GENES AND THE BRAIN


4

Social Modulation of Hormones

SARI M. VAN ANDERS

SOCIAL NEUROENDOCRINOLOGY

Though it is an advance in many ways to conceptualize the mind as operating with biological and socioenvironmental spheres, contextualization of the mind’s function should not end there. Rather than employing a unidirectional hierarchical perspective whereby only the mind is understood to be sensitive to biology in exclusion to the converse, with biology thus positioned at the top of an artificial chain of command, contextualizing the mind within biology should be more nuanced. Hierarchies that include social context and biology are dynamic, continually in flux, and mutually influencing.

In this chapter, I specifically argue that social context in various forms can fundamentally alter and influence endocrine function, and that these hormonal changes can be best discussed within an evolutionary framework of adaptation and functionality—a research approach known as *social neuroendocrinology* (van Anders & Watson, 2006b). This approach represents a truly interactionist perspective that requires attention to both social context and biology, and a conscious move away from biological determinism or assumptions of evolutionarily “hardwired” effects. As I discuss more thoroughly in the following sections, we can reasonably expect evolution to “select” for endocrine responses to social contexts, since hormones are related to many sexual processes. For example, sperm need to be produced after ejaculation, and hormones are involved in sperm production. To test evolutionary questions of hormones influenced by social and sexual context, one first needs context;
that is, we could not logically expect to see evidence for evolved sexual modulation of hormones in the absence of sexual context of some kind. Additionally, many processes we reasonably consider to be influenced by evolution are influenced by past context, as when previous parenting experience modulates present hormonal responses to parenting. As such, *social neuroendocrinology*, by definition, attends to the joint and mutual influences of social context and hormones.

The endocrine system is a paramount exemplar of the need for a nuanced situating of the mind contextualized within biology: Hormone cascades “begin” with the hypothalamus (but see Kriegerfeld, 2006, for a review of upstream neuroendocrine controls of hypothalamic hormone releasers), but the hypothalamus receives converging inputs with socially relevant information. Hypothalamic function therefore is sensitive to social context, and hormonal function resulting is as well. Hormones can also serve as a context for other hormonal actions, as when some hormones have inhibitory effects on other hormones, but this has received little empirical attention in social neuroendocrinology.

Social neuroendocrinology addresses hormonal function as situated within social context, and the research agenda is to examine social modulation of hormones (which is the focus of this chapter), bidirectional influences, and feedback–feedforward effects. The examination of how social context affects hormones is not a unidirectional endeavor, however, as the implicit and explicit goal is largely oriented to questions of effect (e.g., What are the sequelae of social context modulating hormones?) and function (e.g., Why does social context modulate hormones?) As I argue in this chapter, social neuroendocrinology represents a fundamentally important perspective in understanding the mind in context; the mind does not sit quietly in a corner, waiting for biology to tell it what to do. Social neuroendocrinology helps to reinforce a dynamic contextualization of the mind.

In this chapter, I review how social context modulates endocrine function. I focus on social contexts—parenting and sexuality—that are evolutionarily significant and have received empirical attention. Studying how social context modulates hormones necessitates an evolutionary framework, as there is no other way to examine why social context modulates hormones except through an evolutionary lens. By social context, I include the following:

1. Contextual cues that can be transferred from one individual to another (and therefore are socially communicated information); the information in these cues and/or their transmission can be physiological, behavioral, and so forth.
2. Social behaviors of selves or others.

3. Perceptions and anticipation of cues relevant to social context.
4. Information related to social contexts that have been transmitted intergenerationally. As such, social contexts can be immediate (e.g., infants crying) and/or in the past (e.g., past parental experience), brief (e.g., sexual anticipation) and/or longer-lasting (e.g., pregnancy), and modulatory (e.g., stage of pregnancy) or a cue itself (e.g., erotic films).

**PARENTING AND PREGNANCY STIMULI AND HORMONES**

*Pregnancy as a Social Influence on Expectant and New Fathers*

Conceptualizing social contexts, by definition, necessitates envisioning individuals embedded within perceived social networks. As such, social influences on endocrine function could include addressing how the social contexts of some individuals affect the endocrine states of others. States of one individual that would affect endocrine states in another should be evolutionarily relevant, like reproductive states. Reproductive states should have a highly potent social context; as such, the pregnancy status of a woman can be thought of as an extremely salient, evolved social signal—especially to those who are fundamentally invested in the outcome of the pregnancy. Humans tend to form pair-bonds, and human fathers are part of a small number of mammalian species with relatively high paternal investment and involvement (Wynne-Edwards, 2001). Though a mother can provide the gestating fetus and resulting baby with nutritional resources, additional support and resources from other figures (e.g., coparents, family) are likely necessary to support a woman through pregnancy, birth, and childrearing (Hrdy, 1997). As such, it would be adaptive if endocrine changes in a coparent co-occur with a woman’s pregnancy, to potentiate and facilitate parental responsivity. Research has focused on fathers and paternal endocrine responses to infant and pregnancy stimuli, but could (and should!) be extended to examine any persons taking on a coparenting role.

Expectant fathers do show endocrine changes alongside their female partners’ pregnancies. Various changes occur in men over the early and late prenatal stages (i.e., when their female partners are pregnant), in the immediate period surrounding parturition (birth), and in the postnatal period. For example, prolactin (PRL) increases in fathers over the pregnancy (Storey, Walsh, Quinton, & Wynne-Edwards, 2000), cortisol (C) increases near birth and decreases afterwards (Berg & Wynne-Edwards,
2001, 2002; Storey et al., 2000), and testosterone (T) shows an opposite pattern to C, with decreases near birth and increases afterward (Berg & Wynne-Edwards, 2001, 2002; Storey et al., 2000). The decline in fathers’ T is actually consistent with decreases in males of other species that show extensive paternal care (see, e.g., Wynne-Edwards, 2001, for discussion).

Pheromones/chemosignals are one possible mechanism by which this occurs (i.e., chemosignals passing between individuals). Chemosignals from pregnant women may increase sexual desire and fantasy in nonpregnant women (Spencer et al., 2004), buttressing the possibility that pregnant women could affect male partners through chemosignals, and that pregnancy states have social effects on others. Consideration of pheromones as social modulators of hormones adds an important perspective to this discussion; pheromones are social context, since they pass between individuals as social signals.

Why would T decline in new fathers? Possible speculations include decreased sexual desire, as T has been related to desire (e.g., Alexander, Sherwin, Bancroft, & Davidson, 1990), which could be adaptive in directing new fathers’ focus away from sexuality and toward the mother and baby in caring ways. Another speculation is energy redistribution from reproductive and anabolic processes to stress processes, which may be important in attending to the newborn infant. In many species, T inhibits forms of paternal care (e.g., Wingfield, Hegner, Dufty, & Ball, 1990). In humans, men with lower T exhibit better paternal responsiveness (Fleming, Corier, Stallings, & Steiner, 2002) and better father–child relationships (Julian & McKenry, 1985), so decreased T around birth may facilitate paternal care.

Infants as Social Cues on Hormones, and Modulation by Pregnancy

In addition to pregnancy states, cues from offspring should provide an extremely salient social context relevant to endocrine systems because offspring are crucial to reproductive fitness. Infants can themselves be social cues via visual, chemical, and vocal signals or direct contact. Studies have examined effects of the context of having an infant on parental hormones, again, most often looking at fathers. Researchers generally use not only aversive auditory stimuli (e.g., pain or hunger cries) but also videos of pregnancy stimuli or ask men to hold baby dolls. Some have used all three in a likely attempt to maximize the “infant” experience without the difficulty and lack of control that could accompany the presence of real, live infants.

Fathers’ hormones are significantly altered after exposure to infant stimuli, and this socially modulated change in hormones can further be influenced by female partners’ stage of pregnancy. For example, men show larger decreases in C in response to infant cues in the late prenatal phase relative to other phases (Storey et al., 2000). PRL does not appear to change in response to infant cues (Fleming, Corier, et al., 2002), but T does show a significant increase in expectant fathers after some infant cues (Storey et al., 2000), with the largest increase occurring in the early postnatal phase (Storey et al., 2000).

Increased T upon infant cues seems counterintuitive given the possible functionality of low T described, evidence that T inhibits some parental behaviors in other species (Wingfield et al., 1990), and research showing that T is negatively associated with paternal–child bonding (Julian & McKenry, 1989). However, an increase in T specific to the early postnatal phase may reflect some evolutionary history of the need for infant defense in this phase. Parental behavior should not be understood to be a monolithic phenomenon, and I have theorized elsewhere (van Anders & Gray, 2007) that infant cues associated with close intimacy should be classified as bond maintenance and thus predictably lead to decreased T. In contrast, infant cues that might signal need for interventions such as protection or defense should be classified as competitive and lead to increased T. Since many of the infant cues in these studies include aversive baby cries, it may be that these cues a competitive rather than a bond-maintenance response. Additionally, evidence in other species suggests that the largest increases in T in response to social stimuli are seen during phases of lower T, and that androgen sensitivity to social contexts such as challenge are greatest during times of high parental care, and not times of regular social challenge, as counterintuitive as this may seem (Wingfield et al., 2000). Similarly, in human studies, the largest increases in men’s T in response to infant cues are seen during the phases when they have the lowest T (i.e., around birth). Fascinatingly, fathers’ current T levels can thus serve as a context for socially modulated changes in T.

Perhaps ironically, given societal conflation of mothers and infants, fewer researchers have studied effects of infant stimuli on maternal endocrine function (apart from lactation; see Ellison, 2001), though it should be noted that, overall, research on the modulation of infant stimuli on paternal hormones is also limited. Still, some studies have examined infant modulation of maternal endocrine function, and expectant and new mothers show increases in PRL after holding babies (Delahunty, McKay, Noseworthy, & Storey, 2007). Women’s endocrine response to infant contextual cues can also differ depending on their own parturi-
tion status and context; after exposure to infant cues, PRL shows significant increases in pregnant but not in nonpregnant women (Storey et al., 2000). This is likely adaptive, since pregnant women’s bodies should be ramping up the ability to respond to infants with lactation, and PRL is involved in this milk letdown.

**Previous Infant Experience and Infant Cues on Hormones**

Behavioral neuroendocrine research with animals often focuses on priming of the endocrine system, and previous parenting experience has been used as a possible context for or modulator of the endocrine axes in response to subsequent infant stimuli. In humans, researchers have thus examined how social context involving previous parenting experiences affects present social modulation of hormones.

For example, new, but not experienced, fathers show elevated C in response to cry stimuli (Fleming, Corter, et al., 2002). The social salience of baby cries may change depending on past experience, and this difference in social salience may elicit parallel changes in endocrine responses. In contrast to C responses, experienced fathers show a larger increase in PRL after hearing cries than do new fathers (Fleming, Corter, et al., 2002), and a similar pattern holds for fathers holding babies after birth, with experienced fathers showing increases in PRL and new fathers showing decreases (Delahunty et al., 2007). Men with younger siblings also show an increase in PRL in response to infant stimuli, but men with none show a decrease in PRL (Storey et al., 2000). These parallel findings suggest that the context of previous bond-maintenance experience with infants/children (whether with offspring or siblings) influences subsequent endocrine responses to infant stimuli. Which aspects of experience with infants might sensitize the brain to respond to subsequent infant stimuli with characteristic hormone responses is unclear at present because humans have received little empirical attention.

**Transgenerational Effects of Parenting on Offspring Endocrine Axes**

Research examining the effects of parental context on infant endocrine function and subsequent parenting has generally been carried out in nonhuman species (e.g., rats, mice) exposed to experimentally or naturally varied amounts and patterns of maternal care. Research with nonhuman species (e.g., rats) shows profound effects of parenting context on offspring endocrine function and behavior, especially in terms of hypothalamic-pituitary-adrenocortical (HPA) axis function in general situations, and HPA responsivity to stress (see, e.g., Fleming, Kraemer, et al., 2002). And, these effects show intergenerational transmission (e.g., Meaney, Szyf, & Seckl, 2007). Research with primates in cross-fostering studies has shown that maternal behavior of individuals is altered by the maternal behavior these individuals received as infants, and that changes in neurotransmitters (e.g., serotonin and dopamine), as well as HPA hormones (e.g., epinephrine), are implicated (Maestripieri, Lindell, & Higley, 2007). Therefore, influences of social contexts on hormones are likely to be long lasting, transmittable to subsequent generations, and of high import in future human research.

**SEXUALITY AND HORMONES**

Like pregnancy and parental/nurturant behavior, sexuality and reproductive behaviors should be a prime site for evolutionary pressures. Sexuality-related context should exert strong effects on endocrine function (e.g., van Anders & Watson, 2006b) because of the prime importance of sexuality in both fitness and sexual selection. Hormones have strong and direct influences on fertility in terms of ovulation and sperm production, menstruation, and also on morphological sexual differentiation. Social context can include sexual anticipation, in which the expectation of sexual activity might affect hormones, and these can be direct or embodied expectations. Sexual context can also include sexual stimuli (e.g., erotic movies) or sexual activity with another partner.

**Sexual Anticipation Influences on Hormones**

Though we might conceptualize effects of sexual activity on endocrine function as limited to actual sexual activity, expectation of sexuality should also be a highly salient signal. It could be adaptive for the body to expect and/or prepare for sexuality, since sexual activity involves a number of potentially hormonally mediated processes and cognitions. Of the few studies relevant to anticipatory effects of sexuality on hormones, most have found supporting evidence. Thus, the anticipation of a sexual context, or even the experience of a psychologically (but not physically) sexual context, can lead to endocrine alterations.

One of the most widely known and earliest reports of anticipatory effects of sexuality on physiology is by Anonymous (1970), who reported on his experience as a researcher on a deserted island; he was alone except when he traveled back to the mainland to visit his female romantic partner and engage in sexual activity. During his island stay,
Effects of Sexual Cues on Hormones

Unlike sexual anticipation, sexual cues involve transmission of information. For example, people may view sexual stimuli, though engagement with two-dimensional stimuli lacks many of the social cues inherent to interaction with a live person. Still, the evolutionary development of the neuroendocrine system might be seen as unlikely to reflect this distinction.

Visual sexual cues from videos do lead to changes in hormones. Men's T is increased following sexual movies compared to neutral and/or aggressive films (Hellhammer, Hubert, & Schirrmeyer, 1983; Pirke, Kockott, & Dittrar, 1974; Rowland et al., 1987; Stolero, EnnaJJ, Cournot, & Spira, 1993). However, nongonadal steroids, such as C or PRL, have not been found to increase following sexual stimuli in men (Exton et al., 2000). Interactions with live women also alter heterosexual men's hormones, as shown when men's T and C are increased following conversations with women (Roney, Lukaszewski, & Simmons, 2007; Roney, Mahler, & Masetripi, 2003). Conversations should not be understood as sexual interactions; more specifically, Roney and colleagues (2003) found that men's T increases were correlated with their flirtatious behaviors. This suggests that the social perception of a context as potentially sexual and/or romantic and performing relevant behaviors are associated with T increases.

Hormone changes in response to sexual context might be functional in similar ways to sexual anticipation; that is, increased T may facilitate sperm production or genitai vasocongestion, influencing fertility parameters or sexual pleasure. Increases in C may reflect stress responses, but Roney and colleagues (2007) noted that participants' C was uncorrelated with perceptions of situational stress. Increased C may thus be more related to attention to arousal or social stimuli, such as facial emotions (Reolof, Baskis, Hermans, van Pelt, & van Honk, 2007). Additionally, C has been shown to facilitate pair-bonding in species that regularly form monogamous pair-bonds (e.g., corticosterone in prairie voles: DeVries, DeVries, Tymans, & Carter, 1996), so increased C in a sexual context may be facilitatory for pair-bonding.

Sexual Activity Effects on Hormones

Engaging in sexual activity with a partner should also have endocrine effects, but whether this context should be stronger than sexual anticipation and cues, because it involves live people and their concomitant social cues, has not really been tested. Since sexual activity generally involves ejaculation on the male's part, whereas anticipation or cues do
not: always, sexual activity may be a stronger sexual cue to the endocrine system. Humans often engage in sexual activity within the context of some sort of relationship or pair-bond, so sexual activity with others may influence hormones in ways that are relevant to promotion or maintenance of the pair-bond. Indeed, sexual activity itself can facilitate pair-bond formation in prairie voles (Young, Murphy Young, & Hannock, 2005). And women feel more intimate with their partners the morning following partnered sexual activity compared to partnered exercise (van Anders et al., 2007). Fewer studies have examined how partnered sexual activity might affect oxytocin (Otx) in humans, but Carter (1998) notes that mating and especially vaginocervical stimulation in females of other species both increases Otx and facilitate pair-bond promotion.

Studies examining the immediate effects of sexual activity on men's T have generally not found empirical support (e.g., Stearns, Winter, & Faiman, 1973), though one more recent study has (Dabbs & Mohamed, 1992). However, studies have found that men's T is increased at a latency following sexual activity (Knussmann et al., 1986; Kraemer et al., 1976), with especially large increases the morning following sexual activity with multiple or unfamiliar partners (Hirschhausen, Frigerio, Grammer, & Magnusson, 2002). And Knussman and colleagues (1986) found higher T in 48-hour periods surrounding orgasm in men.

Researchers have also examined the effects of sexual stimuli and masturbation to orgasm, finding significant increases in PRL following orgasm in both men and women, with elevations remaining for at least 1 hour (Exton et al., 2001). This increase in PRL appears to be orgasmdependent, and is thought to be a sexual satiety signal. And solitary masturbation increases men's T (Purvis, Landgren, Cekan, & Diezfalusy, 1976; cf. Krüger et al., 1998), even with no latency, whereas sexual activity with a partner does not. Could the social presence of a female partner inhibit T releases in response to sexuality? Since partnered men tend to have lower T (e.g., van Anders & Watson, 2006a) and T may inhibit pair-bonding in other species (Wingfield et al., 1990), this seems a possible though speculative conclusion.

T levels are increased in women immediately following intercourse with male partners, but no significant increases are apparent as yet in longer-term measures (e.g., the next morning) (van Anders et al., 2007). However, the social cues leading to increased T are not limited to partnered sexual involvement, since women also show significant increases in T following cuddling. In fact, the increase in T after cuddling was larger (though nonsignificantly) than the increase following intercourse. One interpretation is that the close physical intimacy of both activities leads to increases in T. Another interpretation is that cuddling leads to sexual anticipation, and because sexual anticipation is associated with increased T in women, postcuddling increases in T might be mediated by anticipation of partnered sexual activity.

CONCLUSIONS

Social Modulation of Hormones via Parental and Sexual Context

Social contexts that are especially relevant to evolution and reproductive fitness are the best candidates for examining social modulation of hormones; these influences, in turn, are interpretable only when evolutionary considerations are taken into account. Thus, social neuroendocrinology is inherently evolutionary, regardless of the home disciplines of its practitioners. As is evident in the preceding sections, examining the effects of social context on hormones is also an inherently interactionist endeavor and can only be accomplished with the explicit recognition that evolved responses occur only within specific social contexts. As such, social neuroendocrinology is perhaps uniquely situated to challenge biological determinism; evolved physiological responses—by definition—require social context to occur. And given the modulatory effects of past context (e.g., parenting experience) on the influences of current context (e.g., infant exposure) on hormones (e.g., increased PRL), there are many points at which considerations of social context are prerequisites to understanding potentially evolved mechanisms.

Sexuality-related stimuli are particularly relevant to social neuroendocrinology because of their importance in reproduction and the involvement of hormones in processes such as fertility, sexual development, and sexual morphology. The extensive research foundation on sexuality and hormones in nonhuman species provides an experimental literature resource from which human researchers can draw. As described, sexual context does affect endocrine function in a multitude of ways that can be understood to exist under a monolithic sexuality category or a subdivided group of avenues of influence. However, setting sexuality up as a monolithic, undivided category is unlikely to provide for the level of detail needed to make key insights. For example, how do social cues inherent to interaction with people, viewing sexual stimuli, or solitary sexual pursuits differentially affect endocrine responses?

The functional implications of endocrine changes in response to sexual stimuli range from fertility to physiological preparations for intercourse (e.g., lubrication), but all remain speculative, since little research has actually examined the possible sequelae of sexually-stimulated endocrine changes. Empirical investigations into functionality, and not just presentations of convincing speculations, are needed and important.
for understanding basic questions of hormone-sexuality associations, in addition to furthering the social neuroendocrinology research agenda. Understanding the actual, as opposed to attractive, sequelae will increase the relevance of social neuroendocrinology to other disciplines, including clinical practice with sexual therapy or infertility.

Like sexuality, parenting-related contexts are prime targets for social neuroendocrinology because of their key association with reproductive fitness and survival, and because hormones are already implicated in known parental processes (e.g., lactation). Similarly, parenting has been extensively studied in nonhuman species, with comprehensive linkages among neural circuits, hormones, and maternal behavior. The focus on intergenerational transmission of socially modulated endocrine function has provided exceedingly important insights in the nonhuman literature, and a major challenge and opportunity is to examine these issues in humans (daunting though the timescales might appear). Additionally, the elision of subcategories within infant stimuli likely undermines the development of a solid empirical and theoretical foundation. Researchers need to examine how different contextual modalities (e.g., live baby vs. vocal only vs. visual only) and contextual valences (e.g., crying vs. happy) differentially elicit endocrine changes.

**Challenges and Future Directions**

Like most newly emerging disciplines, social neuroendocrinology faces both a challenging and promising future. A major initiative involves incorporating a focus on the functionality of social neuroendocrinology (van Anders & Watson, 2006b); researchers allude to tantalizing and interesting possible adaptive functions of socially induced endocrine alterations but need to conduct empirical studies. As noted earlier, the elements of social context need to be more closely examined. What social cues in social context elicit (which) hormone changes? The use of "sexual" or "parental" or even "social" context needs to allow for and provide opportunities to determine how individuals engage with these stimuli (perception, etc.), and how this engagement then influences hormones. A major challenge lies in the need for independent replication of results, which can be a difficult premise given that human researchers often focus on idiosyncratic though overlapping questions. A major advantage is that social neuroendocrinology allows for transdisciplinary collaborations to examine questions of the evolved physiology of social behavior rather than parallel work using different methodologies.

Methodological issues have been and will likely continue to be a challenge. Analyses are not really that expensive, until researchers think about the inclusion of multiple hormones, multiple sampling points, and sufficient sample sizes with women and men. Attending to all of these is as yet an unreached ideal. For example, some studies have pointed to the importance of time of day (another context in itself), with sociality-hormone associations apparent in the afternoon but not the morning (e.g., Roney et al., 2007). Other studies have pointed to latency between context and sampling, with delays needed after some types of social contexts but not others, which can lead to "null" findings despite significant associations (if only hormones were measured later or earlier). Fortunately, important insights have already been gleaned with these introductory methodologies; as the field matures, methodological insights and improvements are certain to follow as researchers are able actually to test both methodological and conceptual questions that are crucial to social neuroendocrine research.

Social neuroendocrinology provides a novel but powerful approach to understand the evolved physiology of social behavioral contexts. Hormones may influence social behaviors and perceptions, and brain areas may develop as substrates for specific kinds of social behavior (e.g., sexuality- or parenting-related), but the mind should not just be contextualized as lying within a larger biological sphere of influences. Instead, the mind should be understood to be an active component within this larger physiological sphere, as social context and hormones actively engage in a complex and dynamic relationship, affecting each other with degrees and direction of influence that change in response to specific social contexts—a socially apt process for the social modulation of hormones.

**REFERENCES**


