Future Directions in Human Behavioral Endocrinology

Lisa L. M. Welling and Todd K. Shackelford

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Edited by Lisa L. M. Welling and Todd K. Shackelford

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Abstract and Keywords

Research within behavioral endocrinology has produced substantial advances over the past few decades. Knowledge of the biological mechanisms involved in human behavior informs evolutionary perspectives on selection pressures in our ancestral past, which encourages the development of more complete theories and more refined research questions. Yet, despite these advances, many unanswered questions remain. This chapter outlines broad suggestions for future hormone research within the topics of development and survival, reproductive behavior, and social and affective behavior. It concludes with several general suggestions for the field, including more research using hormonal assays, longitudinal and experimental designs, exogenous hormone administration, and cross-cultural work. It also suggests that researchers continue to consider the function of other endocrine traits (e.g., carrier proteins) and measure or manipulate hormones in combination with assessing hormone receptor genes. Behavioral endocrinology is a field replete with important future research directions that will contribute important insights into the evolution of our own and other species.

Keywords: Behavioral endocrinology, endocrinology, evolutionary psychology, hormones, behavior, future directions

The bidirectional relationships between hormones and behavior have received attention in several fields, such as biology (e.g., Stricker & Verbalis, 1988), social psychology (e.g., Campbell, 2010), evolutionary psychology (e.g., Welling et al., 2007), medicine (e.g., Hollander et al., 2001), and anthropology (e.g., Whitten, Brockman, & Stavisky, 1998). Contributors to this volume have outlined current research within behavioral endocrinology, highlighting how these findings add to our understanding of the evolution of our species. However, although this diverse literature encourages the development of more complete theories and more refined research questions, much remains to be

investigated. Here, we outline several broad suggestions for future research within each of the three themes of this volume: development and survival, reproductive behavior, and social and affective behavior. We conclude by presenting several general suggestions for the field.

Development and Survival

In addition to being responsible for growth and the development of secondary sexual characteristics, hormones mediate several development and survival behaviors across the lifespan. Although research is progressing, relatively little is known about how hormones mediate life history strategies in humans (reviewed in Vitousek & Schoenle, this volume). Future research should address how hormones across the lifespan influence these strategies while paying particular attention to individual differences (i.e., why individuals within a population differ in life history strategy; e.g., Williams, 2012) and within-subject context flexibility (i.e., how life history strategy changes over time in reaction to environmental changes; e.g., Wingfield, 2015). Moreover, interactions with biological sex across development (see Benenson, this volume) require further study, and animal models could be useful in this work. (p. 434) Although there is some evidence of cross-species similarities in developmental sex differences (e.g., Alexander & Hines, 2002; Hassett, Siebert, & Wallen, 2008), a great deal remains to be explored. For example, comparative work could investigate hormone-mediated differences in the onset of sex-differentiated social behaviors across primate species. The examination of similarities and differences across primate species affords educated inferences regarding ancestral pressures that may have applied to humans, which can further our understanding of sex-typical behaviors.

Comparative work also provides evidence for the Organizational–Activational Hypothesis (e.g., Gurney & Konishi, 1980; Phoenix, Goy, Gerall, & Young, 1959), which posits that sex differences in cognition result from differential hormone exposure during critical periods that organize brain circuitry to later produce behavior under appropriate hormonal conditions (reviewed in Hampson, this volume). There is significant empirical evidence in favor of organization/activational influences of hormones on human cognition (e.g., Puts, McDaniel, Jordan, & Breedlove, 2008; Resnick, Berenbaum, Gottesman, & Bouchard, 1986; Shute, Pellegrino, Hubert, & Reynolds, 1983), but the majority of research has focused on mental rotation ability, and so future work might investigate other aspects of cognition in more detail. One way to ethically investigate differential hormone exposure on human cognition is to compare populations with disorders of sex development (many of which are characterized by abnormal hormonal profiles during critical periods) with controls. Use of populations such as women with congenital adrenal hyperplasia (e.g., Resnick et al., 1986), who are exposed to higher than normal levels of androgens in utero, can provide an important avenue for assessing the contributions of hormones to the development of psychosexually differentiated behaviors. However, relatively few studies test these hypotheses on clinical samples. Similarly, the impact of pubertal timing on cognition (e.g., Beltz & Berenbaum, 2013) could be investigated using clinical populations

such as those with idiopathic hypogonadotropic hypogonadism, a condition whereby puberty is not triggered naturally and patients are given hormone replacement therapy to begin the process (i.e., the timing of puberty is precisely known, unlike nonclinical samples). Use of clinical populations could also inform research on other aspects of cognition that are influenced by sex steroids, such as learning and memory (for a discussion on hormonal influences on learning and memory, see Ervin & Choleris, this volume).

Given the importance of hormones on development and cognition, we need additional research on endocrine-disrupting chemicals, compounds in the environment that block or mimic hormones (see Vandenberg, this volume). The potential negative impact of endocrine-disrupting chemicals, commonly found in pesticides and other modern products like plastics, has been known for several decades (Carson, 1962). Yet, endocrine-disrupting chemicals are still commonplace and can have a profound influence on wildlife. For example, atrazine, which is among the most common herbicides used worldwide, is found in ground, surface, and drinking water. Hayes et al. (2010) found that amphibian males exposed to atrazine were chemically castrated and completely feminized as adults, and suggested that atrazine and other endocrine-disrupting chemicals may play a role in the global decline of amphibians. In humans, many endocrine-related disorders have increased over a relatively short period of time, which suggests that environmental changes such as increases in endocrine-disrupting chemicals may be responsible (Bergman et al., 2013). However, the effect of endocrine-disrupting chemicals on human behavior remains unexplored.

Reproductive Behavior

Considerable research on many species, including humans (see, e.g., Gangestad & Thornhill, 2008; Gildersleeve, Haselton, & Fales, 2014), suggests that hormones affect reproduction-related behaviors in functional ways. Despite some disagreement (e.g., Harris, Pashler, & Mickes, 2014; Wood, Kressel, Joshi, & Louie, 2014), putative shifts in adaptive behaviors and preferences across the female menstrual cycle have received substantial attention (reviewed in Welling & Burriss, this volume). As noted previously (e.g., Gangestad et al., 2016), disagreement about the results of research in this area may be partly attributable to inconsistencies in the methods used to estimate cycle phase. Researchers should use within-subject designs where possible, follow published guidelines when estimating cycle phase, and use sufficient power so that the results of research will be easier to compare across studies (Gangestad et al., 2016; Jones et al., in press). This will serve the additional benefit of reducing Type 1 and Type 2 errors.

Many women have chosen to control their menstrual cycles and fertility using the synthetic hormones (p. 435) found in hormonal contraceptives since their introduction in the 1960s (Mosher & Jones, 2010), which may affect aspects of mate choice (e.g., Roberts, Gosling, Carter, & Petrie, 2008; see Hahn & Cobey, this volume, for a review of synthetic hormones and women’s mating psychology). Although research into the use of

these popular synthetic hormones has progressed steadily, most of this work (with a few notable exceptions; e.g., Cobey, Klipping, & Buunk, 2013) compares women currently on hormonal contraceptives with women not currently on hormonal contraceptives (e.g., Welling, Puts, Roberts, Little, & Burriss, 2012), rather than comparing the same women multiple times. Also, synthetic hormones are not identical; for example, some progestins (e.g., levonorgestrel) are androgenic, whereas others (e.g., drospirenone) are antiandrogenic. Hormonal contraceptives are also administered multiple ways (e.g., injectable, pill, vaginal ring) and can be monophasic (i.e., deliver a constant level of synthetic hormones) or multiphasic (i.e., the synthetic hormone dose varies across the regimen). Some research has compared different doses of synthetic hormones (Cobey, Pollet, Roberts, & Buunk, 2011; Welling et al., 2012; Welling, 2016) or the type of synthetic hormone (Grøntvedt, Grebe, Kennair, & Gangestad, 2017). However, there is a need for additional research that considers different types of synthetic hormones (e.g., levonorgestrel vs. drospirenone) and different types of hormonal contraceptives (e.g., injectable vs. pill, monophasic vs. multiphasic) on women's mating psychology (e.g., mate preferences, sexual behavior), especially using a within-subject design. Correspondingly, although some have argued that menopause is accompanied by a shift away from mating-oriented psychology (e.g., Hawkes, O'Connell, Jones, Alvarez, & Charnov, 1998) and a reduction in behaviors aimed at acquiring and securing a mate (e.g., Vukovic et al., 2009), the impact of hormone replacement therapy (HRT) on many mating and family-related behaviors has yet to be investigated. Given their increasing popularity among women and men (i.e., androgen replacement therapy), HRT is a fruitful area for additional investigation.

Mate preferences fluctuate across the lifespan, but few studies employ longitudinal within-subject designs, and even fewer measure hormone concentrations (reviewed in Boothroyd & Vukovic, this volume). The lack of within-subject designs is a methodological weakness that needs to be addressed to rule out confounding influences of individual differences on mate preferences. Given changes in preferences during periods characterized by marked hormonal changes, such as puberty (e.g., Boothroyd, Meins, Vukovic, & Burt, 2014) and menopause (e.g., Vukovic et al., 2009), hormonal mediation seems likely, but the relative lack of hormonal assays in developmental work makes it uncertain. Furthermore, variation in methods used to assess mate preferences (e.g., peer-aged vs. young adult stimuli; Jones, Vukovic, Little, Roberts, & DeBruine, 2011; Vukovic et al., 2009) and pubertal timing (e.g., puberty scales vs. age of menarche; Jones, Boothroyd, Feinberg, & DeBruine, 2010; Saxton et al., 2010) hinders comparisons across studies. These shortcomings yield ample opportunities for future research into developmental changes across the lifespan and into how hormonal exposure during critical periods organizes mate preferences. Similarly, we need additional research on the hormonal components involved in developing gendered behaviors, gender identity, and sexual orientation (reviewed in Neibergall, Swanson, & Sánchez, this volume).

In addition to influencing mate preferences, hormones influence parental behavior. In men, aggression and mating effort are linked in that testosterone is positively related to both (reviewed in Goetz, Weisfeld, & Zilioli, this volume). Thus, it is perhaps unsurprising

that testosterone declines with fatherhood, which likely functions to decrease aggression and mate seeking and, in turn, increase investment in children (reviewed in Boyette & Gettler, this volume). Using longitudinal data from the Philippines, Gettler and colleagues (Gettler, McDade, Agustin, Feranil, & Kuzawa, 2015; Gettler, McDade, Feranil, & Kuzawa, 2011; Gettler, McKenna, Agustin, McDade, & Kuzawa, 2012) found that men experience significant declines in testosterone when transitioning into fatherhood, and that this decline is greatest among men who are more involved in caregiving. More recently, this lab found that young men's androgen functionality (i.e., androgenicity) before fatherhood predicted whether they were later involved as direct caregivers, with moderately androgenic men being more involved than those low or high in androgenicity (Gettler et al., 2017). Other evidence suggests that other hormones, like prolactin and oxytocin (see Gordon, Zagoory-Sharon, Leckman, & Feldman, 2010), play a role in paternal behavior similar to the role these hormones play in maternal behavior (e.g., Uvnäs-Mobcrg, Widström, Nissen, & Björvell, 1990). Furthermore, maternal behavior is associated (p. 436) with estradiol and progesterone, and their ratio, during gestation (e.g., Glynn, Davis, Sandman, & Goldberg, 2016), but their influence in male paternal behavior is unexplored in humans. The independent and interdependent effects of these hormones on parenting and other social behaviors, including social bond paradoxes (i.e., the seemingly contradictory activating function of certain hormones when applied to different circumstances, such as nurturing vs. infant-defense parenting behaviors; see Witczak, Simmons, & Bales, this volume), deserves additional attention. Specifically, researchers should continue to differentiate the hormonal trade-offs involved in balancing mating, parenting, and affiliative social bonds and behaviors.

Social and Affective Behavior

Social and affective behaviors can be prosocial (e.g., nurturance) or antisocial (e.g., aggression). The endocrine system is important in regulating social-affiliative processes that contribute to the initiation and maintenance of human social bonds (for a review of the endocrinology of social relationships, see Anderl, Saphire-Bernstein, & Chen, this volume). The Challenge Hypothesis suggests that there is a dynamic relationship between testosterone and aggressive behavior such that testosterone promotes aggression when it benefits the individual from a reproductive standpoint (i.e., pursuing a mate, mate guarding, and intersexual competition to ward off male rivals; Wingfield, Hegner, Dufty, & Ball, 1990). Indeed, considerable research has found an association between testosterone and competitive, status-seeking behavior (reviewed in Casto & Mehta, this volume; Geniole & Carré, this volume). Competition-induced testosterone changes are influenced by competitive outcome (i.e., win vs. loss; e.g., Gladue, Boechler, & McCaul, 1989; Mazur, Booth, & Dabbs, 1992; Mehta, Snyder, Knight, & Lassetter, 2015; Pound, Penton-Voak, & Surridge, 2009), and these testosterone fluctuations may in turn influence future competitive behavior by promoting such behavior when it may enhance status (discussed in Mehta et al., 2015). A methodological limitation of this (and other) work is reliance on correlations instead of experimental manipulations, which, particularly given that the relationships between testosterone and aggressive and competitive behavior are

bidirectional (i.e., the behavior follows the increase in the hormone and vice versa; e.g., Carré, Campbell, Lozoya, Goetz, & Welker, 2013; Geniole, Bird, Ruddick, & Carré, 2017), does not inform our knowledge of causal relationships. Testosterone administration studies are becoming more common (e.g., Bos, Panksepp, Bluthé, & Van Honk, 2012; Carré et al., 2017; Welling, Moreau, Bird, Hansen, & Carré, 2016; Wibral, Dohmen, Klingmüller, Weber, & Falk, 2012), but more work using exogenous hormone administration, including with other hormones like estradiol and progesterone, would be useful. Also, investigations into the long-term effects of hormone surges could generate novel information.

Testosterone secretion and action on target tissues is influenced by cortisol level (e.g., S. Chen, Wang, Yu, Liu, & Pearce, 1997), and predictions surrounding testosterone and social status have not been fully supported (see review by Mazur & Booth, 1998). Research on testosterone and status (Mehta & Josephs, 2010) and aggression (Dabbs, Jurkovic, & Frady, 1991; Popma et al., 2007) suggests that the interaction between testosterone and cortisol may be more important than looking at a single hormone in isolation. For instance, Mehta and Josephs (2010) found that testosterone is positively related to dominance behaviors in men and women, but only if the individual is low in cortisol level. Future research should explore this dual-hormone effect in more detail by, for example, examining other behavioral and personality correlates (discussed in Casto & Mehta, this volume). Additionally, the influence of these hormones on status-seeking and related behaviors should be considered with reference to the social group in which they occur (e.g., group hierarchies, intergroup and intragroup competition, nonfamilial vs. familial groups) to more comprehensively investigate within-group social dynamics. Evidence suggests that testosterone can promote prosocial behaviors under certain contexts, such as when interacting with in-group versus out-group members (e.g., Diekhof, Wittmer, & Reimers, 2014; Reimers & Diekhof, 2015), reciprocating prosocial behavior (Boksem et al., 2013; Dreher, Dunne, Pazderska, Frodl, & Nolan, 2016), or (in women) reconciling after a conflict or competition (Casto & Edwards, 2016). However, despite attempts at formulating models outlining the functions of testosterone (e.g., Eisenegger, Haushofer, & Fehr, 2011; van Anders, Goldey, & Kuo, 2011), the contexts and individual differences according to which testosterone promotes positive versus negative behaviors remain unclear (see discussion in Hamilton, Carré, Mehta, Olmstead, & Whitaker, 2015).

Other research on the endocrinology of social relationships has focused on the peptide hormone oxytocin (for a review of oxytocin research, see Grebe & Gangestad, this volume). In addition to its **(p. 437)** functions in parturition and lactation, researchers have argued that oxytocin evolved to facilitate parental (especially maternal) behavior, but that it has been co-opted and modified to function in other relationship contexts (e.g., friendships, kin, in-group members; e.g., Carter, 2014; Donaldson & Young, 2008). Although there is evidence in favor of this hypothesis (e.g., Feldman et al., 2010), more work is needed to clarify oxytocin's role and range of functions. For instance, oxytocin is known to attenuate the cortisol response to stress (Cardoso, Ellenbogen, Orlando, Bacon, & Joober, 2013) and may interact with opioids to influence social outcomes (reviewed in

Gangestad & Grebe, 2017). In rats, estradiol and progesterone proliferate oxytocin receptors in the brain and enhance the influence of administered oxytocin on sexual receptivity (McCarthy, 1995; Schumacher, Coirini, Frankfurt, & McEwen, 1989; Schumacher, Coirini, Pfaff, & McEwen, 1990). Also, oxytocin is related to both prosocial and antisocial behaviors (reviewed in Shamay-Tsoory & Abu-Akel, 2016). Mixed findings have led to several attempts to conceptualize oxytocin's various influences into a unified framework (e.g., Bethlehem, Baron-Cohen, van Honk, Auyeung, & Bos, 2014; Churchland & Winkielman, 2012; Crespi, 2016; Numan & Young, 2016; Shamay-Tsoory & Abu-Akel, 2016), but no consensus has been achieved. Scholars should continue to test the different oxytocin hypotheses to determine which has the most support, and should integrate evidence of associations with other hormones (e.g., vasopressin, estradiol, progesterone, cortisol).

One putative function of oxytocin is that it acts to protect a person from the negative effects of stress by reducing stress hormones (Cardoso et al., 2013) and encouraging affiliative social behavior (e.g., Carter, 1998). Although stress hormones may be adaptive under short-term acute conditions (providing energy for fight-or-flight responses; e.g., Cannon, 1929), chronic stress can have severe long-lasting consequences (reviewed in Mogilski et al., this volume). However, the role that cortisol plays in dysregulating bodily functions and increasing susceptibility to disease through behavioral and immune function changes is not well understood. Recent advances in research have increased our understanding of how maternal/gestational stress and child maltreatment impact the hypothalamic-pituitary-adrenal (HPA) axis and mental and physical health (reviewed in Deer, Bernard, & Hostinar, this volume), but little is known about the degree to which the observed effects are moderated by timing (e.g., during different stages of gestation). Also, as noted elsewhere (e.g., Heim, Newport, Mletzko, Miller, & Nemeroff, 2008), there are few longitudinal studies investigating these issues. Similarly, interactions between genetic variation and stressful experiences, and how they influence psychological behavior and psychiatric outcomes across the lifespan, deserve additional attention. Other methodological issues in this area, such as inconsistent assessment, retrospective designs with adult samples, and small sample sizes, have been noted (McCrory, De Brito, & Viding, 2010; Pollak, 2015; see also Deer et al., this volume) and hinder the comparison of results across studies. Finally, how individual differences mediate responses to acute and chronic stress may have applications for the treatment of certain clinical disorders.

The HPA axis (e.g., Burke, Davis, Otte, & Mohr, 2005; Ciufolini, Dazzan, Kempton, Pariante, & Mondelli, 2014; Stetler & Miller, 2011), estrogen and progesterone (e.g., Newhouse & Albert, 2015; Schmidt, Nieman, Danaceau, Adams, & Rubinow, 1998; Wyatt, Dimmock, Ismail, Jones, & O'Brien, 2004), and testosterone (e.g., Almeida, Waterreus, Spry, Flicker, & Martins, 2004; Bromberger et al., 2010; Giltay et al., 2017) have been implicated in mental health issues such as depressive disorders (reviewed in Ellenbogen, Tsekova, & Serravalle, this volume). Hormones may be important causes or consequences of certain clinical disorders and may be useful in targeted treatments (see, e.g., Herbert, 2013). Research in this area has begun (e.g., Block et al., 2017; DeBattista et al., 2006; Guastella, Howard, Dadds, Mitchell, & Carson, 2009; Spierling & Zorrilla, 2017),

including research that considers matching genetic markers associated with hormone functioning with the response to treatment (O'Connell et al., 2018), but this research remains sparse. Researchers could also further examine how short-term fluctuations in hormones or disruption of natural hormonal cycles (e.g., circadian rhythms; reviewed in Cissé, Borniger, & Nelson, this volume) impact mental health and other behaviors.

Conclusion

Research in behavioral endocrinology informs evolutionary theories surrounding ultimate ("why") questions by providing the proximate ("how") explanations. Although considerable advances have been made, much is left to uncover. We need more research using hormonal assays, longitudinal designs, and experimental designs with exogenous hormone administration. Additional cross-cultural research could illustrate important hormone interactions with (p. 438) the environment, or otherwise provide important replications of key findings. Another major frontier in endocrine research involves exploring the complex regulatory networks that connect neuroendocrine systems and their connection with other physiological systems (e.g., immune and metabolic systems; Martin & Cohen, 2015). Behavioral endocrinology research typically focuses on a single hormone's influence on a given trait, but physiological systems are interconnected (e.g., Cutolo et al., 2004). Understanding the interactions between physiological systems and behavior would provide important insights. Correspondingly, investigating interactions between multiple hormones (e.g., Heinrichs, Baumgartner, Kirschbaum, & Ehlert, 2003; Mehta & Josephs, 2010; Tackett et al., 2015) is imperative. These interactions should be both measured endogenously and manipulated exogenously in multiple samples.

The literature would benefit from additional work on hormone gene activation and how selection shaped the expression and function of other endocrine traits, such as hormone receptors and carrier proteins. Furthermore, measuring or manipulating hormones in combination with assessing hormone receptor genes (e.g., F. S. Chen et al., 2015; Eisenegger, Kumsta, Naef, Gromoll, & Heinrichs, 2017; Roney, Simmons, & Lukaszewski, 2010) can more thoroughly address whether it is the hormone itself or other aspects of biology related to the hormone that are influencing changes in behavior. Future work of this nature may reveal that relationships between hormones and behavior are more complex than previously supposed. Certainly, there are multiple directions scholars can pursue moving forward, which may eventually generate comprehensive models of how hormones influence development, survival, reproduction, and social behaviors across the lifespan.

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Lisa L. M. Welling

Oakland University, Rochester, MI, USA

Todd K. Shackelford

Oakland University, Rochester, MI, USA