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Evolutionary Psychology and Endocrinology

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OVERVIEW: THE ROLE OF ENDOCRINOLOGY IN HUMAN EVOLUTIONARY PSYCHOLOGY

Evolutionary psychology posits that the human mind in its basic design is composed of a collection of specialized processing mechanisms that were naturally selected to address specific adaptive problems, such as mate choice, food choice, social exchange, and parenting (Buss, 2012; Tooby & Cosmides, 1992; chapters in this volume). The primary empirical project for psychological science entailed by this perspective is the discovery and characterization of the functional information-processing features of each of these specialized mechanisms. Although the information-processing (or "cognitive") level of explanation may be privileged since natural selection will act primarily on the functionality of mappings between stimulus inputs and behavioral outputs (see Tooby & Cosmides, 1992), a complete understanding of human psychology also requires empirical characterization of each mechanism's ontogeny, phylogenetic origins, and neurobiological implementation (see Tinbergen, 1963). The systematic mapping of these four levels of explanation on a mechanism by mechanism basis comprises a method for the cumulative construction of an increasingly complete model of human nature.

Research that investigates endocrine signals may be especially productive in promoting the comprehensive mapping of psychological adaptations, for two basic reasons. First, knowledge of endocrine mechanisms typically cuts across the four types of explanation for biological traits such that characterization of the functional roles of

hormonal signals holds the potential to produce unusually complete explanations for specific psychological adaptations. Endocrine signals are known to be produced and received by specific brain structures, the phylogeny and ontogeny of which are often well-characterized; as such, research demonstrating that hormonal signals can produce functional linkages between contextual circumstances and behavioral outputs often carries implications for the neurobiology, ontogeny, and phylogeny of the relevant mechanisms.

Second, endocrine signals may play an especially important role in solutions to the adaptive problem of mechanism coordination that arises as a consequence of the modular organization of the mind. A collection of mechanisms specialized for the solution of different types of adaptive problems raises the problem of determining which problems are currently most pressing in order to assign priority to the processing algorithms of those mechanisms that best solve those problems, while inhibiting mechanisms the outputs of which would disrupt such solutions (see Cosmides & Tooby, 2000). Hormonal signals are ideally suited to contribute to mechanism coordination since they are often released into the general circulation and can thereby simultaneously broadcast information to mechanisms distributed throughout the brain and the rest of the body. In effect, endocrine signals may announce the present importance of specific adaptive problems, and prime organism-wide configurations of mechanism settings that tended to facilitate solutions to those problems over the course of human evolution.

In this chapter, I will describe one specific example of how endocrine signals may produce functional linkages between specific situations and specific configurations of mechanism settings. The example concerns the suite of physiological and psychological

changes that occur when individuals are exposed to potential mates. The chapter is not intended as a literature review of human endocrine research in general, but instead as an example of how research in this area might contribute to the empirical project of mapping the set of human psychological adaptations.

ENDOCRINE SIGNALS AND MATE PURSUIT

EMOTIONS AND THE PROBLEM OF MECHANISM COORDINATION

Cosmides and Tooby (2000) proposed a functional account of emotions as superordinate programs that address the adaptive problem of mechanism coordination. These programs detect ancestrally recurrent cues indicative of a fitness-relevant problem, communicate the presence of this problem via an internal signaling system, and via this communication prime and inhibit distinct mechanisms based on their relevance to solving the problem in question. On this account, emotions may be much more numerous and specific than the traditional set of emotion terms used in language, including emotions such as “being stalked by a predator” that were designed to address recurrent adaptive problems in the ancestral past. In the stalking example, a large number of mechanisms related to other adaptive problems may be inhibited (e.g., those pertaining to food or mate search, sleep, digestion, etc.), while a specific suite of programs and sub-programs calibrate attention, motivation, behavioral thresholds, and physiological patterns toward those settings that on average facilitated escape from danger in this situation.

"Mating opportunity" may comprise an emotion in the sense proposed by Cosmides and Tooby (2000). In sexually reproducing species, the presence of a potential mating partner who exhibited signs of accessibility or interest would have been a recurrent and highly fitness-relevant situation. The fitness benefits of successful mate pursuit likely made it functional for organisms to shift attentional, motivational, physiological, and behavioral priorities away from other adaptive problems and toward mate acquisition upon detection of this situation. The relevant emotion program should implement decision rules regarding whether and how intensely to activate particular mechanism settings based on input cues related to the specific opportunity (e.g., what is the mate value of the potential partner?), the internal state of the organism (e.g., am I in good enough physical condition to engage in mate competition?), and other aspects of the social context (e.g., are competitors present who could thwart efforts at mate attraction?). These decision rules may in effect calibrate the intensity of the internal signals sent to mechanisms throughout the brain and body in order to determine the degree to which the organism is snapped into configuration settings geared toward mate pursuit.

Hormones may be used by many emotion programs as important internal signals that link detection of an adaptive problem to the organism-wide coordination of mechanism settings designed to address that problem. This appears to be especially true for the problem of mate attraction, as specific hormonal responses to cues from potential mates have been demonstrated in a wide array of vertebrate species. In what follows, I first review evidence for these responses in nonhuman species, with an emphasis on how hormone increases may index decision rules regarding behavioral pursuit of mating opportunities. The nonhuman literature provides a model for the possible design of

human mechanisms. I then review evidence that humans express homologous emotion programs that use similar endocrine signals to activate a suite of mechanisms directed toward the problem of mate acquisition.

ENDOCRINE SIGNALS AND MATE PURSUIT IN NONHUMAN SPECIES

Males. Across a wide range of nonhuman vertebrate species, males respond to females or their stimuli with reactive increases in testosterone and corticosterone concentrations that appear to help signal the current importance of mating as an adaptive problem (for a review, see Meisel & Sachs, 1994). These effects are rapid but transient, being first detectable within 10-60 min. of exposure to female stimuli (often peaking near 30 min.) but with concentrations returning to baseline within 1-2 hours. The responses do not require physical contact, as they can be induced via proximity to females placed behind transparent barriers (e.g., Amstislavskaya & Popova, 2004; Batty, 1978; Bonilla-Jaime et al., 2006; Popova & Amstislavskaya, 2002; Purvis & Haynes, 1974) and in some cases by chemosensory stimuli such as urine or vaginal secretions (e.g., Cerda-Molina et al., 2006; Pfeiffer & Johnston, 1994; Ziegler et al., 2005). Finally, these responses are absent after comparable exposure to conspecific males (e.g., Amstislavskaya & Popova, 2004; Macrides et al., 1975; Pfeiffer & Johnston, 1992), which argues for their functional sensitivity to mating-relevant stimuli.

Male behavioral and hormonal responses to females are regulated by a phylogenetically conserved limbic-hypothalamic pathway (for reviews, see Meisel & Sachs, 1994; Paredes & Baum, 1997). Lesions to key structures within this pathway –

such as the medial amygdala and especially the medial preoptic area – have been shown to abolish or significantly reduce male sexual (Paredes & Baum, 1997), courtship (e.g., Lloyd & Dixson, 1988; McGinnis & Kahn, 1997; Riters & Ball, 1999), and hormonal (Kamel & Frankel, 1978) responses to females. These structures express the highest density of androgen receptors of any brain region (Pfaff, 1981) and the signaling properties of this pathway are clearly regulated by androgens like testosterone: castration (and thus removal of testosterone) eliminates or severely reduces male courtship responses to conspecific females, but selective implantation of testosterone into pathway structures such as the medial preoptic area can restore such behaviors to normal levels in castrated males (e.g., Matochik et al., 1994; Nyby et al., 1977; Sipos & Nyby, 1996). Likewise, pharmacological blockade of androgen receptors in this pathway eliminates or reduces male behavioral responses to females (Harding & McGinnis, 2004; Raskin et al., 2009). In sum, a conserved limbic-hypothalamic pathway appears to act as a type of gating mechanism that implements decisions rules about the extent to which cues from females trigger coordinated behavioral and hormonal responses in males. This gating mechanism is in turn modulated by androgens via the androgen receptor such that males are less responsive to female stimuli when testosterone falls to very low concentrations or when the number of occupied androgen receptors is otherwise low.

The signaling properties of the limbic-hypothalamic gating mechanism produce functional modulation of male responses to females under a range of natural conditions. Seasonally breeding species often undergo a type of reversible castration, for instance, in which testosterone falls to castrate levels during the nonbreeding season (in response to cues such as reduced photoperiod) concomitant with an absence or reduction of male

behavioral and hormonal responses to females (e.g., Anand et al., 2002; Riters et al., 2000). Likewise, male rodents that have reached a state of sexual satiety via frequent ejaculation fail to respond both behaviorally and hormonally to novel females (Bonilla-Jaime et al., 2006; Bronson & Desjardins, 1982), and the behavioral effects of satiety are strongly correlated with changes in the density of androgen receptors within the limbic-hypothalamic pathway. Receptor density drops as satiation sets in but then recovers with the resumption of sexual responses to females (Fernandez-Guasti et al., 2003; Romano-Torres et al., 2007). These patterns suggest the functionality of this emotion program's decision rules: under conditions in which pursuit of mates is less functional – as when females are not fertile during the nonbreeding season or when sexual exhaustion has produced sperm depletion – this pathway is down-regulated such that cues from females are no longer mapped onto behavioral and hormonal responses in males.

Various social conditions are also modulators of male hormonal responses to cues from females. In cynomolgus macaques, for instance, an estrous female introduced into a group of males for 20 min. triggers testosterone and cortisol increases in dominant but not in subordinate individuals; however, subordinates exhibit hormonal responses to females under experimental conditions in which the dominant male was removed from their group (Glick, 1984; for similar effects on longer time scales in squirrel monkeys, see Mendoza et al., 1979). Among male marmosets, who form pair-bonds and provide paternal care for offspring, the vaginal secretions of novel females triggered testosterone increases in unpaired and pair-bonded males without offspring, but failed to trigger hormonal responses in males who were currently caring for juveniles (Ziegler et al., 2005); paternal males will often respond to novel females with aggression, furthermore,

suggesting the absence of testosterone responses when males are not treating females as potential mating partners.

Overall, the literature on hormonal responses to potential mates in vertebrate males suggests an endocrine code that indexes a motivational state directed toward mate acquisition: when males respond to females with courtship and sexual behaviors, they also tend to exhibit transient, rapid increases in testosterone and glucocorticoid concentrations. These hormonal responses are diminished or absent under those circumstances in which males do not pursue mating opportunities: during the nonbreeding season when baseline testosterone is very low, when in a state of sexual exhaustion, when in the presence of dominant males who are likely to attack subordinates who make mating attempts, and when engaged in paternal care for offspring. While other signals may also be implicated in this motivational state, testosterone and corticosterone appear to be consistent components of responses to mates across many species, and are thus phylogenetically conserved components of an internal signaling system that broadcasts the current pursuit of mating opportunities.

Reactive hormone increases, in turn, have been implicated in a wide range of downstream effects, consistent with their proposed role as calibrators of organism-wide mechanism settings. Testosterone injections that experimentally simulate reactive increases, for instance, have been shown to have a number of rapid effects (for reviews, see Gleason et al., 2009; Nyby, 2008). Male mice injected with testosterone mount females faster than do control males at 30 min. post-injection, which approximates the time delay between first encounters with females and onset of copulation (James & Nyby, 2002). Testosterone injections likewise induce preferences for places in which they

occurred (e.g., Alexander et al., 1994), rapidly reduce males' risk-aversion (Aikey et al., 2002), and increase the probability of attacking other males (Gleason et al., 2009). In addition to these behavioral effects mediated via brain mechanisms, testosterone has been shown to rapidly promote both penile reflexes (reviewed in Nyby, 2008) and glucose uptake in muscle cells (Tsai & Sapolsky, 1996), with such effects occurring within 1-10 min. of hormone administration.

A simple example may help clarify the functions of hormonal responses in nonhuman males. Rodents are typically averse to open spaces as a predator avoidance tactic. Exposure to female urine triggers both reactive testosterone increases and increased exploration of open spaces in male mice, with such exploration being reproduced by testosterone injections alone (Aikey et al., 2002). In effect, the testosterone increases act as an internal signal for a mate pursuit emotion program that reduces aversion to predation risk when cues of mating opportunities alter the likely cost-benefit profile of exploratory behaviors. This assignment of relative priority across mechanisms with incompatible behavioral outputs (e.g., avoidance vs. exploration of open spaces) is the general function of emotion programs, and all of the downstream effects of reactive testosterone increases reviewed above appear consistent with assignment of priority to those mechanisms that facilitate the successful pursuit of mating opportunities.

Females. Emotion programs related to mating behaviors appear to be activated differently in females than in males across many vertebrate species. Rather than being cued by stimuli from potential mates, such programs appear to respond primarily to internal signals associated with ovulation and thus current fecundity. Interactions with males or their stimuli are the proximate triggers of ovulation in a minority of species

(such as rabbits, ferrets, and cats) with induced ovulation (for a review of such cases, see Bakker & Baum, 2000). In the vast majority of mammals, however, females ovulate according to cycles of endogenous signals with sexual receptivity and proceptivity restricted to fertile regions of the cycle characterized by elevated estrogen (for reviews, see Blaustein, 2008; Carter, 1992).

The likelihood of ovulation occurring within a given time period is in turn a function of energetic variables for most vertebrate and especially mammalian species. The high energetic costliness of mammalian gestation and lactation have led to the evolution of mechanisms that suppress ovulation (and thus fecundity) under conditions in which energy availability is below that necessary for successful gestation (for a review, see Wade & Jones, 2004). Conditions of low energy availability occur regularly during events such as lactation or seasonal drops in food supply, and during such times it is clearly functional for females to allocate priority to mechanisms addressing adaptive problems such as maternal care, foraging, or thermoregulation. The general chain of causation in female mating programs appears to run from energy availability to ovulation and its associated release of hormones to prioritization of mating mechanisms in response to such hormones.

Ovarian hormones act as internal signals for female mating programs in ways analogous to the effects of testosterone in male mating programs. A similar limbic-hypothalamic circuit to that involved in males has been shown to regulate female responses to potential mates, with key structures such as the ventromedial nucleus of the hypothalamus directly affecting behavioral indicators of receptivity (such as the lordosis posture) under the influence of estradiol (for a review, see Pfaff & Schwartz-Giblin,

1998). Estradiol has been shown to have positive effects on female sexual motivation across a broad range of vertebrate species (Blaustein, 2008; Carter, 1992), though evidence occasionally supports positive effects of testosterone in some species, especially with respect to proceptive behaviors (Fernandez-Guasti et al., 1991) or preferences for gonadally intact males in partner preference experiments (e.g., Xiao et al., 2004). Consistent with a mechanism coordinating function for hormones, the increased sexual motivation associated with fecund regions of the estrous cycle appears to be coupled with reduced motivation for other behaviors, as exemplified by substantial drops in foraging and eating when sexual receptivity is heightened near ovulation (for reviews, see Fessler, 2003; Schneider et al., 2013).

Rapid hormonal responses to interactions with potential mates as demonstrated in males have rarely been tested in nonhuman females, probably because of the known effects of endogenous changes in hormones on female sexual motivation. In humans, however, the common formation of long-term pair bonds in mating relationships may have selected for rapid hormonal responses as a means of activating mate acquisition programs independent of time in the menstrual cycle. Given that long-term mates could be met at any time of the cycle and not just on fecund days, reactive hormone increases may have allowed phylogenetically conserved brain structures that respond to ovarian hormones to be activated even outside of the fertile window when women met men who were perceived as attractive potential mates. This logic underlies the prediction that both men and women will exhibit hormonal responses to potential mates as internal signals that coordinate mechanism settings associated with a mating opportunity emotion program.

Males. The limbic-hypothalamic structures that regulate male hormonal and behavioral responses to potential mates exhibit extensive neuroanatomical and functional homology across vertebrate species (e.g., Baum, 1992), which raises the possibility that human males have likewise inherited homologous structures that play similar regulatory roles in a mating opportunity emotion program. Two general empirical patterns are expected if human males express homologous mechanisms. First, men should exhibit hormonal responses to potential mates that are similar to those exhibited in nonhuman vertebrate males. Second, the reactive hormone increases should produce organism-wide downstream effects on mechanism settings that are consistent with facilitation of mate pursuit. Evidence supports both of these patterns.

With respect to hormonal responses to potential mates, controlled laboratory experiments have demonstrated that young men exhibit rapid increases in concentrations of both salivary testosterone (Roney et al., 2003, 2007, 2010; van der Meij et al., 2008) and cortisol (Roney et al., 2007, 2010; van der Meij et al., 2010) after brief social interactions with female confederates. These responses are absent after similar interactions with male confederates. Field studies have also demonstrated reactive increases in testosterone after exposure to or social interaction with women under more ecologically realistic circumstances: after dancing with a woman versus engaging in the same movements without a partner (Murcia et al., 2009), after performing skate-board tricks in the presence of a young woman vs. in the presence of a young man (Ronay &

von Hippel, 2010), after engaging in sporting events with a greater versus lesser ratio of women to men present (Miller et al., 2012), and after naturally occurring social interactions with young women in a Dominican village (Flinn et al., 2012). Finally, men's testosterone (Cerda-Molina et al., 2013; Miller & Maner, 2010; cf. Roney & Simmons, 2012) and cortisol (Cerda-Molina et al., 2013) concentrations may undergo more positive changes after exposure to olfactory stimuli collected from women near ovulation than after exposure to various types of control odors.

The hormonal responses in human males exhibit many parallels to those demonstrated in nonhuman species. The effects occur on a similar time-scale, being first detectable on average within about 15-30 min.; both testosterone and cortisol (corticosterone in nonhuman species) are released; and responses are absent after comparable exposure to other males. One study demonstrated that testosterone responses to conversations with women were larger among men with more sensitive androgen receptors as indexed by shorter CAG codon repeat lengths in the androgen receptor gene (Roney at al., 2010). This is consistent with regulation of the hormone response by similar limbic-hypothalamic structures as in nonhuman species, given the known role of androgen receptors in modulating the responsiveness of this brain pathway to cues from females among male rodents. Taken together, these similarities with nonhuman responses argue for the likely phylogenetic conservation of the same basic system across human and nonhuman species.

Other lines of evidence suggest that the probability and size of men's hormonal responses to potential mates are modulated in functional ways by other variables, and, as in nonhuman males, the hormone increases may comprise an endocrine code that indexes

a motivational state directed toward mate pursuit. Flinn et al. (2012), for instance, demonstrated that men did not exhibit reactive testosterone increases after interacting with young women who were mates of their friends, which suggests the absence of hormonal responses under conditions in which men are unlikely to behaviorally pursue a mating opportunity. Likewise, men who self-reported higher dominance were found to exhibit larger testosterone responses to interactions with young women (van der Meij et al., 2008), which suggests parallels to nonhuman primate studies that have reported larger responses among dominant males (e.g., Glick, 1984; Mendoza et al., 1979), and is consistent with modulation of mating effort by relative levels of intrasexual competitiveness. Such modulation suggests that the decision rules that determine courtship effort are sensitive to the possible costs as well as the benefits of pursuing mating opportunities.

Perhaps consistent with such cost-sensitivity, Roney et al. (2010) found that higher baseline cortisol concentrations predicted smaller testosterone responses to interactions with young women. Many of the conditions that cause elevated baseline cortisol (e.g., energy shortage, immune activation, psychosocial stress; see Dickerson & Kemeny, 2004; Peters et al., 2004) may make mate competition temporarily less functional, explaining the relative suppression of a mate pursuit emotion program when baseline cortisol is elevated. In sum, conserved brain structures appear to implement decision rules regarding mate pursuit based on various costs and benefits associated with specific opportunities, and, when decisions are positive, cause reactive increases in hormone concentrations as internal signals of those decisions.

Although the precise functions of reactive hormone increases in humans have not been definitively determined, a number of lines of evidence suggest that such increases have a range of downstream effects that are consistent with an organism-wide orientation toward courtship and mate competition. Cortisol increases are known to promote short-term glucose availability (for a review, see Peters et al., 2004) and can facilitate enhanced attention, concentration, and memory consolidation in response to motivationally significant events (for a review, see Erickson et al., 2003). Cortisol increases in response to interactions with potential mates may therefore act as rapid energy mobilizations in support of courtship efforts. High baseline cortisol, however, may indicate poor condition for mate competition given its elevation during energy shortages, such that baseline cortisol could negatively index the energetic resources currently available for mating effort, while cortisol responses to potential mates may represent the marginal increases in energetic resources that can be devoted to such effort.

Reactive testosterone increases in humans have been associated with a range of effects that are logically related to willingness and ability to compete for mating opportunities. van Honk and colleagues in a series of experiments have induced large spikes in testosterone in women via exogenous hormone delivery and then measured psychological and behavioral outcomes within a few hours of drug administration. These studies demonstrated that testosterone administration relative to placebo triggered reduced fear responses (Hermans et al., 2006a, 2007; van Honk et al., 2005), reduced empathy and sensitivity to others' facial expressions of emotion (Hermans et al., 2006b; van Honk & Schutter, 2007), and increased risk-taking and reward sensitivity (van Honk et al., 2004). Although the extent to which such effects would generalize to men is

uncertain, all of these outcomes are consistent with a general orientation toward greater boldness and competitiveness. In addition, a number of studies have tested correlations between the size of men's testosterone responses to experimental manipulations and the magnitudes of behaviors performed just after the hormone responses. These studies have found that the size of hormonal responses to competitive tasks positively predicts self-reports of willingness to compete again (Carre & McCormick, 2008; Mehta & Josephs, 2006), the magnitude of aggressive behaviors directed toward other participants (Carre et al., 2009, 2013; see also Klinesmith et al., 2006), and the magnitude of courtship-like behaviors directed toward a young woman (van der Meij et al., 2012). Finally, a recent study reported that the size of testosterone responses to short film clips, including an erotic film, positively predicted subsequent weight lifting performance among trained athletes (Cook & Crewther, 2012). As in nonhuman species, then, evidence supports organism-wide changes in response to transient hormone increases, ranging from adjustments in behavioral tendencies to possible increases in physical strength.

In summary, there is now fairly strong evidence for the expression of a mating opportunity emotion program in human males. Upon exposure to stimuli from potential mates, men exhibit reactive hormone increases that are highly similar to the responses found among nonhuman vertebrate males, which argues strongly for their regulation by homologous brain structures. These hormone increases, likely in conjunction with other signals, appear to act as an endocrine code announcing the present importance of mate pursuit as an adaptive problem. Consistent with this, the reactive hormone increases have been associated with a range of downstream effects that logically would have facilitated courtship effort and intrasexual mate competition, including increased competitiveness,

boldness, aggressiveness, physical strength, and expressions of courtship-like behaviors directed toward young women. Although many details of this emotion program remain to be worked out, the evidence to date suggests positive prospects for achieving a fairly complete description of an adaptive psychological system in which endocrine signals play a central role.

Females. Little research has assessed reactive hormone changes in women after exposure to potential mates. Most instead has assessed effects of menstrual cycle phase on specific aspects of women's sexual psychology and behavior. In an important exception, Lopez et al. (2009) tested and found evidence for reactive increases in women's salivary testosterone and cortisol concentrations after viewing a video of a physically and behaviorally attractive man who was directing courtship behaviors toward a woman (the subjects were instructed to imagine themselves in place of the target woman). These effects were detected at 30 min. after the onset of the video and were absent among women in control groups who viewed a nature documentary, a video containing an attractive woman, or a video containing an unattractive man. Furthermore, among the women who viewed videos containing a man, magnitudes of changes in both testosterone and cortisol were significantly positively correlated with ratings of the man's attractiveness, desire to have sex with the man, and desire for a relationship with the man.

The results of the Lopez et al. (2009) study suggest that the same hormones that serve as internal signals of a mating opportunity emotion program in men may play similar signaling roles in women. Increases in testosterone and cortisol may help signal the presence of an attractive mating opportunity and cause downstream adjustments in mechanism settings that on average facilitated successful efforts at mate attraction.

Experimental manipulations of testosterone pulses in women suggest in particular that reactive testosterone increases may reduce fear responses (Hermans et al., 2006a, 2007; van Honk et al., 2005) and increase risk-taking and reward sensitivity (van Honk et al., 2004), all of which might plausibly increase the display of receptive and proceptive signals to prospective partners, although future research is necessary to specifically test links between hormonal changes and behaviors directed toward potential mates. Baseline concentrations of testosterone (and in some cases cortisol) have also been linked to some measures of aggressive and competitive behaviors in women (e.g., Cashdan, 2003; Denson et al., 2013), such that reactive increases in these hormones might prime competition with intrasexual rivals for the attention of a highly desirable potential partner. In short, the Lopez et al. (2009) study provides an important proof of concept for women's hormonal responses to potential mates, but as the only study of its kind there is a clear need for further research that both replicates the effect in actual social interactions and tests downstream consequences of the reactive hormone changes.

Emotion programs related to mate choice and mate pursuit appear to be calibrated by endogenously generated shifts in ovarian hormones associated with cycle phase physiology in women, in addition to being triggered by exposure to attractive potential mates. Women tested during the fertile window relative to other times in the cycle tend to express stronger attraction to putative heritable fitness indicators in men, such as more masculine or symmetrical features (for reviews, see Gildersleeve et al., in press; Jones et al., 2008; Thornhill & Gangestad, 2008); may exhibit increased sexual desire and initiation of sexual behavior (for a review, see Wallen, 2001); and appear to increase their proceptivity in the form of adopting more attractive and revealing clothing choices

(Durante et al., 2008; Haselton et al., 2007). Less research has addressed the endocrine signals that may regulate such shifts, although studies have supported elevated testosterone as a predictor of preferences for more masculine faces (Babst et al., 2014; Welling et al., 2007), elevated estradiol as a predictor of preferences for cues of higher circulating testosterone in men (Roney & Simmons, 2008; Roney et al., 2011), and the combination of elevated estradiol and low progesterone as a predictor of within-cycle increases in subjective sexual desire (Roney & Simmons, 2013). The theorized functions of these cycle phase shifts have been covered in detail elsewhere (e.g., Gangestad, this volume; Thornhill & Gangestad, 2008; cf. Roney, 2009). The key point here is that the diverse effects associated with ovulatory timing are consistent with endogenous hormonal changes acting as internal signals for mating-related emotion programs. Essentially, endocrine signals associated with current fecundity may broadcast the current importance of mating as an adaptive problem in the service of calibrating mechanism settings such that preferences for specific cues are sensitized, behavioral proclivities toward display of attractiveness is increased, and motivation for contact with mates is elevated.

An interesting direction for future research is the investigation of how endogenously generated endocrine signals associated with cycle phase dynamics may affect and interact with more transient hormonal responses to potential mates. Hormonal signals associated with high current fecundity may create a baseline motivational state directed toward mate search and mate evaluation, with hormonal responses to actual potential partners then triggering a more specific emotion program (or subprogram) directed toward pursuit of a particular target partner. Whether reactive hormone responses to attractive potential mates may be more likely or larger in magnitude

depending on baseline hormone concentrations is largely unknown since the Lopez et al. (2009) study was underpowered to address this question. However, Lopez et al. (2009) did report that testosterone responses to the attractive man video were absent among women using hormonal contraceptives, which is consistent with the inhibition of reactive hormone responses to potential mates when baseline hormones are reduced due to the absence of dominant follicle maturation. If lower baseline ovarian hormone concentrations are associated with a higher threshold for activation of mate pursuit emotion programs, this may have evolved to allocate greater priority to adaptive problems other than mate attraction during natural conditions associated with suppressed fecundity, such as during lactational amenorrhea or after menopause (see Roney, in press). Future research could directly assess whether reactive hormone responses to potential mates are larger or more likely in ovulatory as opposed to anovulatory natural cycles (or in cycles with higher vs. lower estradiol concentrations) as a first step toward testing more complete models of the possible roles of endocrine signals in women's reactions to potential mates.

FUTURE RESEARCH IN EVOLUTIONARY ENDOCRINOLOGY

The mate pursuit examples described above were intended to demonstrate the potential heuristic value of treating endocrine signals as important components of evolved emotion programs as defined by Cosmides and Tooby (2000). This framing, in fact, may be the key to understanding the functions of hormones in general. Other

endocrine signals share with sex hormones the property of release into the general circulation and thus the ability to manipulate organism-wide parameter settings that determine the relative priority of distinct mechanisms based on the current importance of particular adaptive problems. This makes other hormonal signals – such as oxytocin, vasopressin, and prolactin – ideal messengers to act as internal signals in various emotion programs. Development and empirical testing of theories regarding the design of the emotion programs that use such signals may thus be the best method for elucidating the evolved functions of human hormones. Conversely, the relatively unique ability of hormones to simultaneously activate and inhibit multiple mechanisms throughout the brain and body suggests that endocrine signals will often have key roles in adaptive emotion programs such that knowledge of endocrinology may be crucial for achieving a full understanding of the design of many human psychological adaptations.

The emotion program framing is not widespread in the extant literature on human hormones, however, which has often focused on attempting to derive the most parsimonious descriptions of the functions of endocrine signals. Historically, for example, testosterone has at various times been proposed as a status or dominance or aggression hormone, with debates regarding which description best describes its effects and an implicit appeal to a parsimony principle in which the most encompassing description is considered scientifically superior. Similar arguments exist in the expanding literature on oxytocin, with proposals for general descriptions of oxytocin as a bonding or trust hormone.

The argument that hormones play key roles as internal signals in emotion programs does not suggest that these general descriptions of hormones are necessarily

inaccurate, but instead that they are likely to be incomplete given that the very function of such signals is the simultaneous calibration of multiple mechanism settings. Testosterone, for instance, has wide-ranging physiological effects in addition to calibration of behavioral tendencies, including influences on immune function, fat catabolism, blood hemoglobin, muscle anabolism and glucose uptake, and rates of spermatogenesis (for reviews, see Ellison, 2001; Ellison & Gray, 2009; Muehlenbein & Bribiescas, 2005). These multiple diverse effects resist simple reduction to a broad category such as status or aggression, but may make functional sense as coordinated components of emotion programs activated under specific circumstances. These considerations recommend an empirical shift of emphasis away from attempting to find the most generalized descriptions of specific hormones' effects and toward the systematic mapping of the broader emotion programs that use hormones as signals and are activated in response to cues of ancestrally recurrent adaptive problems. This shift would seamlessly integrate the study of human endocrinology with the adaptation-mapping project of human evolutionary psychology.

An interesting question concerns the potential breadth of this integration of endocrinology with evolutionary psychology. While hormones clearly play important roles as internal signals with respect to mating adaptations, is this also the case for many other adaptive problems? In theory, hormones might be expected to act as signals whenever the broad coordination of multiple mechanisms is an adaptive response to ancestrally recurrent cues of specific problem domains. Such coordination is clearly important in response to events such as the birth of a child, and in fact a variety of hormonal signals have been studied as intermediaries between perception of this event

and diverse psychological and behavioral responses (for reviews, see Fleming & Gonzalez, 2009; Rilling, 2013; Saltzman & Maestripieri, 2011). Parenting adaptations thus represent another example in which the emotion program approach is likely to productively integrate evolutionary psychology with endocrinology.

Even beyond the broad motivational categories typically associated with behavioral endocrinology research (e.g., mating, parenting, feeding, aggression), it is possible that endocrine signals have specific coordinating roles associated with many psychological adaptations. In social exchange, as just one example, information indicating that an exchange partner has cheated or benefited you may have cascading implications both for your relationship with that particular partner and for your broader position within a social group. An adaptive response to those implications might then entail the adjustment of multiple mechanism settings related to levels of vigilance, proclivities toward risk-taking, levels of sociality, thresholds for aggression, and so on. Perhaps consistent with an endocrine signal of such adjustments, recipients of even a brief expression of trust in a neuroeconomics experiment demonstrated rapid increases in serum oxytocin (Zak et al., 2005). Future research will be necessary to determine how widespread endocrine signals actually are in psychological adaptations, but the diffuse messages carried by hormones suggest that they are likely to be common devices for recalibrating diverse mechanism settings in response to cues of functionally relevant circumstances.

Specific hormonal signals could play roles in multiple emotion programs, such that an additional empirical task for a field of evolutionary endocrinology may be the discovery of how emotion programs interact with each other or are differentiated from

one another. The types of testosterone responses exhibited after interactions with potential mates have also been demonstrated after aggressive and competitive interactions in both human and nonhuman species (for reviews, see Archer, 2006; Gleason et al., 2009; Mazur & Booth, 1998), which suggests use of similar internal signals by multiple emotion programs. A possible explanation for this is that similar downstream mechanism settings are functional after both exposure to potential mates and events such as competitive victories. Competitive victories may prime mating motives secondary to increased attractiveness and mating opportunities may prime increased competitiveness in the service of potentially defending a valuable reproductive resource (see Ainsworth & Maner, 2012; Gleason et al., 2009). This is not to say that mate pursuit and competitive interaction emotion programs are identical. They are presumably activated by distinct cues with distinct decision rules regarding the release of internal signals for production of specific mechanism settings. Some of these downstream settings, however, may in fact be overlapping. Furthermore, hormones are very unlikely to be the exclusive signals employed by emotion programs – hormone-mediated communication is slow compared to most neurotransmitter-mediated signals and many emotion programs will require very rapid effects (see Cosmides & Tooby, 2000) – such that mate pursuit and competitive interaction programs probably involve the rapid activation of distinct neural networks via transmitter-based signaling, with the common downstream modulation of mechanism settings via testosterone responses occurring at a more delayed time-scale.

Another possibility, however, is that distinct combinations of hormonal responses may act as de facto endocrine codes that distinguish specific emotion programs. If, for instance, exposure to mates was associated with oxytocin increases but competitive

interactions were not, or specific combinations of catecholamines accompanied testosterone release in one case but not the other, then even the downstream mechanism settings associated with reactive testosterone increases might be differentiated in subtle ways across the two emotion programs. These types of issues present challenging empirical problems for future investigation.

The emotion program approach to understanding hormones almost necessarily requires collaborative and interdisciplinary approaches to future research in evolutionary endocrinology. Understanding whole organism calibration of mechanism settings, for instance, requires either collaboration between scholars with expertise in different types of psychological and physiological mechanisms or uncommonly broad interdisciplinary training in individual researchers. Future research in this area may entail teams of scholars mapping out distinct pieces of emotion programs in order to collaboratively build models that specify specific activating cues, release of endocrine signals in response to those cues, and, finally, the set of downstream mechanism settings triggered by endocrine signals and directed toward the solution of specific adaptive problems.

In conclusion, endocrine signals are likely to play important explanatory roles in the expanding field of human evolutionary psychology. A modular collection of specialized processing mechanisms requires functional means of coordinating when specific mechanisms are activated and inhibited, and hormonal signals are ideally suited to act as messengers of such coordination. In effect, hormones act as conductors of the real-time symphony of mechanism activation and inhibition that links patterns of behaviors to the specific circumstances in which those behaviors were most functional

over the course of human evolution. No model of human nature will be complete without a clear understanding of the functional roles of these chemical messengers.

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