In P.T. Ellison and P.B. Gray (eds.) *The Endocrinology of Social Relationships.*
Cambridge, MA: Harvard University Press. 2009.

CHAPTER ELEVEN

The Role of Sex Hormones in the Initiation of Human Mating Relationships

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A LARGE BODY of research has demonstrated that sex hormones play important roles in mate choice and mate attraction across a broad range of nonhuman vertebrate species (for reviews, see Becker, Breedlove, and Crews, 1992; Nelson, 2005). The general story that emerges from this literature is that sex hormones increase when conditions are advantageous for mating, and elevated hormone concentrations in turn enhance attractiveness, cause attraction to opposite-sex conspecifics, and promote behavioral and physiological investment in mate choice and mate attraction. Although the effects of sex hormones on human fertility and sexual physiology have been well-investigated (for reviews, see Carter, 1992a; Ellison, 2001), relatively little research has investigated the role of sex hormones in human mate choice and mate attraction. The goal of this chapter is to review existing evidence regarding the possible importance of endocrine variables in human relationship initiation. Using the nonhuman literature as a guide, the chapter will focus on three specific research questions: (1) whether sex hormones regulate perception of others' mate attractiveness, (2) whether sex hormones predict individuals' attractiveness to others, and (3) whether sex hormones increase in reaction to interactions with potential mates. Preliminary findings on these questions seem promising enough to suggest that further incorporation of endocrine variables into human research may significantly enhance our basic understanding of human mating psychology.

Elucidation of hormonal mechanisms may mesh particularly well with evolutionary psychological approaches to understanding human mating psychology. Evolutionary psychology posits that the human mind is composed of a set of domain-specific psychological mechanisms that were naturally selected to address specific adaptive problems, such as mate choice, food choice, social exchange, and parenting (Tooby and Cosmides, 1992). An interesting consequence of any such modular organization of functionally distinct brain mechanisms is the need for some type of signaling process that couples the activation of specific mechanisms to the circumstances in which this activation is functional, especially if, as seems likely, some mechanisms produce contradictory or otherwise functionally incompatible outcomes (for example, aggressiveness promoted by mate competition mechanisms versus gentleness promoted by parenting mechanisms). Sex hormones may have an interesting role to play in any such signaling process, given that the information they carry is diffusely broadcast throughout the brain and body (recent evidence, for instance, supports a broad distribution of sex hormone receptors throughout both subcortical and cortical brain regions; see DonCarlos et al., 2006) and is therefore positioned to broadly adjust physiological and psychological parameter settings associated with functionally distinct mechanisms. As discussed below, sex hormone concentrations in women may largely index nutritional status and other energetic factors in such a way that specialized mating mechanisms are up- or downregulated depending on the degree to which current physiological conditions would likely support a successful pregnancy. In men, on the other hand, sex hormone concentrations may be largely responsive to the presence and potential availability of fertile mates, in addition to being calibrated by energetic considerations associated with functional resource allocation to mating effort versus maintenance of physical health. In both sexes, then, sex hormones may turn on and off the domain-specific mating mechanisms envisioned by evolutionary psychology, with sex hormones in turn calibrated to condition-dependent circumstances that index the current functional utility of energy investment in mating effort. If sex hormones are in fact priming mating mechanisms in a condition-dependent way, then members of the opposite sex could also use observable cues of sex hormone concentrations as indicators of condition that could inform mate preferences. As such, sex hormones may calibrate mate choice mechanisms, respond to cues of mating opportunities, and in part determine attractiveness to members of the opposite sex.

Sex Hormones and Perceptions of Mate Attractiveness

Females' Perception of Males

Individual conspecifics can be evaluated along any number of functional social dimensions—such as potential mates, kin, competitors, and social exchange partners—and sex hormones may promote attention to, and evaluation of, stimuli relevant specifically to judgments of mate attractiveness. Among a range of nonhuman vertebrate females, for instance, ovarian hormones tend to promote attraction to androgen-dependent cues that may mark conspecific males as potential mates. Ovariectomized female rodents exhibit no preferences for associating with males over females or intact over castrated males, but ovariectomized females administered estradiol and progesterone show clear preferences for gonadally intact males over both females and castrated males (Edwards and Pfeifle, 1983; Xiao, Kondo, and Sakuma, 2004). Natural variations in ovarian hormones appear to produce similar preference shifts, with stronger preferences for male stimuli among females tested during fertile versus nonfertile phases of the estrous cycle (for example, Beach et al., 1976; Johnston, 1979; Clark et al., 2004) and during the breeding versus nonbreeeding season (for example, Ferkin and Zucker, 1991; Michael and Zumpe, 1993). These differential reactions to male stimuli may be hormonally modulated even at the level of perceptual inputs, as estrogen-treated ovariectomized mice exhibit greater fos-immunoreactivity in the vomeronasal organ in reaction to soiled bedding from intact males than do ovariectomized females without hormone replacement (Halem, Cherry, and Baum, 1999). In sum, a large body of evidence in nonhuman species suggests that ovarian hormones modulate attraction to androgen-dependent male stimuli.

Ovarian hormone concentrations are in turn calibrated to physiological conditions that support the functional allocation of energy to reproductive efforts. In seasonally reproducing species, for instance, it is widely accepted that gonadal quiescence during the nonbreeding season functions to conserve energy under conditions in which food scarcity or thermoregulatory challenges reduce energy availability beneath levels necessary to support both basic physiological processes and reproductive activities. Seasonal inhibition of ovarian activity represents only the extreme end of a continuum, though, in which energetic stress can inhibit ovarian activity. Food deprivation or increased energy expenditure has been shown to rapidly reduce ovarian hormone concentrations, fertility, and sexual receptivity across a wide range of mammalian species, with the key variable appearing to be the net availability of oxidizable fuels (for example, Schneider and Wade, 1990; Williams et al., 2001; for a review, see Wade and Jones, 2004). The hormonal calibration of attraction to androgen-dependent male stimuli may therefore function to couple the activation of mate preference mechanisms to the conditions under which mating effort is most adaptive: during conditions of suppressed fertility, attention and behavioral effort are probably better allocated to problem domains such as foraging, thermoregulation, predator avoidance, immune function, or maternal investment in offspring.

An intriguing recent line of research suggests that ovarian hormones may also calibrate attraction to androgen-dependent stimuli in humans. Growing evidence suggests shifts in women's evaluations of men across distinct phases of the menstrual cycle, with the time near ovulation associated with stronger preferences for facial masculinity (Penton-Voak et al., 1999; Penton-Voak and Perrett, 2000; Johnston et al., 2001), deeper voice pitch (Puts, 2005; Feinberg et al., 2006), olfactory cues associated with body symmetry (Gangestad and Thornhill, 1998; Thornhill and Gangestad, 1999), and more forward and aggressive behavioral displays (Gangestad et al., 2004). The traits that are more preferred near ovulation may be unified by their associations with higher androgen concentrations, as faces perceived as more masculine tend to belong to men with higher testosterone concentrations (Penton-Voak and Chen, 2004; Roney et al., 2006), androgens are known to promote deeper voice pitch (reviewed in Feinberg et al., 2006), and various lines of evidence suggest positive correlations between testosterone and aggressive or competitive behaviors (for reviews, see Mazur and Booth, 1998; Archer, 2006). On the perceiver end, preferences for the above traits tend to increase from approximately the midfollicular phase until ovulation, a time period when estradiol concentrations are also rising. In addition, a recent study reported that women with higher estradiol concentrations had stronger preferences for the faces of men with higher testosterone concentrations and that women's testosterone preference and estradiol curves tracked one another across days of the cycle (Roney and Simmons, 2008; compare Welling et al., 2007). The human data thus exhibit patterns that are quite similar to those seen in nonhuman species in that studies converge in finding that women are more attracted to masculine, androgen-dependent traits during high estrogen times of the cycle, and preliminary evidence suggests that estradiol itself may be the physiological signal that regulates these effects.

The most prominent proposed explanation for cycle phase shifts in women's attractiveness judgments is that they are products of an adaptation designed to facilitate extra-pair copulations under circumstances in which women may obtain higher-quality genes than may be available from their primary partners (for example, Penton-Voak et al., 1999; Gangestad, Thornhill, and Garver-Apgar, 2006). This argument is predicated on the assumption that cues to androgen concentrations may serve as heritable fitness indicators (see discussion below) combined with a cost-benefit analysis that posits that the potential costs of infidelity are constant across the menstrual cycle (such costs could include abandonment or violence if infidelity is discovered), but the potential genetic benefits are realizable only near ovulation when conception is actually possible. As such, ancestral women may have maximized their reproductive fitness via a mixed strategy in which they sought material support from high-investing long-term partners but also opportunistically sought better-quality genes from higher androgen men during extra-pair copulations that occurred during fertile portions of the menstrual cycle. Proponents of this position argue that cycle phase shifts in preferences for masculinity appear inexplicable otherwise, as there would be no functional reason to downregulate interest in masculine features at nonfertile times of the cycle, absent the potential costs of a discovered infidelity (for example, Gangestad, 2000).

The broader context provided by the nonhuman literature suggests possible alternative explanations for menstrual phase shifts in women's attractiveness judgments. As reviewed above, ovarian hormones promote attraction to androgen-dependent male stimuli in species such as rats and mice that do not form pair-bonds, thus excluding extra-pair mating as a possible cause of estrous cycle shifts in such attraction. Rather, sex hormones appear to modulate the categorization of conspecifics along sexual versus nonsexual dimensions, depending on the current relevance of mating as an adaptive problem domain, with sex hormones in turn indexing changes in fertility associated with estrous cycle physiology and energetic conditions. Insofar as humans have inherited similar mechanisms that calibrate ovarian hormones and fertility to energetic conditions, the menstrual cycle shifts in women's mate preferences may have less to do with special design for infidelity and more to do with adaptive allocation of attention to mate evaluation during stretches of the life cycle in which women experience higher fertility.

A large body of research demonstrates that women's fertility and ovarian hormones are in fact positively associated with energetic conditions that are favorable for sustaining successful pregnancies and ensuing lactation (for reviews, see Ellison, 2001; also see Ellison, this volume). It is well established that fertility and ovarian hormone concentrations are suppressed during lactation, for instance, and a number of studies have demonstrated that energy balance is the key variable regulating the degree of suppression (for example, Lunn et al., 1981; Ellison and Valeggia, 2003; Valeggia and Ellison, 2004). Likewise, in industrialized societies, even moderate exercise (for example, Bullen et al., 1985; Ellison and Lager, 1985; Schweiger et al., 1988) and weight loss (for example, Pirke et al., 1985; Lager and Ellison, 1990) have been associated with reduced estradiol or progesterone concentrations, and similar effects of both calorie intake restrictions (for example, Ellison, Peacock, and Lager, 1989; Panter-Brick, Lotstein, and Ellison, 1993; Bentley, Harrigan, and Ellison, 1998; Vitzthum et al., 2002) and elevated energy expenditure (for example, Panter-Brick and Ellison, 1994; Jasienska and Ellison, 1998) have been shown in natural fertility populations. Recent evidence also implicates stress as a possible suppressor of ovarian hormones (Nepomnaschy et al., 2004), which may complement mechanisms sensitive to energetics in delaying reproduction when aversive circumstances reduce the prospects for a successful pregnancy.

The sources of ovarian suppression discussed above would likely have entailed that women in ancestral environments usually experienced suppressed fertility and only in rare months between births would have experienced fertile cycles with elevated ovarian hormone concentrations (see Strassmann, 1997). This may have created circumstances loosely analogous to breeding seasons in nonhuman species in which evaluation of male sexual attractiveness is downregulated during stretches of suppressed fertility (when other adaptive problems are more pressing) but then upregulated when fertility returns. I propose that women may exhibit temporal shifts in their mate preferences due to the operation of a mechanism that uses elevated estradiol as a signal that women are currently experiencing high fertility cycles and thus upregulates evaluation of men's sexual attractiveness across cycle days in these more fertile months; since estradiol also peaks near ovulation within individual cycles, though, this mechanism might generate within-cycle preference shifts even if it were primarily designed to shift psychology across different cycles.

A full discussion of empirical tests of this between-cycle alternative to the extra-pair mating theory is beyond the scope of this chapter. Briefly, though, the extra-pair mating explanation predicts that preference shifts should be tightly coupled to the "fertile window" (the portion of an ovulatory cycle when conception is possible), while the between-cycle alternative explanation predicts that preferences for androgen-dependent traits should correlate with ovarian hormone concentrations more broadly at various times in the cycle. The luteal phase of the cycle is especially interesting since conception is not possible at this time, but estradiol is still likely to be higher in the luteal phases of more versus less fertile cycles: the extra-pair mating position thus predicts that attraction to masculine traits should be uniformly downregulated during the luteal phase in order to avoid the costs of infidelity when genetic benefits are impossible to obtain, while the between-cycle position predicts that higher luteal phase estradiol should predict stronger attraction to masculine traits since elevated estradiol signals a more fertile cycle. Figure 11.1 presents data from Roney and Simmons (2008) demonstrating that women's luteal phase estradiol predicted the strength of their preference for the faces of higher testosterone men. Although certainly not definitive, this result provides at least preliminary evidence for the proposed between-cycle position.

In summary, the human and nonhuman data present intriguing parallels with respect to the role of sex hormones in females' perceptions of male attractiveness. Attraction to androgen-dependent cues is enhanced when fertility is elevated, and both experimental manipulations in nonhumans and correlational work in humans suggest that estradiol may be the physiological signal that regulates these effects. The precise functional explanation for these temporal shifts in women's mate preferences is still a matter of some debate and may provide interesting directions for future empirical research.

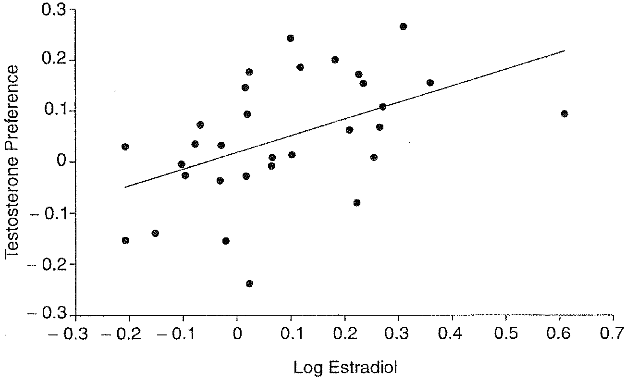

Figure 11.1 Relationship between luteal phase estradiol levels in women and the strength of their preference for the faces of higher testosterone men. From Roney and Simmons, 2008.

Males' Perception of Females

Sex hormones also modulate males' preferences for cues of fertility in females. Male rodents' preference for odors from estrous versus ovariectomized females is eliminated by castration (Xiao, Kondo, and Sakuma, 2004), for instance, and preferences for estrous over nonestrous odors can be restored after gonadectomy via testosterone replacement (for a review, see Gandelman, 1983). As in females, seasonal fluctuations in male preferences for opposite-sex stimuli are largely mediated by concomitant shifts in sex hormones (for example, Ferkin and Gorman, 1992) and may function to distribute attention, energy, and motivation away from mating effort when the absence of fertile females reduces or eliminates reproductive return on such effort.

There do not appear to be any extant studies testing whether fluctuations in men's hormone concentrations are associated with shifts in attractiveness judgments analogous to those documented among women across different phases of the menstrual cycle. Experimental induction of hypogonadism via gonadotropin-releasing hormone (GnRH) antagonists produces reductions in sexual desires and behaviors that can be reversed with testosterone supplementation, but the replacement concentrations necessary to restore normal sexual function are well below the normal baseline concentrations of circulating testosterone (Bagatell, Heiman, Matsumoto, et al., 1994; for a general review, see Bancroft, 2005). Such results suggest that male sexual interest may require a fairly low threshold concentration of androgen, as opposed to exhibiting a more continuous dose-response relationship across the normal range. If such a pattern extends to mate choice, it may turn out that variations in men's sex hormone concentrations do not generally predict preferences for particular features in potential mates. This is an empirical question, though, and future research could examine whether higher testosterone men exhibit stronger preferences for, say, more feminized facial or bodily features that may index higher fertility in women (see below). The relatively low cost of sperm production and the potentially large reproductive benefits from copulation with fertile mates lead one to expect that men's attraction to cues of women's health and fertility will be robust across most conditions. Rather than modulating libido and mate preferences, then, men's sex hormone concentrations may primarily modulate whether energy is invested in mate competition and courtship effort versus being invested in the maintenance of physical health (Ellison, 2001).

Sex Hormones and Attractiveness to Others

Female Attractiveness

Ovarian hormones appear to index fertility and energetic conditions across mammalian species, and, as such, males could use observable cues of sex hormone concentrations in mate choice decisions. At least two somewhat related types of information might be provided by such cues. First, hormone-dependent cues could mark the window of fertilizability within ovulatory estrous cycles. The well-established finding that gonadally intact males exhibit stronger preferences for cues from estrous versus nonestrous or ovariectomized females (see partial review above) provides strong evidence for this function. A second possible type of information provided by such cues might pertain to distinctions in female quality when position in the estrous cycle is held constant: if two females are both in a fertile portion of an ovulatory estrous cycle, might cues associated with differing sex hormone concentrations make one female more attractive to males than the other? In general, there is very little evidence that mammalian females produce ornamentlike cues that may indicate health or fecundity independent of indicating position in the estrous cycle (Andersson, 1994). A possible exception may be sexual swellings produced by some nonhuman primates. Emery and Whitten (2003) reported that chimpanzees with larger sexual swellings exhibited greater estradiol concentrations across equivalent portions of the cycle than did females with smaller sexual swellings. They also reviewed evidence demonstrating that cycles with greater estradiol are associated with higher conception probabilities and that male primates tend to exhibit stronger attraction to larger sexual swellings. The tendency for females to advertise and males to pay attention to more continuous hormonal signals of fertility may be associated across species with slower rates of reproduction and greater energetic costs of offspring production, as such conditions reduce the number of highly fertile mating opportunities and thus limit the potential payoffs of male strategies that involve relatively indiscriminate mate choice in the service of maximizing the quantity of copulations. The pattern of large energetic investment in a small number of offspring characterizes humans, of course, and leads to the expectation that observable cues of sex hormone concentrations might in part determine women's attractiveness to men.

Human menstrual cycles that result in successful conceptions are characterized by higher ovarian hormone concentrations than are ovulatory nonconception cycles that were similarly exposed to unprotected intercourse (Lipson and Ellison, 1996; Venners et al., 2006). This pattern suggests adaptive advantages for male mate choice mechanisms that could identify not only external signs of ovulatory versus anovulatory cycles but also any available cues of continuous gradations in women's ovarian hormone concentrations. Elements of body shape may provide just such cues, as women with larger breasts and smaller waist-to-hip ratios were found to have higher salivary estradiol and progesterone concentrations than other women when compared on equivalent days across the menstrual cycle (Jasienska et al., 2004). Other research has provided evidence that these body dimensions are in fact attractive to men (Singh, 1993). Likewise, women's late follicular estradiol concentrations were significantly correlated with attractiveness ratings of their faces, at least among women who were not wearing makeup (Law-Smith et al., 2006). The faces of higher estradiol women were also subjectively rated as more feminine, and a large body of research consistently demonstrates that feminized facial features are attractive in women (for a review, see Rhodes, 2006). These studies provide the most direct evidence that men's attractiveness judgments are informed by morphological cues of women's hormone concentrations, though indirect evidence supports this possibility as well. Some evidence suggests that higher estradiol may be associated with higher voice pitch (Abitbol, Abitbol, and Abitbol, 1999), for instance, and men rate higher frequency voices more attractive in women (Collins and Missing, 2003). Other research suggests that women's facial attractiveness correlates with both their vocal attractiveness (Collins and Missing, 2003; Feinberg et al., 2005) and their body attractiveness (Thornhill and Grammer, 1999), which implies that underlying hormonal condition may have feminizing effects on multiple phenotypic cues that men's mate choice mechanisms could in turn use as indices of likely fertility.

The studies by Jasienska et al. (2004) and Law Smith et al. (2006) suggest that facial and bodily cues of women's attractiveness may indicate relative differences in fertility across women when time in the menstrual cycle is held constant. Other research has examined whether phenotypic cues may indicate the window of fertilizability within given menstrual cycles. When presented with photographs of the same women taken during the late follicular and luteal phases, raters judged the follicular phase photos more attractive at rates that were slightly above chance (Roberts et al., 2004). This effect could be a product of ovarian hormone fluctuations altering soft tissue traits. A number of other studies have provided evidence that women's scent is rated more attractive by men when odors are collected near ovulation as opposed to at other times in the cycle (Singh and Bronstad, 2001; Thornhill et al., 2003; Kuukasjarvi et al., 2004; Havlíček et al., 2006; cf. Thornhill and Gangestad, 1999), and such studies have been interpreted as further evidence that ovulatory timing is not entirely concealed.

Although the above studies are presented as supporting the existence of choice mechanisms in men that are attuned to cues of women's ovulatory timing, the results are equally consistent with mechanisms designed to promote greater attraction to women with chronically higher estradiol concentrations. The Havlicek et al. (2006) scent study, for example, found that between women variance in odor attractiveness was far greater than within-women variance associated with phase of the menstrual cycle. This means that the odors of some women outside the fertile window were judged more attractive than scents of other women near ovulation, which is a pattern inconsistent with a mechanism designed to identify the timing of ovulation in order to target short-term mating effort toward currently fertilizable women. This study also found that scents collected during the luteal phase were judged more attractive than scents collected during menstruation: estradiol concentrations are higher in the luteal phase versus at menstruation, but fertilizability is zero in both cases. These patterns are consistent with a mechanism designed to track cues of estradiol across the cycle in order to promote attraction to more fertile women, with greater attraction to ovulatory scents simply following from the presence of higher estradiol concentrations at midcycle.

Alternatively, a true ovulation-detection mechanism might have evolved in order to target men's mate guarding to fertile portions of their partners' cycles. Some research indicates greater mate guarding near ovulation (Gangestad, Thornhill, and Garver, 2002), but another study found that this pattern held only for relatively less attractive women and that men paired with more attractive women showed no shift and, if anything, engaged in greater guarding during the luteal phase (Haselton and Gangestad, 2006). Given that more attractive women appear to exhibit higher estradiol concentrations than other women throughout most of the cycle (for example, Jasienska et al., 2004), this pattern is again consistent with a mechanism that responds to cues of absolute estradiol concentrations rather than being targeted specifically to ovulation. In sum, the state of the evidence in humans appears to be the reverse of that found in nonhuman species: the existence of hormone-dependent cues that differentiate women's fertility at equivalent points in the cycle is more strongly supported by evidence than is the existence of cues that reliably indicate the window of fertilizability within specific cycles.

Although initial evidence suggests that observable cues of sex hormone concentrations in part determine women's attractiveness, research in this area is just beginning, and there are many unanswered questions. It is unclear, for example, to what extent facial and body attractiveness are statelike cues that may change within women with temporary changes in circumstances as opposed to being more stable traitlike cues that may better index lifetime fertility than cycle-to-cycle fluctuations. Do variables like facial femininity and waist-to-hip ratio change concurrent with drops in ovarian hormone concentrations that have been documented in response to seasonal increases in energetic stress within subsistence societies (for example, Ellison, 1994)? Such traits do change with age (for a review, see Singh, 1993) and parity (Lassek and Gaulin, 2006), but degree of short-term change within age and parity classes appears unknown. It is also not entirely clear what circumstances might ensure that external cues of sex hormone concentrations are in fact honest signals of health or reproductive condition. Some authors have suggested that only healthier women can afford higher estrogen due to the possibility that high estrogen may handicap the immune system (for example, Thornhill and Grammer, 1999), but evidence for immunosuppressive effects of estrogen is mixed at best, and many components of the immune response appear to be improved under conditions of high ovarian hormones (for reviews, see Beagley and Gockel, 2003; Bouman, Heineman, and Faas, 2005). Body shape dimensions that involve specialized fat storage may provide signals of reproductive condition that would be especially difficult to fake under conditions of either current or developmentally experienced energetic stress. Facial femininity, on the other hand, does not intuitively appear to have high production costs, and it thus seems uncertain why the development of feminine features could not be decoupled from hormonal influences as a means of dishonestly signaling a fertile hormonal profile. Theoretical arguments related to the selection pressures that may have promoted men's attraction to phenotypic cues of ovarian hormones are thus needed in addition to further empirical work linking variability in hormone profiles to variability in attractiveness.

A final avenue for future research concerns cross-cultural work on possible hormonal correlates of women's attractiveness. The extant studies that have examined hormonal correlates of facial and body attractiveness have been performed in industrialized countries, and similar findings in subsistence societies could substantially bolster the case for species-typical psychological adaptations in men that are attuned to phenotypic cues of women's hormonal status. Consistent with the existence of such adaptations are findings showing fairly strong agreement in judgments of facial attractiveness among raters from diverse cultures (for example, Cunningham, 1986), including the finding that neotenous and feminized facial features that may plausibly reflect estrogen exposure tend to be preferred cross-culturally (for example, Jones, 1995).

The case for species-typical standards for women's bodily attractiveness, on the other hand, is complicated by studies showing that men in some cultures seem to prefer higher overall body fat and not lower waist-to-hip ratio (for example, Yu and Shepard, 1998; Marlowe and Westman, 2001). Although these findings could be artifacts of a failure to use a range of body weights typical of the local population (see Sugiyama, 2004, 2005), another intriguing possibility is that the morphological cues of ovarian hormones and thus fertility differ according to food availability in the local environment. Jasienska et al. (2004) found that women with low waist-to-hip ratio and large breasts actually had lower body mass index (BMI) than women with other body shapes but nonetheless had higher estradiol concentrations. An interesting question posed by Jasienska et al. is whether under conditions of food shortage BMI itself would be a better predictor of ovarian hormones and fertility than would waist-to-hip ratio. Cross-cultural research on the endocrine correlates of body shape and attractiveness would be necessary to test this idea and thus determine whether men's preference mechanisms are designed to facultatively track different phenotypic cues depending on the nature of local conditions.

Male Attractiveness

The role of androgens in signaling male attractiveness has played a prominent role in tests of handicap models of sexual selection within evolutionary biology. Folstad and Karter (1992) proposed that the immunosuppressive effects of androgens allow androgen-dependent traits to honestly signal immunocompetence. There has been confusion in the ensuing literature regarding whether such a model should predict high or low correlations between measured androgens and parasite loads, however, and empirical studies have reported conflicting findings (for a review, see Muehlenbein and Bribiescas, 2005). This debate may be based on misconceptions, as there seems no clear reason to expect correlations in either direction. Trade-offs between investment in androgen-dependent traits and investment in immune function are presumably enforced by finite energy availability. Assume that males in a population vary in their energy budgets due to some underlying, at least partly heritable aspects of their physiology. Males with larger budgets can, other things equal, afford larger investments in both secondary sex traits and immune function. Depending on factors such as the intensity of mate competition and the rate of future discounting (for example, the number of remaining breeding seasons), males with larger budgets may sometimes need to invest so much energy in courtship signaling to outcompete other large-budget rivals that their immune function is compromised to the level of smaller-budget males who have equivalent immune functioning but could not also afford to grow larger ornaments. In other conditions in which the intensity of mate competition is more relaxed, larger-budget males may be able to afford both better immune functioning and larger ornaments. In all circumstances, though, ornament size should correlate positively with size of energy budget, and females' offspring should always benefit from inheriting larger budgets (assuming that energy can be allocated to survivorship or mating effort in a plastic manner). Thus, an androgen-mediated energy trade-off model of this sort makes no predictions about relationships between ornament size and parasite load but clearly entails two other predictions: (1) that androgen concentrations will correlate positively with ornament size and (2) that females will prefer larger ornaments. These two predictions are in fact fairly well supported in the nonhuman literature (for reviews, see Folstad and Karter, 1992; Andersson, 1994; Parker, Knapp, and Rosenfield, 2002).

The handicap model implies that circulating androgen concentrations should directly correlate with male attractiveness, though the size of the correlation should be attenuated by imperfect relationships between androgens and secondary sex traits and between secondary sex traits and female judgments of attractiveness. Female preferences for intact versus castrated males (see partial review above) supports this correlation at the extreme end of the distribution but does not demonstrate that continuous variation in androgens covaries with degree of mate attractiveness. Ferkin et al. (1994) may have provided the strongest evidence for such covariation among mammals by demonstrating a dose-response relationship between the amount of testosterone injected into castrated male meadow voles and the attractiveness of their odors to females. Other research suggests that androgen doses may in fact signal immune status. The odors of male mice experimentally infected with sheep red blood cells are less attractive to females than the odors of control males, for example, but testosterone administration in conjunction with red blood cell infection can restore odor attractiveness (Litvinova et al., 2005). Although immune responses to testosterone manipulations are not always consistent across species or across studies within species (Muehlenbein and Bribiescas, 2005), and although much more research is needed on androgen mediation of overall energy distribution, the results in the nonhuman literature on the whole suggest that females may often use androgen-dependent phenotypic cues as signals of good condition in males. This renders plausible the possibility that androgens also play a role in determining human male attractiveness.

There is fairly strong evidence that men's androgen concentrations at least coarsely index their general condition. Bribiescas (2001a) has proposed an energy allocation model in which higher circulating androgens are associated with greater energy investment in the construction of men's skeletal muscle mass, as opposed to investment in either energy storage in adipose tissue or energy allocation to immune function. He reviews evidence in humans showing that chronic or acute food deprivation is associated with decreases in testosterone and muscle mass, as are certain illnesses and physical traumas (see also Muehlenbein and Bribiescas, 2005). Testosterone administration, on the other hand, stimulates fat catabolism and has been associated with very large and rapid increases in muscle mass and measures of physical strength (Bhasin et al., 2001). Likewise, in vitro studies in human cell cultures have generally shown that testosterone inhibits components of immune responses such as immunoglobulin production (for example, Kanda, Tsuchida, and Tamaki, 1996), though in vivo studies have been less conclusive (Muehlenbein and Bribiescas, 2005). Taken together, these findings imply that women could use phenotypic cues of high androgen concentrations as signals that men are in good enough condition to afford allocating energy away from functions such as fat storage and immune responses.

Despite common appeals to the idea that men's testosterone concentrations may correlate with their heritable fitness (for example, Penton-Voak et al., 1999), there is surprisingly little research that has directly examined correlations between men's circulating testosterone and ratings of their attractiveness. Neave et al. (2003) reported that attractiveness ratings of men's face photographs were uncorrelated with men's salivary testosterone concentrations. Another study found a small but significant tendency for raters to choose composite faces constructed from the upper half of the testosterone distribution as more attractive than composites constructed from the lower half of the distribution when judgments were made in forced-choice tests; similar forced-choice tests performed on the original faces, however, revealed no significant effect of testosterone (Penton-Voak and Chen, 2004). Roney et al. (2006) reported a small but significant relationship between men's salivary testosterone and women's ratings of the men's faces for short-term mate attractiveness; for subsequent samples of faces collected in my lab, though, we have not always found positive correlations between facial attractiveness and circulating testosterone (unpublished data). With respect to men's facial attractiveness, then, there appears at best a weak positive influence of circulating testosterone concentrations.

Facial architecture may be relatively stable after puberty, though, and so may not provide the most sensitive index of condition-dependent fluctuations in androgen concentrations. Androgen-dependent changes in odor attractivity similar to those seen among nonhuman mammals could provide a more transient signal of condition, and researchers have suggested that more attractive scents among men with lower fluctuating asymmetry could be mediated by higher androgen concentrations in such men (for example, Gangestad and Thornhill, 1998). Nonetheless, in the only study that seems to have directly measured the relationship between men's testosterone concentrations and their odor attractiveness, there was no correlation between women's ratings of men's T-shirt odors and the men's salivary testosterone measures (Rantala et al., 2006). Although research has found that women express attraction to deeper voice pitch (Collins, 2000), muscularity (Maisey et al., 1999; Dixson et al., 2003), and some types of behavioral displays (Gangestad et al., 2004), there do not appear to be any studies that have directly assessed whether attraction to these traits classifies men according to their circulating testosterone concentrations.

The relationship between androgens and attractiveness may be complicated in humans by women's mate preferences for signs of paternal quality that could either conflict with, or at least be independent of, androgen-mediated cues of physical condition. Some research suggests that women may infer poor paternal potential from highly masculinized faces (Perrett et al., 1998; Johnston et al., 2001), and similar inferences for other androgen-derived cues could attenuate relationships between testosterone concentrations and rated attractiveness. Future research might test whether cues of higher androgen concentrations become more attractive under conditions in which women are provided information that assures them that the men in question are relatively high in kindness, interest in children, and so on.

A potentially more difficult problem in testing the role of sex hormones in men's attractiveness relates to the fact that androgen-mediated energy allocation might produce downregulation of testosterone production during circumstances in which elevated concentrations are not necessary for courtship or intrasexual competition. In olive baboons, for instance, testosterone concentrations do not correlate with dominance under stable social conditions but correlate positively during conditions of social instability in which dominance is being challenged (Sapolsky, 1983). Perhaps analogously, female mice exhibited no preferences between scent marks of male mice that were or were not infected with foreign antigens unless the males were first exposed to female urine before marking (such exposure causes transient increases in testosterone; see below), in which case the females preferred marks from the uninfected males (Zala, Potts, and Penn, 2004). In both cases, basal testosterone concentrations may not distinguish males based on their condition—perhaps because the higher-condition males gain energy savings by reducing testosterone when it is not necessary for competition or signaling—but the males in better condition are better able to upregulate concentrations during challenge. The expression of similar energy allocation mechanisms in humans would imply that the relationship between men's androgen concentrations and their attractiveness might be revealed most clearly under conditions of energetic, immune, or social challenge. Although empirical tests of this idea would likely be challenging, the successful demonstration of positive correlations between androgens and attractiveness during conditions of challenge could represent an important advance in our understanding of the physiological determinants of men's attractiveness.

Effects of Mating Stimuli on Sex Hormones

Male Reactions to Female Stimuli

The energy allocation model reviewed above is predicated on the presumption that androgen-mediated investments in muscle development, competitive behavior, and ornament growth are functional only if the mating benefits of such investments outweigh the costs of diverting energy away from survival-related processes such as fat storage and immune function. This implies that testosterone concentrations should be sensitive to cues of mating opportunities. Androgen suppression during the nonbreeding season among seasonally breeding species supports this general position, as it strongly suggests that the benefits of testosterone elevation are coupled specifically to mate competition (see Daly and Wilson, 1983). Breeding season reactivation of gonadal function may be triggered in part by cues from fertile females, furthermore, as male macaques exhibited testosterone elevations after exposure to females who were artificially brought into estrous during the nonbreeding season (reviewed in Michael and Zumpe, 1993), and male Siberian hamsters failed to exhibit breeding season restoration of luteinizing hormone pulses under conditions of long-day photoperiod unless they were also exposed to females (Anand et al., 2002; see also Hegstrom and Breedlove, 1999). Even within breeding seasons or among continuously breeding species, though, mating opportunities vary over time, and we might therefore expect to see androgen-mediated variations in energy allocation over much shorter time scales. Among continuously breeding chimpanzees, for instance, males exhibited both higher testosterone concentrations and more aggressive behaviors on days when parous females displayed maximal sexual swellings (Muller and Wrangham, 2004a). This demonstration potentially extends to primates evidence for the "challenge hypothesis" developed for avian species in which testosterone elevations above those necessary for sperm production promote mate competition behaviors during periods of pair formation (Wingfield et al., 1990). These studies together suggest that male androgen production and its sequelae are functions not only of male condition but also of cues to mating opportunities that can alter the cost-benefit structure of energy investment in mating effort versus survival.

Male hormonal reactions to conspecific females have been demonstrated even more conclusively at shorter time scales than those addressed in the above studies. Across various species, testosterone increases are typically reported within about 20 minutes of onset of exposure to females placed behind transparent barriers (Purvis and Haynes, 1974; Batty, 1978; Popova and Amstislavskaya, 2002; Amstislavskaya and Popova, 2004; Bonilla-Jaime et al., 2006) or to female chemosensory stimuli such as urine or vaginal secretions (for example, Macrides et al., 1974; Pfeiffer and Johnston, 1994; Richardson et al., 2004; for demonstrations specifically in primates, see Ziegler et al., 2005; Cerda-Molina et al., 2006). Testosterone increases are not reported after comparable nontactile exposure to other males (Macrides, Bartke, and Dalterio 1975; Pfeiffer and Johnston, 1992; Amstislavskaya and Popova, 2004), which suggests mechanisms that are designed to respond more specifically to cues of mating opportunities. Other research suggests that common brain mechanisms may regulate behavioral and hormonal reactions to females. Courtship behaviors emitted during exposure to female stimuli have in some cases been found to correlate positively with the magnitude of testosterone responses at about 30 minutes after exposure onset (Pinxten, Ridder, and Eens, 2003; James, Nyby, and Saviolakis, 2006), and lesions to subcortical forebrain structures such as the medial preoptic area disrupt both courtship behaviors (for example, Lloyd and Dixson, 1988; McGinnis and Kahn, 1997; Riters and Ball, 1999) and testosterone reactions to females (Kamel and Frankel, 1978). Castration is also known to reduce or abolish behaviors such as ultrasonic courtship vocalizations in response to female urine (Nyby et al., 1977), but, interestingly, testosterone implantation localized to only the medial preoptic area can restore these reactive vocalizations to normal levels (Matochik et al., 1994; Sipos and Nyby, 1996). A limbic-hypothalamic pathway including structures such as the medial preoptic area may therefore act as a gating mechanism that determines the extent to which cues from females trigger behavioral courtship effort and the upregulation of testosterone production (see also Wood, 1997). Since the hypothalamus processes numerous sources of information regarding male condition (for example, stress hormone concentrations, energetic status, immune activation), furthermore, this pathway may integrate information about mating opportunities with signals of male condition to generate decision rules regarding current investment in mating effort.

The function of short-term testosterone increases is less clear than changes over time scales of, say, breeding seasons, as transient elevations might not substantially adjust energy allocation processes. Transient elevations could play a role in priming longer-term shifts in androgen production and energy allocation if multiple exposures to mating cues have positive feedback effects on neuroendocrine mechanisms—perhaps by upregulating receptors in the limbic-hypothalamic circuit—though I am not aware of systematic tests of this idea. Short-term testosterone spikes might also play a role in regulating behavioral response strategies on short time scales. In particular, cues to mating opportunities may dramatically alter the momentary potential benefits of risky and competitive behaviors. Consistent with a risk-modulation function, Aikey et al. (2002) demonstrated in mice that exposure to mating stimuli, injections of testosterone, and injections of metabolites of testosterone known to act as gamma-aminobutyric (GABA) agonists (such as 3-alpha-androstanediol) each independently produced anxiolytic effects on males within 30 minutes of the respective manipulations. Similar manipulations have also been shown to reduce mount latencies in tests with receptive females (James and Nyby, 2002). Other research has shown that testosterone administration can enhance muscle metabolism within minutes in vitro (Tsai and Sapolsky, 1996), and such effects could plausibly support mate-seeking behaviors. Although rapid adjustments of risk aversion and competitiveness might be accomplished via neurotransmitters without the need for changes in hormone concentrations, it may be functional to maintain some hormonal modulation if androgen production is in fact coupled to general condition. A male in poor condition due to pathogen-based or energetic stress, for instance, may have less functional reason to reduce risk aversion than a male in better condition, and coupling behavioral adjustments to condition-dependent testosterone responses may therefore allow for a better integration of cues to condition with cues to mating opportunities.

The evidence supporting the condition dependence of androgen production in men (see partial review above) supports the functionality of human males also using cues to mating opportunities as moderators of testosterone concentrations. Rapid testosterone responses to cues from potential mates are amenable to experimental tests and could suggest that homologous brain mechanisms produce reactive hormone increases across human and nonhuman mammals. Some studies have provided evidence that exposure to sexually explicit films can trigger testosterone increases within about 20 minutes of exposure onset (Hellhammer, Hubert, and Schurmeyer, 1985; Stoleru et al., 1993; Redoute et al., 2000; but for negative results, see also Carani et al., 1990; Kruger et al., 1998), though the ecological validity of such manipulations seems uncertain. Roney, Mahler, and Maestripieri (2003) reported that men's salivary testosterone increased significantly over baseline concentrations 20 minutes after the onset of a conversation with a woman confederate. The magnitude of testosterone change was also positively correlated with the women confederates' ratings of the degree to which the subjects tried to impress them, which is consistent with the possibility that common mechanisms regulate the behavioral and hormonal responses. Subsequent research has provided further evidence for rapid testosterone increases in men after social interactions with women (Roney, Lukaszewski, and Simmons, 2007). Although the amount of human data is fairly limited, the studies to date present interesting parallels with the nonhuman literature both in terms of the time course of testosterone increases and the correlations between courtshiplike behaviors and time-lagged hormonal responses.

No studies directly address the functions of men's short-term testosterone reactions to mating stimuli. Rapid anxiolytic effects as in nonhuman species are a possibility, and studies that have administered testosterone to subjects have found some evidence for reduced fear responses within a few hours (for example, van Honk, Peper, and Schutter, 2005; Hermans et al., 2006). Although rapid adjustments in risk aversion may seem unnecessary in modern environments in which adults may meet opposite-sex strangers on a fairly regular basis, it is important to keep in mind that encounters with novel young adult women may have been fairly rare events in the small group environments commonly thought to characterize ancestral living arrangements. A face-to-face conversation with an unattached, unfamiliar young woman may have signaled a new mating opportunity that could have rapidly altered the cost-benefit structure of investment in mating effort. If so, transient elevations after initial encounters may play a role in priming longer-term testosterone increases (and hence adjustments in energy allocation) if subsequent encounters suggest the possibility of relationship initiation. Perhaps consistent with this is the finding that although men in relationships typically have lower testosterone than unattached men, men within the first few months of a new relationship had higher testosterone concentrations than even single men (Gray, Chapman, et al., 2004)—such men may be exhibiting the culmination of an energy reallocation process that began at the initial encounter. Reduced risk aversion and rapid adjustments in courtship motivation within hours of meeting a potential mate may also be crucial in modulating mating success if initial impressions play an important role in women's mate choice. Coupling such adjustments to condition-dependent androgen production could in turn ensure that mating effort is calibrated to potential costs as well as benefits. All of this is speculation at this point but could be tested in research designs that look at the effects of testosterone increases in reaction to encounters with potential mates: greater testosterone increases could predict outcomes such as lower risk aversion, greater willingness to engage in competition, or greater willingness to approach women when such outcomes are measured not during the encounters with potential mates but at least 30 minutes after such encounters when testosterone increases have been detected in past studies.

Other evidence supports the idea that men's testosterone concentrations are calibrated to levels of mating effort over longer time scales. Perhaps the strongest support for this possibility comes from studies that have shown that testosterone is lower among men who are in committed relationships or who are fathers (see Gray and Campbell, this volume), as the costs of androgen-mediated energy allocation away from fat storage and immune function may not be functional in men who are not actively seeking mating opportunities. Consistent with the idea that degree of mating effort may be an important variable here, McIntyre et al. (2006) reported that men in relationships who expressed interest in extra-pair sex maintained higher levels of testosterone. Regardless of motivation for pair formation, though, androgen production should also be reduced over longer time periods in the absence of available mating opportunities. Anecdotal evidence from men performing field research away from women suggests that testosterone may fall during such times and then rise again when men are reunited with women (Anonymous, 1970; Bribiescas, 2001a). Over more intermediate time scales, a correlational study found that degree of self-reported, psychological sexual stimulation (estimated by amount of exposure to stimuli such as reading materials, photos, or actual women) predicted serum testosterone concentrations measured the following day (Knussman, Christiansen, and Couwenbergs, 1986). Various lines of evidence are thus consistent with the possibility that motivation for pair formation and/or exposure to stimuli from potential mates can modulate men's sex hormones over a range of different time scales.

The evidence that higher testosterone concentrations actually do improve men's ability to compete for mates is entirely circumstantial. A couple of studies have reported positive correlations between either circulating testosterone (Bogaert and Fisher, 1995) or dihydrotestosterone (Mantzoros, Georgiadis, and Trichopoulos, 1995) and self-reported number of sex partners, though direction of causality is ambiguous. Correlational studies have also reported positive associations between testosterone and personality characteristics that would logically facilitate courtship and intrasexual competition, such as disinhibition, self-confidence, assertiveness, extraversion, and sensation seeking (Daitzman et al., 1978; Daitzman and Zuckerman, 1980; Dabbs, Hopper, and Jurkovic, 1991; Gerra et al., 1999; Aluja and Torrubia, 2004). Likewise, various lines of evidence suggest that higher testosterone individuals are generally more focused on maintaining personal power (Schultheiss, Campbell, and McClelland, 1999), status (Josephs et al., 2003), and dominance (for reviews, see Mazur and Booth, 1998; Archer, 2006), and other research suggests that such characteristics may enhance men's mate attractiveness (for example, Sadalla, Kenrick, and Vershure, 1987). Unclear in all of this correlational research is the extent to which these traits may change over time within individuals concurrent with changes in testosterone concentrations—if men becoming fathers experience drops in testosterone, for instance, do they also exhibit reduced disinhibition or sensation seeking? An androgen-mediated energy allocation model clearly predicts such within-individual changes, but direct empirical evidence will require longitudinal research designs that may be especially challenging to implement. Also needed are empirical studies that can more directly assess whether higher testosterone concentrations predict greater courtship effort in ecologically realistic circumstances. In sum, the available evidence suggests that mating stimuli can affect men's sex hormone concentrations across a range of time scales, though more evidence is needed regarding the functional effects of these physiological adjustments on the initiation of mating relationships.

Female Reactions to Male Stimuli

Interactions with males trigger GnRH release in species with induced-ovulation such as rabbits, ferrets, and cats, but even among spontaneous ovulators there is evidence in various species that exposure to chemosensory or tactile stimuli from males can in some cases advance the preovulatory luteinizing hormone (LH) surge and thus the timing of ovulation (for a review, see Bakker and Baum, 2000). The functionality of any such responses in humans seems uncertain, as it would appear that selection pressures for calibration of fertility to energetic conditions sufficient for successful pregnancy would be far greater than selection pressures for increasing fertility on perception of available mating opportunities—mating opportunities are essentially irrelevant if a woman does not have sufficient energy resources for pregnancy. Nonetheless, there could be marginal functional benefits to advancing ovulation as a means of cryptic female choice in the context of multiple mating or longer-term benefits in terms of energy savings associated with the calibration of ovarian hormones to social circumstances such as relationship status.

Some correlational research has suggested that women who self-report sexual activity or otherwise greater contact with men tend to have shorter and more regular cycles than women who are less exposed to men (for example, McClintock, 1971; Veith et al., 1983), though the direction of causality in these studies seems uncertain. Cutler et al. (1986) experimentally manipulated exposure to male axillary secretions but reported only nonsignificant trends toward shorter or "less aberrant" cycle lengths; furthermore, this manipulation had no effect on ovarian hormone concentrations. Another study that also exposed women to men's axillary secretions found that the time to next LH pulse was reduced after axillary exposure relative to control exposure, but the physiological significance of this effect was uncertain, given that the manipulation had no effect on number of LH pulses, pulse amplitude, or total secretion of LH over the course of the testing session (Preti et al., 2003). It thus appears that there is not yet any direct evidence that exposure to stimuli from men can affect sex hormone concentrations in women.

Conclusion

The energetic costliness of internal gestation and lactation in mammalian reproduction may have selected for females designed to convert energy into offspring and males designed to convert energy into mating opportunities with females (Daly and Wilson, 1983). Evidence for the role of sex hormones in human mating psychology—although very preliminary—appears generally consistent with this position. Women's ovarian hormone concentrations are highly sensitive to variables like energy balance (Ellison, 2001; also see Ellison, this volume), and cycle phase shifts in women's mate preferences suggest that hormone concentrations may in turn calibrate attraction to androgen-dependent traits in men. Ovarian hormones may thus function to couple women's fertility and mate preferences to propitious reproductive conditions. Men's sex hormone production is not as finely sensitive to energetic conditions as in women (Bribiescas, 2001a) but does appear to respond to cues of mating opportunities in ways that have not been demonstrated in women. This suggests a chain of causality in which favorable energetics upregulate women's ovarian hormones (and hence fertility), and men's perception of cues to enhanced fertility in turn upregulates men's androgen production. If sex hormone allocation of energy to fertility in women or courtship effort in men is essentially condition dependent because of finite energy availability, furthermore, then cues of elevated hormone concentrations may enhance attractiveness by honestly indicating good condition. Some direct evidence now indicates that women's physical attractiveness may correlate with their estradiol and progesterone concentrations. The evidence that men's attractiveness correlates with their testosterone production is more indirect, but this relationship may be complicated by the possibility that men may reduce androgen production when it is not needed for mate competition such that correlations with attractiveness may be revealed consistently only under conditions of challenge.

Greater understanding of the role of sex hormones in human mating psychology may substantially advance an area of research that has heretofore been dominated by self-report survey methodologies. Not only can hormonal investigations potentially integrate psychological measures with neurobiological mechanisms and phylogenetic patterns, but the linkages between sex hormones and systems regulating immune function and energy storage suggest that research on sex hormones may be crucial to understanding how mating mechanisms function within the context of multiple systems that have been designed to interact in adaptive ways. This chapter was intended to lay out what little is already known about the role of sex hormones in human mate choice and mate attraction, but clearly this is an area with broad opportunities for further investigation.