 2011; Mazur & Michalek, 1998) studies have provided evidence for drops in men's testosterone after entry into committed romantic relationships, with even larger declines when partnering is coupled with the birth of children. In an important recent synthesis of this literature, Grebe et al. (2019) used meta-analysis to show that both relationship status and fatherhood are reliably associated with declines in men's testosterone when considering both published and unpublished studies. This pattern is consistent with the decline in testosterone associated with the hatching of offspring and onset of paternal effort in pair-bonding birds (Wingfield et al., 1990; for a review of similar patterns in nonhuman primates, see Muller, 2017), and represents an important endocrine signature of adaptive design for pair-bonding and paternal investment in humans.

C29.P51 Roney and Gettler (2015) characterized these temporal shifts in testosterone as a "testosterone-relationship cycle" in which a current focus on mate-seeking increases testosterone, testosterone promotes mating effort that increases the probability of entering a long-term relationship, but then relationship entry feeds back to reduce testosterone and further mating effort. Some longitudinal evidence does support higher baseline testosterone increasing the probability of long-term relationship entry (Gettler et al., 2011), as well predicting dominance-related behaviors during mate competitions that enhanced perceptions of attractiveness (Slatcher et al., 2011). Furthermore, the importance of mate-seeking as a key variable is supported by evidence that men in relationships who maintain high sociosexual desire (i.e., interest in and arousal by extra-pair partners) maintain elevated testosterone despite being partnered (e.g., Edelstein et al., 2011; McIntyre et al., 2006). Edelstein et al. (2014) showed that men's testosterone concentrations were negatively associated with both their own and their partners' relationship satisfaction in a dyadic study of romantic couples, suggesting that increased testosterone was a cause

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or consequence of relationship dissatisfaction that may in turn be associated with seeking alternative mates. Indeed, other longitudinal research has reported that men's testosterone concentrations positively predict their future probability of divorce (Booth & Dabbs, 1993).

C29.P52 Research on men's testosterone has focused on its role in calibrating mate competition and status striving rather than predicting variability in men's sexual motivation. In many nonhuman species, only fairly low thresholds of testosterone production are necessary for full expressions of sexual behavior, and indeed the intermediate, breeding baseline level of testosterone production is sufficient for copulation in pair-bonding birds (Wingfield et al., 1990). A very similar pattern occurs in humans. Chemical suppression of natural testosterone production to very low concentrations does reduce men's desire, fantasy, and sexual behavior, but subsequent testosterone replacement at only half the average baseline concentration is sufficient to restore baseline measures of the sexual variables (Bagatell et al., 1994b). Conversely, supplementing men's natural testosterone production to concentrations much higher than their natural baselines did not increase their sexual desire or behavior (Bagatell et al., 1994a). Thus, testosterone fluctuations within the normal range appear to track men's mate-seeking motivation and mate competition efforts but do not strongly affect sexual desire itself, which instead requires only threshold concentrations of androgen production.

C29.P53 The endocrine regulation of men's sexuality thus appears substantially different than such regulation in women, for whom sexual desire is more continuously calibrated to fluctuations in estradiol and progesterone. Importantly, women's brain mechanisms have direct information regarding temporal fluctuations in fecundity via hormonal signals and can therefore adjust sexual motivation accordingly. If, however, women's ovulation is effectively concealed from other individuals, then an adaptive strategy for men may be to desire sex at regular intervals with their long-term partners in order to capture concealed conception opportunities whenever they occur. Men's rates of sexual initiation appear to be flat across their partners' menstrual cycles (Adams et al., 1978; Caruso et al., 2014; VanGoozen et al., 1997; cf. Harvey, 1987), and some research has reported no changes in men's testosterone across distinct phases of their partners' cycles (Ström et al., 2012; Ström et al., 2018). These patterns are consistent with ovulatory timing being effectively concealed. Men's sexual motivation requiring only low-threshold concentrations of testosterone may facilitate this strategy of somewhat continuous sexual desire as a response to concealed ovulation. In addition, full sexual function in response to low thresholds of androgen production allows men to maintain sexual interest in their long-term partners despite the drops in testosterone that occur in conjunction with relationship entry and fatherhood.

C29.S11 ### *Reactive Testosterone Responses to Social Stimuli*

C29.P54 The changes in testosterone associated with relationship status and fatherhood concern baseline concentrations over timescales of weeks or months. Testosterone is also known

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to exhibit rapid changes on the timescale of minutes to hours in response to more immediate contextual triggers. In a wide range of nonhuman vertebrate species, for instance, nontactile exposure to conspecific females or their stimuli can trigger male testosterone increases within about fifteen to forty-five minutes, with testosterone concentrations usually returning to baseline within one to two hours from the onset of stimulus exposure (reviewed in Roney, 2016b). These responses are regulated by a phylogenetically conserved limbic–hypothalamic neural pathway that implements decision rules regarding the magnitude of responses (Roney, 2016b). Experimental induction of testosterone increases at timescales similar to these natural responses has been shown to promote outcomes such as reduced fear and risk aversion, increased aggression toward other males, induction of place preferences for contexts in which hormone increases occurred, reduced pain sensitivity, and reduced latency for mounting females (reviewed in Gleason et al., 2009; Muller, 2017; Roney, 2016b). Thus, in response to immediate cues of mating opportunities, short-term testosterone responses acutely prime a coordinated set of outputs that calibrate the organism toward competing for mating opportunities.

C29.P55 Evidence supports a phylogenetically conserved reactive testosterone response to potential mates in human males. A series of laboratory experiments has supported reactive increases in men's testosterone after brief in-person social interactions with young women that tend to be absent after brief social interactions with young men (Kordsmeyer & Penke, 2019; Roney et al., 2003, 2007, 2010; van der Meij et al., 2008). Field studies have also provided some corroborating evidence for testosterone increases after men interact with potential mates in a range of nonlaboratory environments (Escasa et al., 2011; Flinn et al., 2012; Murcia et al., 2009; Ronay & von Hippel, 2010). The human responses exhibit various parallels with the nonhuman patterns, furthermore, including similar timescales of effects, the absence of responses after comparable social interactions with other males, and reactive increases in cortisol that co-occur with the testosterone elevations (reviewed in Roney, 2016b). Those parallels support the likelihood that homologous brain mechanisms implement the hormone responses in humans and in nonhuman species.

C29.P56 As in nonhuman species, evidence supports short-term testosterone increases in humans having a suite of effects that should facilitate mate competition efforts. A mix of hormone administration and correlational studies has shown that testosterone elevations may acutely reduce fear responses, increase risk-taking and reward sensitivity, increase willingness to compete with and aggress against other research participants, increase weight-lifting performance, and increase the magnitude of courtship-like behaviors directed toward young women (reviewed in Carré & Olmstead, 2015; Roney, 2016b). These outcomes collectively suggest an enhanced willingness and ability to compete for a potential mate, although the triggers of testosterone increases in these studies were not mating stimuli but instead either hormone administrations or competitive laboratory tasks. Kordesmeyer and Penke (2019), however, did assess downstream correlates of reactive testosterone responses to a series of competitions with another man that were observed by an attractive female

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confederate and found that the magnitude of testosterone increases correlated positively with pre/post changes in both self-reports of men's competitiveness and observers' ratings of men's self-assurance. Thus, reactive testosterone increases after exposure to potential mates may acutely intensify the orientation toward mate competition that is associated with elevated baseline testosterone concentrations in single men, thereby promoting more immediate courtship efforts.

C29.S12 **Functional Roles of Hormones in Human Mating: Summary and Conclusions**

C29.P57 Hormones are coordinating signals that prototypically calibrate organism-wide responses to adaptively relevant input circumstances. Their functions are thus best understood within the context of theoretical frameworks that specify mappings from input conditions to coordinated output effects. The goal of this chapter was to lay out the broad theoretical frameworks that have organized our understanding of the role of hormones in mating psychology and behavior both in nonhuman species and in humans. The frameworks sketched are basic in many respects but can serve as organizing foundations, additions to which can help construct more complete models of the endocrine regulation of human mating.

C29.P58 Hormones play crucial and well-established organizational roles in the development of sex-differentiated phenotypes and behavioral strategies in many nonhuman species. In humans, converging lines of evidence support prenatal androgen signaling and the canalization of androgen effects as important causal factors in the development of sexual orientation. In principle, other individual differences in mating psychology could be traceable to quantitative differences in early androgen exposure, although the relevant pathways are complex and some influences, such as epi-marks, are very difficult to measure. Progress in mapping organizational effects of hormones to individual differences in adult mating psychology may require improved abilities to measure the magnitude of early androgen signaling.

C29.P59 In females of many nonhuman species, estradiol and progesterone act as a simple, two-signal endocrine code that causes shifts in motivational priorities based on temporal fluctuations in fecundity. Recent evidence supports the conservation of the priority-shifting effects of these hormones in humans, with the two-signal code having opposite effects on sexual versus feeding motivation. Pair-bonding in humans may have caused important changes in these hormone effects, however, such as a weakening of hormonal versus social influences on sexual motivation to facilitate an expansion of nonconceptive sexuality. Likewise, effects of progesterone on female odors that are seen in nonhuman species may have been suppressed in humans as a means of concealing ovulatory timing. Future research on the endocrine predictors of variables like odor attractiveness can test whether and how cues of ovulatory timing have been concealed in humans, thus potentially contributing important evidence regarding the evolution of human pair-bonding.

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C29.P60 Versions of dual sexuality theory have argued that ovarian hormones primarily affect women's mate preferences rather than shifts in more general motivational priorities. The infidelity-based mixed-mating hypothesis should predict strong inhibitory effects of progesterone on women's preferences for masculine traits in men given that an infidelity cannot reap genetic benefits during the nonfecund luteal phase when progesterone is elevated. Yet, a series of recent studies have produced null findings for within-women correlations between fluctuations in progesterone and changes in attraction to masculine traits. These findings are still being actively debated, however, and further research may be necessary to reach more definitive conclusions regarding the role of ovarian hormones in women's mate preferences.

C29.P61 The challenge hypothesis has organized many findings on testosterone fluctuations and their effects in nonhuman species. Human males conform to the same basic patterns predicted by this hypothesis. Men's testosterone drops after relationship entry and during fatherhood, and evidence supports a psychological orientation toward mate-seeking as a key variable in these shifts. Further, more immediate social stimuli suggestive of mating opportunities and mate competition can prime rapid, reactive increases in testosterone that may more acutely prime an orientation toward courtship efforts. All of these patterns fit within theoretical frameworks that also incorporate more somatic and physiological effects of testosterone (see fig. 29.1).

C29.P62 Although the frameworks proposed here for ovarian hormones and testosterone may be foundational for understanding the roles of these hormones in human mating, they are nonetheless surely incomplete accounts of endocrine influences on human mating. An important extension of these arguments concerns the roles of other hormones and how they interact with the gonadal hormones profiled here in what may comprise complex endocrine codes indexing specific, adaptively relevant input conditions. As a hint of this complexity, oxytocin production and receptor expression are partly regulated by estradiol (see Shukovski et al., 1989), which raises possibilities for these two hormones jointly affecting variables like sexual desire or relationship intimacy in interactive ways. Likewise, although testosterone responses to social interactions with potential mates may prime outputs that promote possible mate competition, the importance of pair-bonding in human mating raises the possibility that other hormonal signals may play important roles in early responses to potential mates. In prairie voles, for instance, oxytocin (Williams et al., 1994) and corticosterone (DeVries et al., 1996) are casually implicated in the formation of pair-bonds, raising the possibility that reactive changes in these hormones may be part of an endocrine cascade that initiates the pair-bonding process in humans. Research that investigates possible multisignal endocrine codes implicated in human mating may importantly supplement the theoretical frameworks proposed here, and represents an exciting direction for future research in human behavioral endocrinology more generally.

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Notes

1. Gangestad et al. (this volume) devote an entire paragraph to arguing that I have mischaracterized the hormonal predictors of nonhuman primate sexual motivation in Roney (2018) and in this volume. They cite evidence that chimpanzee females may initiate more total copulations on days with lower conception probability than on days with maximum fecundity (when they are more likely to resist all but the most dominant males), and they conclude from this that "chimpanzee sexual motivation does not follow the patterns of hormonal inputs proposed by Roney (2018)." I actually discussed the female initiation findings in Roney (2018) but argued that these patterns still occur within a broader cycle phase pattern in which sexual behavior is positively associated with estrogen production but negatively associated with progesterone concentrations. Indeed, Emery Thompson (2005) directly demonstrated in a sample of wild chimpanzees that female copulation rates peaked on the same days as the females' highest estrogen production, whereas copulations decline precipitously after luteal phase progesterone elevations produce sex skin detumescence. This is very consistent with the pattern of hormonal inputs that I have proposed. Although there are some exceptions (also cited in Roney, 2018), these hormonal predictors of female sexual behavior are found across many nonhuman primate species (see Emery Thompson, 2009; Wallen, 2013).
2. Gangestad et al. (this volume) offer lengthy critiques of motivational priorities theory in their chapter. Unfortunately, given the broader scope of this chapter (hormone effects more generally), space limitations preclude detailed responses to all of their points. Nonetheless, some clarifications are important to avoid misinterpretations. For example, Gangestad et al. criticize the notion of "general sexual desire" or "libido," and they relatedly imply that an upregulation of general desire should motivate taking any sexual opportunity. First, "general desire" has been used in explanations of motivational priorities theory to distinguish its claims from those of specific versions of dual sexuality theory (e.g., dual mating theory) in which it has been alleged that only desire for men with good genes indicators tends to increase within the fertile window, but there is nothing within motivational priorities theory that entails that desire is necessarily detached from representations of specific people. When women answer questions phrased as "desire for sexual contact," they may well be picturing contact with specific mates, and hormonal predictors of women's desire for their own long-term partners and for extra-pair men were similar to those for target-unspecified measures of desire (Roney & Simmons, 2016). Likewise, women have strong mate preferences and nothing in motivational priorities theory suggests that hormonal influences on desire would nullify those standards. This is equally true for nonhuman species for many of which it is generally accepted that female sexual receptivity is restricted to fecund time periods without entailing that females are unselective in their mate choice. In mechanistic terms, fecundity-mediated shifts in desire can be reconciled with strong mate preferences by having the neural structures that regulate sexuality be primed (or inhibited) by ovarian hormones while also requiring social stimuli of sufficient strength for their full activation (see Roney, 2018).
3. The two-input position can also help address some of the criticisms that Gangestad et al. (this volume) level against motivational priorities theory. Gangestad et al. imply, for instance, that the mechanisms posited by motivational priorities theory should have produced maladaptive outcomes by promoting sexual behavior even during cycles in which conception would not have promoted fitness (e.g., when a woman had insufficient social support). Although ovarian hormones may prime neural structures that regulate desire within the fecund regions of such cycles, other inputs are likely to have much stronger inhibitory effects on those same structures. Stress, perception of risk, poor relationship quality, and lack of relationship security may all strongly inhibit sexual desire or behavior, and these inhibitory effects are likely to be much stronger than the hormone priming effects (some evidence for this is reviewed in Roney, 2019). One possibility is that cautionary mechanisms inhibit sexual behavior early in courtship until there is sufficient relationship security to release this inhibition: if so, those inhibitory effects could entail that fecundity-related shifts in sexuality are found more clearly in partnered versus single women, and some evidence does in fact support this pattern (Roney & Simmons, 2016).

   Gangestad et al. (this volume) further suggest, however, that any such cautionary inhibition should be greater during the fertile window when conception is actually possible: in effect, that there should be hormone-mediated conception avoidance mechanisms. I think this is an interesting idea that has a clear functional logic to it, but I also see these as additional mechanisms that may be combined with those proposed by motivational priorities theory. Many different neural architectures could implement such effects. Imagine, for instance, specific neural structures that regulate desire and that have their firing thresholds modulated by ovarian hormones in the ways proposed by motivational priorities theory. Downstream of these structures may be cautionary mechanisms that have inhibitory effects on sexual behavior based on

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variables like relationship insecurity but that are also primed by ovarian hormones in such a way that caution is greater when fecundity is higher (in alternative architectures, such mechanisms might also be upstream of desire). Once a secure pair bond is established, though, these cautionary mechanisms lose the social inputs that cause their activation, and the proposed two-signal pattern of ovarian hormone effects on sexual motivation may then emerge more clearly. Specifying candidate neural architectures of this sort can help focus debates on empirically testable elements of mechanism design. I am attempting to use the nonhuman neuroscience literature to build models of the neural architecture that could implement the two-input pathway ideas described here, though the details of these models are beyond the scope of this chapter.

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