

Hormones and Human Partnering

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Research on the associations between hormones and human partnering represents an exciting advance in understanding human behavior, relationships, and sexuality. We review empirical literature on circulating hormones and human partnering (i.e., pair bonding, sexual/romantic relationships, pairing). We begin by reviewing steroids (e.g., androgens, estrogens, cortisol) and peptides (e.g., oxytocin, vasopressin). We then move on to androgen-partnering associations, attending to early stages of relationships, and partnering behaviors. A major focus includes relevant theoretical frameworks, possible directional or causal associations, and related controversies. We next cover associations between pair bonding, partnering behaviors, and both peptide (e.g., oxytocin) and stress hormones (e.g., cortisol). Following is a discussion of some contextual factors that might be important to understanding hormone-partnering associations, such as pregnancy or menopausal status. We conclude by summarizing and highlighting the main findings of partnering-hormone links and their implications; and we close by describing some of the challenges facing the field and some future directions given the field's current trajectory.

Key Words: androgens, challenge hypothesis, gender, pair bond, partner, relationship, sex.

Judging by the content of our literature, laws, behavior, and preoccupations, sexual and romantic relationships are fundamental aspects of human behavior. Only recently, however, have love and relationships been understood to fall within the purview of bio-scientific foci. Although lay assumptions might conceptualize hormones as the key biological correlate of sexuality, love, and relationships, the findings from recent research suggest that associations with hormones are subtle and intriguing.

Throughout, we use the terms *partnering* and *pair bonding*. This choice replaces *romantic/sexual relationships*, which can be unwieldy,

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or *mating*, which can be problematic when referring to human partnering that includes postfertility, same-sex, or nonreproductive contacts. Unlike pair bonding, partnering does not denote two-person relationships. In this review, we do not address prenatal hormones, menstrual cycles, or nonhuman animal research, except when relevant to human research. We cover hormones that have received sufficient empirical attention to merit inclusion in a review, but this choice does not negate the potential importance of the many others we do not reference.

Research on hormones and human partnering represents an exciting advance, a line of inquiry that approaches one of the frontiers of human biology and behavior. This review is timely—published at a point when the literature is beginning to grow but is still graspable—and, we believe, helpful: It introduces the neophyte to the field, updates the veteran on current findings and theory so as better to appreciate future advances, and both reviews the findings so theorists and empiricists can work to piece together this puzzle and identifies areas in need of empirical investigation.

Brief Overview of Hormones

Steroids

Although peptide hormones, such as oxytocin and vasopressin, have received substantial consideration in pair-bonding research, steroid hormones are also significantly associated with partnering as well as social behavior in general. Steroid hormones are released following a sequence that begins in the hypothalamus, continues to the pituitary, and culminates with steroid release from the gonads or adrenal glands. Steroids are lipid-soluble and often have “carriers” or binding globulins to help them travel through blood. They can arrive at receptors located anywhere in the body that blood can reach. Steroidal action occurs via binding of the steroid to nuclear receptors, which can have genomic effects (e.g., affect transcription), or, as has been more recently suggested, through membrane-bound receptors to exert nongenomic effects (Losel et al., 2003).

Sex steroids. Androgens, estrogens, and progesterone are commonly referred to as “sex steroids.” In humans, estrogens include estradiol (found in higher concentrations than other estrogens), estriol, and estrone. Androgens include the following: testosterone (T), the most common androgen; dehydroepiandrosterone and its sulphate, DHEA and DHEAS, weaker androgens released from the adrenal gland; androstenedione, an androgen precursor; and dihydrotestosterone (DHT), a testosterone metabolite and a potent androgen especially important for genital virilization, among other things (Becker,

Breedlove, Crews, & McCarthy, 2002). These sex steroids influence reproductive and sexual development as well as other physiological processes (e.g., immune function, stress responses); they can also affect sociosexual behaviors (see below).

Sex differences are found in hormone concentrations, with higher levels of androgens in men, and higher levels of estrogens in women. Still, both classes are represented in women and men and play significant roles in the physiology of both men and women. Steroids are released largely via the hypothalamic-pituitary-gonadal (HPG) axis, and also via the hypothalamic-pituitary-adrenal (HPA) axis, although in smaller quantities (adrenal androgens are a higher percentage of overall androgen levels in females because the testes release larger quantities of androgens relative to the ovaries). Steroids are transported through the vascular system via sex-hormone binding globulin (SHBG).

Release of sex steroids from the HPG axis is stimulated by gonadotropin-releasing hormone (GnRH) in the hypothalamus. GnRH then stimulates the anterior pituitary gland to release both luteinizing hormone (LH) and follicle-stimulating hormone (FSH). LH stimulates the Leydig cells of the testes and the thecal cells of the ovaries to release sex steroids. Sex steroids are also produced in peripheral adipose tissue through conversion from precursor hormones. The HPG axis generally functions through negative feedback (i.e., higher sex steroids downregulate gonadotropins, leading to lower gonadal steroid release), but positive feedback can occur under specific conditions as happens, for example, with the pre-ovulatory surge of estradiol during the menstrual cycle or with increasing levels of progesterone over pregnancy. Additionally, GnRH appears to be influenced by other hormones in both a stimulatory (by kisspeptin) and inhibitory (by gonadotropin inhibitory hormone, GnIH) fashion (for a review, see Kriegsfeld, 2006).

All sex steroids are derived from a common pathway starting with cholesterol, from the common hormone precursor pregnenolone. Estradiol and DHT are derived from T, which itself can be derived from DHEA or progesterone pathways (Chung & Hu, 2002). T can be "aromatized" (i.e., converted through the enzyme aromatase) to estradiol and can be converted to DHT through the enzymatic activity of 5- α -reductase; these conversions (T to DHT; T to estradiol) are thought to be unidirectional. Steroids bind to hormone class-specific receptors, that is, androgen receptors (AR), estrogen receptors (ER), and progesterone receptors. Receptors are present in multiple isoforms intracellularly, ER α and ER β , for example, and potentially in a different membrane-bound morph.

Serum measures of sex steroids generally result in “total” or “free” levels (e.g., free T is an estimate based on quantities of total T relative to quantities of SHBG). Free steroids are thought to be the bioactive portion of the hormone (and therefore relevant to questions in behavioral neuroscience), as they represent the unbound portion available to travel throughout the vascular system to receptors; the bioactive component may include the weakly bound (i.e., albumin-bound) portion as well. Related to this, salivary measures are often called “bioavailable” because the portion of the hormone that can be accessed through saliva is the un- or weakly bound fraction that can travel to receptors (and thus potentially influence behavior; Quissell (1993). Salivary and blood serum measures of testosterone have been validated for clinical use and are widely used in research.

Although salivary and free steroid measures correlate with one another (e.g., T: Shirtcliff, Granger, & Likos, 2002; Wang, Plymate, Nieschlag, & Paulsen, 1981), they are not identical. Salivary measures of T, for example, can be both reliable and accurate but may underestimate behavior-hormone relationships in women (Granger, Shirtcliff, Booth, Kivlighan, & Schwartz, 2004), reducing confidence in null effects but not affecting the validity of significant effects. Anecdotally, biomedical researchers favor blood measures, whereas human biologists (e.g., from psychology, anthropology, neuroscience) prefer saliva.

Cortisol. Although most commonly connected to stress and the immune system, hormones such as cortisol (corticosterone in rodents) have also been linked with pair bonding in humans and animals (e.g., Reburn & Wynne-Edwards, 1999; Young, Murphy Young, & Hammock, 2005). Cortisol is released via the HPA axis: Corticotropin releasing hormone (CRH) from the hypothalamus stimulates the anterior pituitary gland to release adrenocorticotropin hormone (ACTH). ACTH stimulates the adrenal cortex to release glucocorticoids, including cortisol. Cortisol binds to the glucocorticoid receptor and may travel through blood attached to a binding globulin.

Peptides

Peptide hormones, such as oxytocin and vasopressin, appear to play important roles in social behavior, including adult sociosexual relationships (Carter, 1998; Carter & Keverne, 2002; Esch & Stefano, 2005; Young & Wang, 2004). These short peptides are synthesized primarily in magnocellular and parvocellular neurons of the supraoptic and paraventricular nuclei in the hypothalamus (Gimpl & Fahrenholz, 2001; Greenspan & Gardner, 2001) and may traverse the neurohypophysis for release from the posterior pituitary into peripheral circulation. They

may also be released centrally from oxytocinergic and vasopressinergic neurons projecting to a variety of neural structures involved in reward and social memory (Young & Wang, 2004).

The oxytocin and vasopressin systems show some sexual dimorphism, with oxytocin potentially exhibiting greater functional organization of female physiology and behavior, and vasopressin doing so in males (Carter, 2007). This pattern in part reflects links with gonadal steroids. Estrogen potentiates oxytocin function, increasing both oxytocin levels and oxytocin receptor expression. T does the same for vasopressin (Sanchez, Parkin, Chen, & Gray, 2007).

Animal research points to the peptide hormones oxytocin and vasopressin as being intimately tied to pair bonding. Researchers examining two species of voles that are closely related but differ in mating systems have implicated oxytocin and vasopressin in adult sexual relationships (Lim & Young, 2006). By comparing the monogamous prairie vole with the polygynous montane vole, neuroendocrine mechanisms underlying species differences in adult mating relationships have been observed. Oxytocin and vasopressin facilitate development of partner preferences in prairie voles in part through activation of dopaminergic reward pathways (Young et al., 2005), and mating appears to play an important role in the development of these partner preferences. Oxytocin and vasopressin levels rise after sexual activity and thus might positively reinforce partner preferences and facilitate pair bonding (Young et al., 2005).

Research findings from nonhuman animals that do not form long-term adult bonds suggests that oxytocin plays a common role in broad social affiliation, and not just reproductively oriented pair bonding. In sheep, for example, rising oxytocin levels at birth are necessary to reinforce offspring recognition and maternal care (Carter & Keverne, 2002). In rats, oxytocin also plays an instrumental role in maternal care (Carter & Keverne, 2002).

Experimental research on rodents also implicates vasopressin pathways in male pair-bonding behavior. Three primary vasopressin receptors (AVP1a, AVP1b, AVP2) have been recognized, with differential expression of the AVP1a receptor in specific brain structures, including greater density in the ventral pallidum, associated with rodent male pair-bonding behavior. Transgenic experiments demonstrate that expression of this AVP receptor in the normally polygynous male meadow vole's forebrain can lead to enhanced interest in spending time with a single female partner, thus showing a role for AVP receptors in facilitating partner preferences and, likely, pair bonding (Lim & Young, 2006). Similar results have been found in normally polygynous rat and vole species (Lim & Young, 2006).

As compelling as these findings are, they should not be blindly extrapolated to humans. Although the endocrine system exhibits considerable conservation across taxa, rodents and primates show differences, including in the key role of estradiol on rodent but not primate sexual differentiation of the brain and in estrogen feedback effects on LH. Other taxonomic differences such as extended sexual pro/receptivity, greater cortical control of behavior, and extended life span in humans argue for appropriate caution and skepticism when drawing connections between nonhuman and human findings.

Pair Bonding and Hormones in Humans

Courtship, Early-Stage Love, and Hormones

The study of partnering and hormones leads to methodological questions that address interesting conceptual issues. For example, when does partnering begin? Does it begin at attraction or upon falling in love? After beginning a committed relationship? Choosing a starting point, necessary for research purposes, sheds light on how partnering and hormones can be associated. Even first interactions of an apparently neutral nature can affect hormones.

In a study examining the effects of interactions on T with women, Roney, Mahler, and Maestripieri (2003) sampled T in 39 heterosexual men prior to and following a brief conversation with a woman or a man. Men who conversed with women, but not men, showed significant increases in T (*Cohen's d* = .99), although average increases did not differ significantly (Roney et al., 2003). Additionally, the increased T occurred mainly in men with prior sexual experience, suggesting either an effect of sexual experience on subsequent physiological responses, or a trait association whereby men who have T increases in response to women are also more likely to engage in sexual activity. What causes these increases? Roney et al. reported that men's increases in T were significantly correlated with their display (courtship-like) behaviors during the conversations, so these behaviors possibly increased T. Another possibility is that men's perception of a situation deserving of show-off behaviors is associated with increases in T, regardless of whether they engage in the show-off behavior. It may be that both perceiving a situation to be deserving of show-off behavior and actually engaging in it is necessary for the increase. In a follow-up replication (Roney, Lukaszewski, & Simmons, 2007), only afternoon testing periods showed an increase in men's T after interacting with women (interestingly, other researchers have found afternoon only associations between relationship status and T as well, for example, Gray, Campbell, Marlowe, Lipson, & Ellison, 2004).

Attractiveness has also been associated with hormones in both individuals and in the people to whom they are attracted. Researchers have highlighted the need to distinguish between preferences for long- and short-term relationships and have provided evidence that hormones may be differentially implicated in attraction to one set of characteristics for long-term relationships versus another set for short-term relationships or sexual encounters. Roney, Hanson, Durante, and Maestripieri (2006) examined 29 women's ratings of male attractiveness relative to male T levels and other factors via photographs of 39 men. Women rated men with higher T as more attractive than lower T men specifically for short-term relationships. Roney et al. also found that T and facial masculinity were moderately correlated ($r = .32$), suggesting that facial masculinity mediated the T-short-term mating preference and that facial masculinity may be a cue to circulating T levels in men. The authors suggested that the preference for higher T men (via facial masculinity) for short-term relationships reflected women's preferences for genetic quality. This suggestion is related to hypotheses concerning the possibly immunosuppressive effects of T, such that "good genes" would allow men to have higher T and still be healthy (the immunocompetence handicap hypothesis: Folstad & Karter, 1992). Such (controversial) hypotheses predict that women should find good genes especially important for short-term relationships, in which men's parental investment would be limited to sperm and little else (e.g., parental care, resources, etc.).

In another study using photographs of 50 men who also had T measures taken, 33 raters judged the masculinity of the faces (Penton-Voak & Chen, 2004). Of these, 19 women also rated the attractiveness of the photographed men. Results showed that composites of higher-T men were judged as significantly more masculine 65% of the time (relative to chance, at 50%). Ratings of attractiveness were not, however, associated with T levels in this study. This result actually does not contradict Roney et al. (2006), because Penton-Voak and Chen did not ask raters to distinguish between the attractiveness of the men for short- and long-term relationships. If higher-T men are rated more attractive for short-term relationships only, then ratings of attractiveness that do not take relationship duration into account would probably not correlate with T. These findings thus suggest that facial masculinity in men may be associated with attractiveness, but only when attractiveness is contextualized for long- or short-term relationships.

Facial femininity in women has been correlated with circulating estradiol (Smith et al., 2006). Over their menstrual cycles, 59 women were photographed and provided saliva samples for endocrine assay;

their photographs were then rated by 15 women and 14 men. Women with higher facial femininity were perceived as healthier and more attractive. This was true even though raters were not asked to judge attractiveness for short- versus long-term relationships, and was true for both men and women raters. This result suggests that, unlike in men, facial cues to women's hormones may not be associated with differential attractiveness for short- and long-term relationships. Both women and men conducted ratings, suggesting that estradiol might be associated with a less sexual, more generalized, attractiveness.

The experience of falling in love is also associated with altered endocrinology. Marazziti and Canale (2004) examined 12 men and 12 women who had recently fallen in love compared to a control group of 12 men and 12 women who were either in no relationship or in a long-lasting relationship. Although the authors found no differences between those who had recently fallen in love and controls on some hormones (LH, E_2 , P, DHEA, A4), others (T, FSH, cortisol) did differ. Specifically, men who had recently fallen in love had lower T (*Cohen's d* = 1.64), lower FSH (*Cohen's d* = 2.18), and higher cortisol than controls (*Cohen's d* = 2.81). Women who had recently fallen in love also had higher cortisol (*Cohen's d* = 1.67) but higher T (*Cohen's d* = 1.90) than controls. At 12-18 months after falling in love, the "in love" participants still in relationships showed similar endocrine parameters to controls, suggesting that their initially altered endocrine states may have returned to normative levels. Early-stage love may thus be associated with lower T and FSH in men, higher T in women, and higher cortisol in both. The authors suggested that higher cortisol is associated with arousal and/or new love's stressful conditions (stress refers to an alteration of the body's equilibrium, neither "bad" nor "good" in a general sense). Stress does facilitate pair-bond formation in voles (e.g., Carter et al., 1995; see also the section on "Relationship Status, Oxytocin, AVP, and Stress Hormones"). Differences between women's and men's FSH and T levels by "love status" were less clear. One reason for the uncertainty could be the unclear constitution of the control group, which included both single and partnered individuals. As we discuss later (see the section on "Partnering and Testosterone"), T differs between people who are single or partnered. Thus, sex differences in the direction of the difference in T may reflect differences in the make-up of the control group by sex (e.g., more singles in the male controls than the female controls).

The beginning stages of possible romantic attachment are thus associated with hormone changes. Brief conversations with women increase men's T, specifically if these men have prior sexual experience with women. And, engaging in show-off behaviors is associated with this

increase in T, although the cause of the increased T might be either the behaviors themselves or their associated cognitions. Hormones can influence how attractive both women and men are perceived to be and can differentially affect the perceived attraction of men for short- or long-term relationships. Finally, early stage love appears to be associated with increased cortisol for men and women, but decreased T and FSH for men and increased T for women. We now move to theoretical frameworks that may contextualize some of these findings and set the stage for examining how hormones (here, mostly T) may be associated with later stages of relationships.

Theoretical Frameworks

Frameworks for contextualizing associations between T and partnering are grounded in evolutionary theory. The "Challenge Hypothesis" (Wingfield, Hegner, Dufty, & Ball, 1990), an empirically grounded theoretical approach to avian endocrinology and reproductive behavior, is most commonly referenced because of its relevance to male mating effort, as the majority of partnering-T research in humans is conducted with men. Wingfield et al. have posited that T should be high around times of social challenges that are directed toward increasing mating opportunities and success. Both T and these behaviors are generally increased during the mating season and can have bidirectional effects. Although the theory was originally proposed to account for avian patterns of male mating behavior, the authors have suggested that it extends to other species (including mammals) and possibly to females under specific circumstances. Thus, researchers have looked for evidence of the Challenge Hypothesis with various species, including humans (for relevant reviews, see Archer, 2006; van Anders & Watson, 2006b), sometimes finding support and occasionally not. Others (e.g., Ketterson & Nolan, 1992) have examined the trade-offs (costs and benefits) of experimentally elevated T on reproductive fitness, including parenting and mating, in male and female birds. These authors have found that, although higher T might promote some indices of reproductive success, higher T also has costs and can reduce other indices. Thus, there is evidence for constraints on selection for atypically high androgens in both sexes (Clotfelter et al., 2004; Reed et al., 2005)

The Challenge Hypothesis posits that androgens inhibit some kinds of effort directed toward offspring. Thus, that high parental effort is linked with low T is sometimes supported in birds (Van Roo, 2004) and mammals including humans (e.g., Fleming, Corter, Stallings, & Steiner, 2002; Gray, Campbell, et al., 2004; Lipson, & Ellison, 2004; Storey, Walsh, Quinton, & Wynne-Edwards, 2000). Specifically, the Challenge

Hypothesis posits that T inhibits one class of parental effort (e.g., nesting) but enhances others (e.g., offspring defense). Thus, offspring defense is associated with high T, and is termed a “low parental effort” behavior, even though the effort expended in offspring defense can be considerable or even higher than “high” parental effort behaviors like nesting.

An additional framework of testosterone trade-offs that is grounded in and extends the Challenge Hypothesis addresses men and women within and outside “mating effort” and beyond seasonality (van Anders & Watson, 2006b). In it, high T is linked with competitive behaviors/states and associated with competition for or defense of a resource (broadly defined, including partners, territory, infants, etc.); competitions can be real or imagined. In terms of partnering, competitive behaviors/states could include, for example, looking for partners or jealousy. As well, low T is linked with bond-maintenance behavior/states: those associated with developing an intimate and caring bond with others (e.g., partner, friend, offspring, etc.). Competitive and bond-maintenance behaviors/states can occur within the pair bond, and their classification would depend on the context. For example, mate guarding should be competitive even though it is directed toward a partner and maintaining the pair bond, because mate guarding is directed toward defending a resource (i.e., the partner). Infant defense would be competitive because it concerns resource defense, even though it is situated around infants. Thus, behaviors are classified by their kind as opposed to their target.

The association between T and social behaviors can be state, where sexual activity increases women’s T (e.g., van Anders, Hamilton, Schmidt, & Watson, 2007), or trait, where higher T may predict divorce in men (e.g., Booth & Dabbs, 1993), or both. Theoretical applications of the Challenge Hypothesis are largely specific to males, and the testosterone trade-off framework provides a supra-sex theoretical foundation that is neither predicated on male mating theory nor attempts to determine if females are “like” or “unlike” males. Instead, it allows for gender/sex as one possible moderating factor between T and, as is relevant to this review, partnering.

Partnering and Testosterone

Endocrine perspectives on partnering in humans have focused mainly on androgens in men for various reasons, including the inability to measure peptide hormones from saliva, theoretical considerations based on the Challenge Hypothesis and male mating effort, or theoretical considerations about androgens and status (e.g., Mazur & Booth,

1998). In this research, investigators generally contrast single versus partnered individuals or examine how T may be associated with measures of marital quality and marital dissolution.

Hormones, "marital quality," and divorce. Using a sample of about 4,000 male Vietnam army veterans, Booth and Dabbs (1993) found that men with higher T have a 43% increased incidence of divorce and were 31% more likely to have separated because of marital discord, relative to men with lower T. Using a sample of about 2,100 male Air Force veterans, Mazur and Michalek (1998) conducted a longitudinal study in which they found that men who remained wed had approximately 9% lower T than men who remained single or who had divorced. Higher T appeared to predict the likelihood of future divorce and was transiently elevated around the time of divorce.

Why should higher T be associated with divorce? Although acknowledging that T can be associated with prosocial traits, some authors (Booth & Dabbs, 1993; Mazur & Michalek, 1998) have suggested that higher T is negatively associated with some traits and behaviors that contribute to marital quality. As related evidence, for example, Julian and McKenry (1989) found that higher T was negatively associated with marital happiness in middle-aged men. Booth and Dabbs found that men with higher T were 12% more likely to have hit their wives and 38% more likely to have engaged in extramarital sex; in general, these men also had a lower quality of marital interaction. This association was not linear (the implications of this are not well understood): Midrange-T men reported the lowest marital quality. Additional evidence links higher-T in men (recruited from social service agencies on the basis of risk factors for HIV/AIDS) with past physical and verbal abuse of wives (Soler, Vinayak, & Quadagno, 2000). It appears likely that marital quality mediates the T-divorce link, but how T contributes to marital quality (temperament? cognitions?) and how contextual factors are relevant is not clear.

Some researchers have examined how T levels within married couples are associated with marital quality. Cohan, Booth, and Granger (2003) considered T levels of 92 newlyweds individually and by couple and found that wives with higher T relative to other wives had wife-initiated conversations with their husbands that were less positive. They also found that husbands were more negative, less positive, and provided less social support to their wives when the husbands had lower T relative to other husbands than their wives' T relative to other wives. The authors suggested that a lack of concordance between couples' relative T levels may be associated with poorer communication patterns and social support, and especially that husbands may behave more neg-

atively when their wives have higher T relative to other wives. Results from this study are suggestive that higher relative T can be associated with lower marital quality when concordance between partners is low. In one other study, Hirschenhauser, Frigerio, Grammer, and Magnusson (2002) included attention to concordance between partners' T. Men's T correlated with their female partners' monthly endocrine patterns, but only if they wanted to have children with the women, suggesting that contextualizing individual T levels within the couple is likely to be important.

Partner status and androgens. Some researchers have focused on how relationship status itself might be associated with hormones (only T, generally) in humans. Although in most of these studies the focus has been on heterosexual men in North America, some researchers have also attended to cultural contexts, gender, and sexual orientation. Most researchers compare groups, attempting to control for other possibly confounding group differences. These controls include time of day (statistically or through time-restricted sampling, [e.g., afternoon only]), body mass index (BMI), abnormally high T levels, and age. Some routinely exclude people using exogenous hormones or medications/drugs or who have medical conditions that affect the HPG axis, control for extrapair sexual behavior (via questions and then exclusion from analyses or statistical checks), or control for seasonality or month of testing.

The earliest studies were conducted to determine if T was negatively associated with marital quality (see our earlier discussion on "Hormones, 'Marital Quality,' and Divorce"). More recently, researchers have provided additional data on the associations between T and partnering, focusing more on ecological context and questions (for a review, see Gray & Campbell, 2007). Gray and colleagues have shown that North American single men have higher T than married men, 32% higher than married fathers and 19% higher than nonmarried fathers (Gray, Campbell, et al., 2004; Gray, Kahlenberg, Barrett, Lipson, & Ellison, 2002). Researchers found varying levels of T for unmarried men who are nevertheless partnered, but lower levels than singles (21% lower T than singles: Burnham et al., 2003; 49% lower T than singles: Gray, Chapman, Burnham, & McIntyre, 2004; 19% lower T than singles: McIntyre et al., 2006). These results clearly indicate that involvement in partnering (marriage or otherwise) is associated with lower T. From this perspective, marriage appears to formalize a relationship process already associated with endocrine differences. Gray and colleagues point out that these findings are consistent with theoretical predictions grounded in male mating effort, specifically, that T should not be high in individuals who engage in less male-male competition for female mates.

Other researchers have explored human diversity in relationship types and approaches to see whether dividing people on the basis of their likelihood of finding partners as per their relationship status might be associated with T (for a review, see van Anders, 2007). For example, in a study using a sample of 76 heterosexual men, van Anders and Watson (2006a) found that unpartnered (single, dating, or in multiple relationships) men exhibited higher T than partnered men (van Anders & Watson, 2006a). This study is the only one to include non-heterosexual men (sexual orientation was dichotomized into exclusively heterosexual and not, via Kinsey, Pomeroy & Martin, 1948): In a sample of 56 men, partnered status was not associated with T in nonheterosexual men (van Anders & Watson, 2006a). Thus, several research groups have confirmed that partnered heterosexual men exhibit lower T than unpartnered counterparts, and findings suggest this pattern is specific to heterosexual men.

Partnering and T have been shown to be associated in women in three studies (as further described below), but the pattern is less clear and sexual orientation appears to be an inconsistent moderator. Partnered women exhibited significantly lower T than unpartnered women, but only in the 55 nonheterosexual women and not in the 75 heterosexual women (although means were in the expected direction) (van Anders & Watson, 2006a). Also, in studies described below, sexual orientation has not been found to modify the partnering-T association; however, these studies were not designed to address this question explicitly.

Some studies have included related contextual variables. Because partner presence is an important cue to being partnered, it might be one mediating factor. Examining 72 single women and 49 single men, in either long-distance relationships or same-city relationships, van Anders and Watson (2007) found that gender might moderate the association between T and partner cues. Same-city partnered women exhibited lower T than single women, with long-distance partnered women in-between (*partial* $\eta^2 = .107$). In contrast, partnered men, regardless of partner presence, exhibited lower T than single men (*partial* $\eta^2 = .166$). Participants in this study were mostly heterosexual, and the results remained consistent when sexual orientation was controlled. This research suggests that partner presence may affect women's, but not men's, T and that partnered men have lower T even if their partners are not present.

Although the majority of research has been conducted using diverse North American populations, research with international populations has been important both in furthering the understanding of T and partnering and in identifying some of the contexts that might predicate

these associations. In fact, international research does not point to as consistent an association between partnering and lower T. For example, Gray, Yang, and Pope (2006), in research undertaken in Beijing with 126 Chinese participants, showed that parental as opposed to partner status was associated with T: Married fathers exhibited lower T than single men or married nonfathers. And, in a study undertaken in Japan, Sakaguchi, Oki, Honma, and Hasegawa (2006) found that, although T tended to be lower in paired compared to unpaired men, this was only a statistical trend, suggesting lower effect sizes. These findings point to the need for contextualized considerations of partnering: Whether fathers in Beijing may be more committed to their relationships, whereas single men and married nonfathers may both be interested in finding new partners is, as yet, unclear. Other data from this study also point to the need for contextual understanding: Married men in Beijing reported high levels of extrapair sexual encounters relative to North American married men. Generally, understanding local conceptualizations of partnering, along with their accompanying normative behaviors and cognitions, is crucial in understanding when and why partnering and T are associated. If partnering is not a way to limit one's sexual encounters, then it may not be associated with lower T.

In fact, other studies of men in multiple relationships suggest just that. Gray (2003) examined polygynous married men, monogamously married men, and single men in a group of 88 Kenyan Swahili and found that polygynously married men had higher T than the other men (43% higher in mornings, 32% higher in evenings). This result fits into the testosterone trade-off framework, in which the possibility of additional wives (as in polygyny) should be associated with higher T. On the other hand, in the same study Gray was unable to rule out alternative explanations for this link between polygyny and T, including developmental impacts of diet and physical activity.

Further showing the importance of contextualization are data from Ariaal men of northern Kenya (Gray, Ellison, & Campbell, in press). The Ariaal are agropastoralists who have well-recognized male age sets and a high prevalence of polygyny. The process of male marriage and reproduction can be linked with age and socioeconomic resources: Men tend to remain single until around age 30 and may acquire additional wives with age, leading some older men (e.g., in their 60s) to marry young wives with whom they continue reproducing. In a sample of about 200 men aged 20 and older, Gray et al. found that monogamously married men had lower T levels than their unmarried counterparts. But, older polygynously married men, particularly those living in settlements, had *lower* T levels than monogamously married men. Here the context suggests that lower T is a

result of age, wealth (livestock and land holdings), and sociopolitical resources (status and family networks) outweighing the importance of T-mediated behavior in the acquisition of wives at older ages. In short, categories such as marital status may not be equivalent proxies for mating effort across all societies and male age itself may be an important variable: T-mediated linkages to partnering may be most apparent among young adults (see also Adkins-Regan, 2005).

In North America, too, instances of partnering extend beyond the traditional monogamous pair. For instance, "cheating," which occurs when an individual seeks extrapartner sexual/romantic encounters in the context of a relationship with another person who assumes fidelity, is linked to higher T (Booth & Dabbs, 1993). No researchers have examined T and partnering in either of these two next contexts. Polygamy (the lay term applied to North American polygyny) consists of multiple marriages between one man and multiple women within religious strictures. Swinging generally occurs within a committed pair when partners encourage or allow each other the opportunity to seek extrapartner sexual relationships (Jankowiak & Mixson, in press).

Less widely known is polyamory, a practice denoting individuals having many loving and committed relationships (Polyamory Society Glossary, n.d.), with the awareness of all parties. van Anders, Hamilton and Watson (2007) hypothesized that polyamory should be associated with higher T because individuals seek more than one partner, making it competitive in the testosterone trade-off framework. These researchers examined 48 women and 47 men who were single, in monoamorous, or polyamorous relationships, or who were "poly lifestyle" (in the polyamory community, but currently not multipartnered). Polyamorous individuals exhibited higher T than single or partnered individuals, in women (*partial* $\eta^2 = .264$) and men (*partial* $\eta^2 = .293$). This difference was not mediated by sexual desire or sociosexual orientation scores (self-reported interest in extrapair sexual encounters: Simpson & Gangestad, 1991). Poly lifestyle men had similar T levels to polyamorous men, suggesting that the man's approach to relationships was more important than his current partner number. Polyamorous women had higher T than women with poly lifestyles, suggesting that partner number, rather than approach to relationships, was associated with higher T in women.

Directionality. Does partnering decrease T? If so, T is associated with relationship status. Conversely, does lower T predict partnering (i.e., a trait effect)? In this case, T is associated with "relationship orientation," that is, the likelihood of entering relationships. This question of whether T is associated with relationship status versus relationship orientation

generates lively debate among researchers for a variety of reasons, including theorizing about mechanisms and hypothesis generation.

Upon encountering the relatively unstudied field of hormones and human relationships, both of us initially (and working separately) approached the T-partnering connection primarily as a state link (i.e., partnering behaviors decreased T) on the basis of evidence that social behaviors affect T (Archer, 2006; van Anders & Watson, 2006b). This approach followed from several nonhuman frameworks showing male T responses to partnering and parenting (Ketterson & Nolan, 1994; Wingfield et al., 1990). However, one of us, van Anders, now sees the evidence as largely supporting a trait effect, especially or specifically in men. Although partnering behaviors may have transient state effects on T, there is no evidence at present that entering or being in a relationship decreases T. For example, Gray, Campbell, et al. (2004) examined whether men's T differed on days spent with families versus at work, but surprisingly found no difference in T according to how a day was spent. van Anders and Watson (2006a), in examining a small sample of women and men longitudinally, found no evidence that entering a relationship decreased T. In a larger, longitudinal study, Mazur and Michalek (1998) found that individuals who changed marital status or remained single had higher T than individuals who remained married. Divorce was associated with a time-linked transient increase in T, but no apparent permanent alteration in T occurred with the change in relationship status. And, van Anders and Watson (2007) found that men who were long-distance partnered and same-city partnered had similarly lower T than single men, suggesting that cues to being partnered and partner-related behaviors are not associated with lower T.

Although there is no evidence that being in relationships decreases T, low T predicts entering relationships and high T predicts exiting them in men. van Anders and Watson (2006a) found that unpartnered individuals with lower T were more likely to enter relationships than those with higher T (the effect of relationship status accounted for nearly 10% of the variance in overall T). As indicated above, that partnered men (regardless of partner presence) exhibited lower T (van Anders & Watson, 2007) is suggestive of a relationship orientation interpretation because cues to partner presence were not necessary for the lower T. Additionally, McIntyre et al. (2006) found that being partnered was *not* associated with lower T if partnered individuals were interested in and expected to engage in extrapair sexual encounters. And, polyamory (current partners or relationship approach) was associated with higher T (Gray, 2003; van Anders, Hamilton, & Watson, 2007). Thus, men's *orientation* toward relationships (e.g., attitudes, likelihood of future behav-

ior, etc.) appears to be more strongly related to T than men's current relationship *status*. This is the case based on current empirical research: Men who are more likely to have a competitive relationship orientation (i.e., more likely to seek out new/multiple partners) appear to have higher T.

Related to this, Gray, Chapman, et al. (2004) showed that single men with prior relationship experience exhibited higher T than men without it. This finding is closely related to Roney et al.'s (2003) finding of greater T increases in sexually experienced men. Prior sexual experience may sensitize the HPG axis, but a more conservative interpretation is that higher T men are more likely to have sexual encounters than that the experiences changed trait levels of T. Again, this result might support a T-relationship orientation interpretation. Only further evidence will clarify whether T is related to relationship orientation or status, or both.

Hormone levels are responsive to social and other stimuli, and as such are measures of contextualized physiology, or people's physiology as they interact with the world. If relationship orientation is associated with T (i.e., if lower trait T is associated with a trait approach to entering relationships) we can still ask: Why is this trait T lower? Heritable genetic or perinatal influences could be relevant but have been minimally explored (Abbott, Barnett, Bruns, & Dumesic, 2005) and may be only one possible direction in which to look. Could childhood or puberty influence an individual's subsequent physiology, including trait T linked with partnering propensities (Flinn, Quinland, Decker, Turner, & England, 1996)? It may well be that personality traits and associated ways of thinking about and engaging in the social world lead to trait T. Engaging with the social world might then directly influence the likelihood of partnering, which might be further influenced by trait T. This is supported by evidence linking afternoon and evening, but not morning, T to partnering. We know that partner-related behaviors do not lead to lower T over the day (Gray, Campbell, et al., 2004). But whether an ongoing trait way of existing in the social world *that is also associated with being partnered* leads to overall trait levels of T is not known.

Further complicating the issue of relationship status/orientation interpretations is the lack of a clear distinction between trait and state effects. Behaviors reducing T are state effects; T predicting partnering is a trait effect. But, if people significantly change their pattern of behavior and thought upon entering relationships, and this change is maintained for the duration of their relationship for up to 10 or even 50 years, does this qualify as a trait effect or state effect?

Androgens and partnering: Summary and further questions.

Researchers have shown that T is higher in single than partnered men, specifically men who are partnered with one woman in a bond-maintenance context associated with little likelihood of looking for additional partners (e.g., Gray, 2003; McIntyre et al., 2006; van Anders, Hamilton, & Watson, 2007). Research with women, as yet in its infancy, suggests an association between partnering and T, the elements of which are not clear. At present, debate continues about directionality, some interpreting the evidence in men to support a relationship orientation interpretation and others to support a relationship status interpretation.

Researchers in this field have generally not included social psychological perspectives on relationships. Diamond (2003), for example, has made a compelling case that romantic love and sexual lust are distinct and may involve different although, nevertheless, interconnected systems; Gonzaga, Turner, Keltner, Campos, and Altemus (2006) reported on different correlates for sexual desire (e.g., arousal) and love (e.g., happiness). Because endocrine researchers have found that bond-maintenance partnering is associated with lower T, whereas sexual activity is generally associated with higher T and intimacy (e.g., van Anders, Hamilton, Schmidt, et al., 2007), including Diamond's perspectives is likely to be helpful in delineating the aspects of partnering that are associated with higher or lower T.

Steroid hormones, such as T, interact with behavior through their modulation of neural activity. Therefore, one might ask whether specific brain areas mediate the T-partnering association. Researchers have described neural substrates related to pair bonding in voles, for example, and this information might be instructive. Do higher T individuals show neural activity related to pair bonding that differs from that of lower T individuals? Are measures other than circulating hormones important? For example, AR density and binding affinity may be important to understanding T-partnering associations. Additionally, few human T and partnering studies have included OT, AVP, or cortisol assessment, and the inclusion of these hormones known to be related to pair bonding may provide additional dimensions to our understanding.

Relationship Status, Oxytocin, AVP, and Stress Hormones

Although most human research has focused more on androgens, some researchers have investigated adult relationships, peptide hormones, and stress hormones. In one study of the link between oxytocin and adult heterosexual relationships, researchers evaluated the importance of warm partner contact on oxytocin in 59 premenopausal women (Light, Grewen, & Amico, 2005). Oxytocin levels were measured at sev-

eral time points, including at baseline and after a speech stressor. When various frequencies of partner behaviors were coded by self-report, baseline oxytocin levels were positively correlated with more frequent hugs. These levels were also negatively related to measures of cardiovascular activity such as systolic blood pressure.

In another study of partner interactions and oxytocin, Grewen, Girdler, Amico, and Light (2005) investigated 38 heterosexual couples who provided pre- and postpartner-contact hormone and blood pressure data. A 10-min warm partner contact session (involving discussion of positive relationship experiences, a brief romantic movie clip, and a 20-s hug) occurred between measurements. Men and women reporting greater partner support exhibited higher oxytocin levels at all time points. Oxytocin in women was also inversely related to blood pressure and norepinephrine levels.

In a third study, Sanchez et al. (2007) measured the plasma oxytocin levels of 30 young women during brief interactions with male partners. Women were primed to seek social support by a researcher asking them about something they wished to change about themselves, and then engaged in follow-up discussions about the same topic with their partners. Oxytocin levels were measured via blood samples before, during, and after partnered discussion. Women receiving greater partner support displayed increased oxytocin levels after the partner interaction. From questionnaire responses, individuals who were viewed as "anxiously attached" showed lower oxytocin levels.

Turner, Altemus, Enos, Cooper, and McGuinness (1999), investigating plasma oxytocin, mood, and interpersonal support among 25 women, found that a greater increase in oxytocin while participating in a standardized lab stressor was associated with being in a romantic relationship. Surprisingly, single women had *higher* basal oxytocin concentrations and were more likely to exhibit potentially unhealthy interpersonal traits such as intrusiveness, anxiety, and coldness. To explain this discrepancy, the researchers suggested this may indicate poor oxytocin regulation in response to social stimuli and was not causal in nature. In another analysis of this sample, Gonzaga et al. (2006) found that performance of affiliative behavioral cues was associated with increased oxytocin.

Collectively, then, the findings from a number of studies lend support to the notion that oxytocin is associated with human relationship dynamics. In four studies, oxytocin levels were positively associated with female involvement in supportive relationships, and in one study similar results held for males. The results raise the question of whether baseline or reactive oxytocin is more meaningfully linked with relationship support.

A complementary line of evidence based on functional imaging also implicates oxytocin and vasopressin in human pair bonding. Women and men were subject to fMRI while looking at photographs of the romantic partner with whom they were in love, as well as control photographs of friends (Bartels & Zeki, 2000). The love stimuli elicited activity in the hypothalamus and ventral tegmental area, areas shown to be rich in oxytocin and vasopressin receptors and involved in rewards pathways. These peptides may have helped establish and perhaps maintain the neural activity associated with romantic bonding. Importantly, too, some areas deactivated (showed suppression) during this procedure were associated with social judgment and negative emotion.

In another fMRI study (Fisher, 2004), both similarities and differences with the preceding study were observed. Here, the ventral tegmental area and caudate nucleus were activated when looking at photographs of beloveds as compared with acquaintances. Other areas, including the anterior cingulate cortex, were activated only among subjects in longer-term romantic relationships, suggesting changes in the neuroendocrine mechanisms underlying relationships over time.

In a small set of studies, researchers have investigated the effects of human partnering on hormonal stress responses. In one of these studies, Roney et al. (in press) tested whether young men displayed different cortisol responses to brief interactions with women in comparison with the control conditions of being alone and interacting with young men. Changes resulting from this type of brief partner interaction has been conceptualized as a "courtship" response. Two different samples of men exhibited greater cortisol increases after interacting with women, compared to control situations. The potential functionality of this hormonal response may be quite different (e.g., to adaptively mobilize energy for courtship), the authors pointed out, compared with the more commonly emphasized impacts of cortisol reactivity (e.g., with negatively valenced stressors).

Researchers at Kiecolt-Glaser's lab at The Ohio State University have conducted the primary studies, with young newlyweds as well as older married couples, investigating the role of endocrine stress responsiveness in established adult sexual relationships (e.g., Kiecolt-Glaser, Bane, Glaser, & Malarkey, 2003). Married couples reported to a research facility where they habituated to the novel environment, completed questionnaires, responded to questions during brief interviews, and had indwelling catheters for repeated blood draws for measuring hormones (and other analytes such as markers of immune function). The key analyses focused on stress responses to discussions of topics generating marital conflict over a 30-min session. Participants in these

studies reported extremely high marital satisfaction, meaning that results may not generalize to all populations.

Younger subjects participating in these studies were approximately 25 years old and included 90 newlywed couples. Blood samples were collected during the early morning, when ACTH and cortisol levels are typically declining. Thus, stress responses appear as attenuated declines in stress hormones across the time of marital conflict. That is, a flatter cortisol slope in this case suggests a greater stress response compared with a more typical, steep decline during this timeframe.

Based on investigations of these participants, higher levels of hostility and negative behavior during marital conflict sessions were associated with increases in ACTH, growth hormone, epinephrine, and norepinephrine, but decreases in prolactin (Malarkey, Kiecolt-Glaser, Pearl, & Glaser, 1994). The most recent analysis suggested that stress responses (ACTH and cortisol) were related to "social-evaluative threat" (Robles, Shaffer, Malarkey, & Kiecolt-Glaser, 2006). For a subset of couples unaccustomed to marital conflict, the research paradigm may have increased wives' stress responsiveness. However, more consistent with initial expectations, discussions characterized by "low positive/high negative" behavior were associated with increased stress hormones. Among women, marital satisfaction was inversely related to cortisol declines: Wives reporting more marital satisfaction had steeper cortisol declines during the session. No significant relationships in these stress hormone profiles were observed among husbands, suggesting asymmetric stress responses during these types of conflict sessions. Moreover, female stress responses predicted the likelihood of divorcing 10 years subsequently (Kiecolt-Glaser et al., 2003).

Kiecolt-Glaser's group conducted a parallel study among older couples ranging in age from 55 to 77 years (Kiecolt-Glaser et al., 1997). In their first report, negative behaviors were positively associated with changes in ACTH, cortisol, and epinephrine levels during the conflict session (Kiecolt-Glaser et al., 1997), paralleling to a large degree the findings among younger couples. In a more recent analysis, women's (but not men's) increased cortisol responses were associated with perceived "wife demand/husband withdraw" behavior during marital conflict sessions (Heffner et al., 2006).

In one other lab-based study, Kirschbaum, Klauer, Filipp, and Hellhammer (1995) investigated the effects of a romantic partner on stress responsiveness to the stressor of public speaking. These investigators provided insight into how an individual might draw support from the presence of a partner and identified important sex differences. Men showed lower cortisol responses in advance of the stressor if their romantic partner were present, compared with men without support or

assigned a stranger to provide support. Women, conversely, showed cortisol increases if their partners were present. These results, like the marital conflict studies summarized above, suggested that women's stress responses are more attuned to relationship dynamics than are men's, that is, the presence of a partner was more likely to activate a woman's stress response.

The findings of these lab-based stress responsiveness studies are supplemented by the results of other types of studies. For example, Adam and Gunnar (2001), in one naturalistic study entailing multiple sample collection across the day, found steeper cortisol declines associated with higher relationship satisfaction in women. Further, Mazur and Michalek (1998), using a large U.S. military sample, reported lower morning baseline cortisol levels among married men compared with their unmarried counterparts. Finally, no differences in baseline morning or early evening cortisol levels were observed among unmarried, monogamously married, or polygamously married Kenyan Swahili men (Gray, 2003).

In summarizing studies of adult stress responses and relationships, several patterns emerge. Stress responses have been linked with relationship dynamics, primarily in lab settings but also in at least one naturalistic study. Stress responses may be activated during the initiation of a relationship and show greater activation in the face of less supportive/lower quality relationships. These patterns have been observed primarily through the assessment of changes in cortisol (e.g., lab studies or diurnal rhythms), suggesting that cortisol reactivity or diurnal rhythms are more meaningful than basal cortisol measures for establishing relations with partnering.

Another pattern is that female stress responses appear more attuned to relationship threats than do male stress responses. This sex effect could be interpreted according to the differential costs/benefits men and women bear through engagement in relationships. From the standpoint of parental investment, women benefiting from male investment might perceive threats to that resource flow as problematic. Or, given sex differences in communication, social cognition (Hines, 2004), or social networks, men may have fewer outlets for emotional intimacy, leading men partnered with women to benefit inordinately from intimate communication with a partner.

Contextual Aspects of Hormone-Partnering Associations

Relationships and Sexual Activity Over Time and With Aging

Both relationships and physiology can change with aging in men and women. Frequency of intercourse within relationships tends to decline

with relationship duration in the U.S. (Laumann, Gagnon, Michael, & Michaels, 1994; Wood, 1994) and other countries (Udry, Deven, & Coleman, 1982), although this decline has not been empirically linked with changes in hormones. However, changes in endocrine parameters may be relevant to changing sexual activity within relationships. T in men and women shows a decline with aging (e.g., Bancroft & Cawood, 1996; Crilly, Marshall, & Nordin, 1979; Gray, Berlin, McKinlay, & Longcope, 1991). In postmenopausal women, however, these declining androgens still represent a larger proportion of sex steroid circulation because estrogens show a larger decrease. The following sections focus primarily on women, because of the larger relevant body of empirical research.

Menstrual Cycles, Menopausal Transition, and Sexual Relationships

Not only can individuals' attractiveness be mediated by their endocrine profiles, it can be influenced by perceivers' endocrine states, as research attending to women's menstrual cycles suggests. A full accounting of this pattern is beyond our scope, but see Pillsworth and Haselton (2006), and Gangestad, Thornhill, and Garver-Apgar (2005) for comprehensive reviews. In short, women's behavior toward and preferences for men may change over the menstrual cycle, and men's behavior may change relative to a woman's cycle. Both midcycle and the luteal phase have been implicated in these changes.

The decline in estrogens that accompanies menopause is associated with changes in some parameters that could influence partnered sexual activity. For example, lower E_2 is associated with decreased vaginal vasocongestion and lubrication (Sarrel, 2000), and some evidence (though still controversial) indicates that sexual desire may also independently decrease with age (Bancroft, Loftus, & Long, 2003; Eplöv, Giraldi, Davidsson, Garde, & Kamper-Jorgensen, 2007; Hayes & Dennerstein, 2005). This decrease has been tentatively (and also controversially) associated with lower androgens (e.g., Greenblatt, Barfield, Garner, Calk, & Harrod, 1950; Lobo, Rosen, Yang, Block, & Van Der Hoop, 2003; Sherwin, 2002; van Anders, Chernick, Chernick, Hampson, & Fisher, 2005). Because the majority of this research has been conducted within a heterosexual paired context, little is known about whether single postmenopausal women or partnered lesbians see changes in sexual parameters that may be associated with endocrine changes.

Pregnancy, Postpartum, and Sexuality

Women experience profound endocrine changes associated with pregnancy and postpartum (Greenspan & Gardner, 2001). During pregnancy, estrogens and progesterone increase to support the growing fetus

and fat deposition for later lactation as does prolactin, in part to facilitate breastfeeding. These changes could influence sexual behavior and relationship dynamics, although currently little or no evidence links these changes with hormones.

For new parents, relationship satisfaction may increase during a woman's pregnancy, especially if the child is desired (De Judicibus & McCabe, 2002). Postpartum, however, decreased relationship satisfaction is frequently reported in Western societies (e.g., Belsky & Rovine, 1990) and elsewhere (Beijing, China: Gray et al., 2006). A variety of factors appear to account for these changes, including inequitable distribution of childcare, fatigue, shifting social orientation toward a new child, and reductions in sexual desire.

Changes in sexual behavior associated with pregnancy and postpartum show considerable interindividual variation, although some general patterns also emerge (reviewed in De Judicibus & McCabe 2002; Reamy & White, 1987). For example, sexual desire may show enhancement early in pregnancy, especially late in the first trimester, perhaps associated with elevated maternal steroid production. By the third trimester, female sexual desire and partner sexual activity commonly decline and remain low until after birth (Bancroft, 2005). Postpartum, after some time, female sexual desire increases, and sexual activity resumes at a typical level (Ford & Beach, 1951), although current data are generally lacking. Breast-feeding delays the return of sexual desire and sexual behavior (Alder & Bancroft, 1988; Hyde & DeLamater, 2000; Rowland, Foxcroft, Hopman, & Patel, 2005), as well as fertility. These effects of breast-feeding may be hormonally influenced—for example, breast feeders exhibit lower T than bottle feeders (Alder & Bancroft, 1988) as part of the delayed resumption of sex steroid production—and/or may stem from other considerations (e.g., less desire for physical contact with a partner given contact with infant). Other factors that commonly predict a lower frequency of postpartum sexual behavior include concerns over physical harm (e.g., vaginal tearing after episiotomy), an infant's health or safety, maternal attractiveness, and fatigue. Cross-cultural evidence shows that intercourse is commonly avoided in the initial weeks postpartum and that resumption of sexual activity is variable (Ford & Beach, 1951). In some societies, it is avoided for months to years, but the latter duration tends to be among societies practicing polygyny where a husband has alternative sexual outlets (Ford & Beach, 1951).

Important hormone changes may also be associated with the transition to parenting. Direct maternal care, including touching, nursing, and interacting with an infant, can increase oxytocin and prolactin levels (Greenspan & Gardner, 2001; Matthiesen, Ransjö-Arvidson, & Nis-

sen, 2001). Elevations in oxytocin may enhance social attachment to an infant and increases in prolactin levels may be part of a "maternal regulatory circuit" that reinforces attachment of the mother to her child (Sobrinho, 2003).

In several studies, researchers have found that fathers exhibited lower T levels than other men (e.g., Berg & Wynne-Edwards, 2001; Fleming et al., 2002; Gray, Parkin, & Samms-Vaughan, 2007; Gray et al., 2006; Storey et al., 2000). In one of these studies, fathers showed inverse relationships between their T levels and responsiveness to infant cues such as tape-recorded infant cries (Fleming et al., 2002), suggesting that reduction of T levels associated with fatherhood may be adaptive. In two studies of Canadian men, fathers also exhibited increases in prolactin levels (Berg & Wynne-Edwards, 2001; Fleming et al., 2002). In a sample of Jamaican men, single men showed declines in prolactin, while sitting alone reading a newspaper, whereas fathers interacting with a partner and child did not (Gray et al., 2007).

The endocrine bases of maternal and paternal care help show how parental physiology can shift toward investment in children. This shift may buttress partnering behavior, which could theoretically occur if oxytocin increases that promote bonding with an infant also promote bonding with an adult partner. An alternative could theoretically occur if breastfeeding-associated decreases in sexual behavior affect partner-related intimacy.

Future Directions and Challenges

Evidence links a variety of hormones with various aspects of partnering, including behaviors, states, and preferences. Flirting-like behavior increases men's T, specifically in sexually experienced men (Roney et al., 2003). Men with higher T are rated more masculine (Penton-Voak & Chen, 2004), more attractive for short-term relationships, and less interested in infants (Roney et al., 2006). Distinguishing between attractiveness for short- or long-term relationships appears to be important in men, but not women; women with higher E_2 are rated as more feminine and generally attractive (Smith et al., 2006). Hormones are also associated with early-stage love, higher cortisol in women and men, and higher T in women but lower in men, relative to others not in early-stage love (Marazziti & Canale, 2004).

Theoretical frameworks linking hormones and partnering often focus on T and male mating effort (e.g., Wingfield et al., 1990) or trade-offs in women and men (van Anders & Watson, 2006b). Higher T has been linked with poorer marital quality and increased divorce in men (e.g., Mazur & Michalek, 1998), as well as with being unpartnered/single in

heterosexual men (Booth & Dabbs, 1993; Burnham et al., 2003; Gray, Campbell, et al., 2004; Gray, Chapman, et al., 2004) although evidence does not extend this pattern to nonheterosexual men (van Anders & Watson, 2006a). Concordance between partners' hormonal profiles appears to be important for contextualization (Cohan et al., 2003), although this element remains understudied. Also receiving limited attention is partnering-T associations in women, where evidence supports an association, albeit a less clear one (van Anders, Hamilton, & Watson, 2007; van Anders & Watson, 2006a, 2007). Evidence does show that multipartnered people, both men and women, exhibit higher T (Gray, 2003; van Anders, Hamilton, & Watson, 2007). International research has further shown the importance of contextualizing partnering, and identifying the meaning or connotations of being partnered is becoming increasingly important. Directionality of effect (i.e., state or trait) is debated, although evidence may support more strongly a relationship orientation (i.e., T predicts partnering) than a relationship status interpretation. More evidence is needed to clarify causality.

In research on partnering, peptides, and stress hormones investigators have found an association with relationship dynamics. For example, neural areas dense in oxytocin receptors in voles show activation in humans using "love" stimuli (Bartels & Zeki, 2000). Also, stressful or hostile marital interactions are associated with increased stress hormones and decreased prolactin in both older and younger couples (Kietcolt-Glaser et al., 1997; Mularkey et al., 1994). And, partner support appears to be associated with increased oxytocin (e.g., Grewen et al., 2005; Light et al., 2005).

Few investigators have examined how contextual factors affect hormone-partnering links, but age, menopausal status, pregnancy, and parturition may prove meaningful, as these are associated with changes in hormones, behaviors, and desires within relationships. Whether these are causally linked remains unclear, except with parenting behaviors, in which, for example, evidence supports decreases in T with some fathering behaviors (e.g., Fleming et al., 2002).

The field can benefit from converging lines of inquiry. For example, partnering-T research could benefit from studies associating neural structures with pair bonding, peptides, and cortisol. Do the same areas show low AR density? Also, further research examining multiple steroids and peptides should be extremely valuable. Investigating hormone receptor involvement in humans is also likely to be informative, as circulating hormone levels provide only a partial picture of endocrine activity. Researchers have already attended to AR density via measurement of AR protein levels in circulating leukocytes (Sader

et al., 2005) and AR sensitivity to androgens via measurement of CAG repeats in the AR gene (Tut, Ghadessy, Trifiro, Pinsky, & Yong, 1997). Partnering-hormone research would benefit from integrating other behavioral neuroscience methodologies (e.g., AR density and binding affinity, neural imaging) and from converging lines of research that are currently parallel.

Research is generally conducted with heterosexual North American men or couples, leaving unexamined such issues as how sexual orientation is implicated, how cultural considerations within North America are relevant, and whether research on various international populations can clarify patterns. An international perspective on stress responses and partnering would be beneficial, including polygynous cultures or less affiliative marital relationships to extend existing research. To address directionality, longitudinal studies should be a major initiative, even though these are often methodologically more problematic and costly than cross-sectional studies.

At present, research findings are tentative and have not been independently replicated; various alternative explanations have yet to be ruled out as well. Although many researchers control for various confounding factors, the need for such controls cannot be overemphasized, especially since making group comparisons has been the goal of many studies. Additionally, the extensive use of medications by growing numbers of the population makes exogenous alterations of hormone profiles an ongoing concern.

Indeed, a large number of individuals use street drugs or take medications or supplements, including hormonal contraceptives and hormone replacement regimens, that alter their endocrine profiles in significant ways. The implications of such usage for both study populations and general populations should receive serious attention. Possible effects of androgen supplementation on partnering profiles would have implications for understanding partnering-T links and, even more relevant, for individuals receiving androgens for health issues—especially those related to quality of life. Some doctors are currently prescribing T to women who report low sexual desire, but what effect does this have on other parameters such as relationship satisfaction or health (if T does show immunosuppressive—or even enhancive—qualities in humans)? Similar questions arise when some doctors prescribe androgens to men experiencing age-related declines in T. The sequelae of these exogenous hormones for partnering-related domains remain unknown.

There may also be implications of hormone-partnering links for the health of healthy people. Married individuals tend to have longer and

healthier lives (e.g., Hu & Goldman, 1990; Kiecolt-Glaser & Newton, 2001), and tend to have lower T (e.g., Booth & Dabbs, 1993). Is there an association between these two? Do healthier individuals tend to have lower T and get married? Does immune function improve during supportive relationships? The positive effects of partner support on stress hormones and peptides, along with the negative effect of stressful partner interactions, suggest some state effects and open further possibilities for examining stress responses, partnering, and general health. The large question of how major life events and changes associated with endogenous endocrine alterations may affect the variety of partnering-related behaviors and states remains largely unanswered. If specific associations could be identified, individuals could potentially be given advice or information to contextualize changing life experiences.

In terms of basic physiology, much remains to be determined. Because vasopressin and estrogens have received little investigation in humans, it remains to be seen how these hormones may be associated with partnering in humans. Oxytocin and T have obviously received more attention, but this research has largely been gendered, focusing on oxytocin in females and T in males. Further attention would be beneficial on the hormones themselves as well as to the relationships among the hormones. Researchers of stress hormones have often attended to the entire HPA axis, but research using T has been limited to the gonadal level. It is likely that attending to the HPG axis will be informative. Further, partnering strategies and evolutionary influences have been theorized for androgen-partnering associations, but somewhat less so for peptide and stress hormones. Increased attention to theoretical considerations is likely to help guide empirical efforts.

Despite the newly emerging status of this field, research on hormones and partnering has provided insights into aspects of human behavior, evolution, and endocrinology. At this stage, the research has been broad and encompassing; future research should refine the questions, use advanced technologies, and seek to specify more detailed and sophisticated relationships between hormones and partnering. Despite these caveats, research into associations between partnering and hormones is providing fascinating insights into evolutionary bases of pair bonding, culturally situated understandings of partnering, links with stress and health, and causal interpretations of hormone-behavior associations. This is a field teeming with interesting, testable, and important questions, and we are confident that current and future researchers will help to provide fundamental advances, clarifying how partnering and hormones are associated, and illuminating links with health, neural activity, and other domains.

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