Oxford Handbooks Online

Integrating Mechanisms and Functions to Understand Behavior

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The Oxford Handbook of Evolutionary Psychology and Behavioral Endocrinology
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Print Publication Date: May 2019
Subject: Psychology, Cognitive Psychology, Cognitive Neuroscience
Online Publication Date: May 2019 DOI: 10.1093/oxfordhb/9780190649739.013.1

Abstract and Keywords

Evolutionary psychology and behavioral endocrinology provide complementary perspectives on interpreting human behavior and psychology. Hormones can function as underlying mechanisms that influence behavior in functional ways. Understanding these proximate mechanisms can inform ultimate explanations of human psychology. This chapter introduces this edited volume by first discussing evolutionary perspectives in behavioral endocrinology. It then briefly addresses three broad topic areas of behavioral endocrinology: (1) development and survival, (2) reproductive behavior, and (3) social and affective behavior. It provides examples of research within each of these areas and describes potential adaptations. The chapter concludes with a discussion on the importance of integrating mechanisms with function when investigating human behavior and psychology.

Keywords: evolutionary psychology, behavioral endocrinology, mechanisms, function, behavior

Hormones are chemical messengers secreted into the bloodstream or tissue fluid system by specialized cells. They travel from their source until they reach target cells with specialized receptors, to which they bind to evoke a response. The three main classes of hormones are steroids, peptide hormones, and monoamines. Steroid hormones in humans include estrogens (e.g., estradiol), progestins (e.g., progesterone), androgens (e.g., testosterone), and corticosteroids (e.g., cortisol). They are lipophilic and must bind to carrier proteins (e.g., sex hormone–binding globulin) to circulate in the bloodstream. Peptides (e.g., oxytocin) and monoamines (e.g., melatonin) are made of one (monoamines) or more (peptides) amino acids. They are hydrophilic and travel freely in the bloodstream. Hormones can change gene expression (e.g., Béchet, 1986), influence signaling pathways (e.g., Goglia, Moreno, & Lanni, 1999), and/or change cell sensitivity by increasing (i.e., up-regulating) or decreasing (i.e., down-regulating) the number of receptors for that or another hormone. For example, pregnancy hormones cause an up-regulation of oxytocin receptors in the uterus during the third trimester (Gimpl & Fahrenholz, 2001), whereas elevated levels of insulin cause a down-regulation of insulin receptors (Fröjdö, Vidal, & Pirola, 2009). In addition to these biological functions, hormones may serve other evolved purposes under certain circumstances by influencing human behavior.

Evolutionary psychology and behavioral endocrinology have progressed as relatively independent fields over the last few decades. Evolutionary psychologists seek to explain human behavior and psychology in terms of functional outcomes of natural and sexual selection across our evolutionary past. Specifically, evolutionary psychology stands on the supposition that selection pressures designed the adaptations of the mind (as well as the body) and these adaptations produced behavior through psychological, neurological, and physiological mechanisms (Tooby & Cosmides, 1992, 2005). Similar to physical adaptations, such as how the human foot is designed to afford long-distance running (e.g., Bramble & Lieberman, 2004; Raichlen, Armstrong, & Lieberman, 2011; (p. 2) Rolian, Lieberman, Hamill, Scott, & Werbel, 2009), evolutionary psychologists maintain that behavior and psychological traits (e.g., memory, learning, perception, personality, preferences) are the result of psychological mechanisms that evolved because they served an adaptive function during our ancestral past (e.g., Buss, 2005; Pinker, 2002). Hypotheses are generated accordingly and tested against alternative explanations using both Western and cross-cultural samples (discussed in Tooby & Cosmides, 2005).

Behavioral endocrinologists investigate the underlying hormonal and neuroendocrine mechanisms that influence or regulate behavior in humans and other animals. Behavioral endocrinology is the scientific study of the bidirectional relationship between hormones and behavior, and of the interactions among the brain, the endocrine system, hormones, and behavior (Nelson, 2010). Although the field arguably dates back to Berthold’s (1849) landmark experiment on castrated chicks, which provided the first formal evidence that the testes produce substances that influence both physiology and behavior, Frank Beach, who wrote the book *Hormones and Behavior* (1948) and cofounded the journal of the same name, first branded and defined the discipline more than a century later (Beach, 1975). Behavioral endocrinologists examine relationships with behaviors of interest using measured (e.g., Denson, Mehta, & Ho Tan, 2013; Hahn, DeBruine, Fisher, & Jones, 2015; Welling et al., 2007, 2008), estimated (e.g., Garver-Apgar, Gangestad, & Thornhill, 2008; Jones et al., 2005; Lukaszewski & Roney, 2009), or manipulated (e.g., Carré et al., 2015; Donaldson, Welling, & Reeve, 2017; Welling, Moreau, Bird, Hansen, & Carré, 2016; Welling, Puts, Roberts, Little, & Burriss, 2012) circulating hormone levels, or through investigating the associated biological circuitry (e.g., receptor-binding sites, gene expression) of these interactions (e.g., Arango et al., 1990; Farfel, Kleven, Woolverton, Seiden, & Perry, 1992; Israel, 2016). Hormones influence gene expression or cellular function, and increase the likelihood of specific behaviors occurring under certain circumstances by affecting sensory (i.e., input) systems, central nervous system processing systems, and/or peripheral effectors (i.e., output systems such as striated muscles; Nelson, 2010).

Scholars of both evolutionary psychology and behavioral endocrinology often study interactions using interdisciplinary methods. Both investigate questions and/or borrow techniques from neuroscience, anthropology, social psychology, genetics, biology, zoology, and other disciplines. The complementary nature of these areas is increasingly recognized; annual conferences hosted by the *Human Behavior and Evolution Society* and the *Society for Behavioral Neuroendocrinology* include a variety of speakers who are investigating the hormonal basis of behavior from an evolutionary perspective. In other words, researchers are acknowledging that integrating mechanisms in our understanding of function provides additional insight that produces more complete theories and hypotheses.

Focusing on underlying mechanisms moves evolution-minded researchers from asking ultimate ("Why?") to proximate ("How?") questions. Ultimate explanations outline the function of a trait or behavior, whereas proximate explanations outline how underlying mechanisms interact with the environment to produce that trait or behavior (Tinbergen, 1963). For example, an ultimate explanation for birds singing is that birds that sang over that species' ancestral past were more likely to attract a mate and pass on their genes (i.e., singing conferred a reproductive advantage), whereas a proximate explanation for birds singing is that seasonal fluctuations in testosterone level cause singing behavior during the breeding season. Proximate explanations deal with mechanisms, whereas ultimate explanations deal with evolved functions. Certainly, understanding how a mechanism works informs the understanding of why a mechanism came to exist in the first place, and hypotheses about why mechanisms exist inform research on how they function. Therefore, both proximate and ultimate explanations should be considered when investigating behavior.

Broad Areas of Behavioral Endocrinology

The current chapter discusses evolutionary perspectives in behavioral endocrinology by introducing and briefly reviewing the three broad topic areas that are the focus of this volume: (1) development and survival, (2) reproductive behavior, and (3) social and affective behavior. Within each of these topic areas, chapter authors discuss research and theory in important subareas. We conclude this chapter with a note on the importance of integrating mechanisms (proximate questions) with function (ultimate questions) to disentangle the how and why of behavior.

Development and Survival

An organism's investment in growth, reproduction, and survival defines its life history strategy (e.g., Roff, 2002; reviewed in Vitousek & Schoenle, this volume), and hormones govern multiple biological processes (p. 3) related to development from conception onward. Differential hormone exposure in utero affects sexual behavior later in life in multiple species (reviewed in Clark & Galef, 1995). Behavioral sex differences are noticeable early on (reviewed in Benenson, this volume) and likely stem, at least in part, from this differential hormone exposure (see Collaer & Hines, 1995). Across primate species, young males are more likely than females to engage in rough-and-tumble play and confrontations over status (e.g., Meaney, Stewart, & Beatty, 1985). Work with rhesus and vervet monkeys documents sex-differentiated toy preferences similar to those documented in human children, with females preferring dolls and cooking pots more than males and males preferring cars and balls more than females (Alexander & Hines, 2002; Hassett, Siebert, & Wallen, 2008). These preferences are unlikely to be about the objects themselves, given that monkeys have no use for cooking pots or cars, but rather are likely about movement, with males preferring toys that move actively through space more than females do. Correspondingly, human girls are more likely than boys to help their parents with child-rearing tasks for their siblings and take more pleasure in caring for infants (e.g., Edwards, 2002). These sorts of sex-conforming behaviors are weaker among girls exposed to testosterone prenatally, such as those girls born with congenital adrenal hyperplasia (reviewed in Bailey & Zucker, 1995).

The Organizational-Activational Hypothesis posits that sex steroid hormones permanently organize neural circuitry during early development (i.e., via exposure to specific steroids at critical developmental periods) to give rise to sexually differentiated behaviors that are activated by steroid hormone exposure in adulthood (reviewed in Hampson, this volume). Most evidence for this hypothesis comes from animal work (e.g., Phoenix et al., 1959), but evidence in humans is accumulating (e.g., Heil, Kavšek, Rolke, Beste, & Jansen, 2011; Vuoksimaa et al., 2010). Indeed, several sex differences in cognition have been identified; for example, women tend to excel at object location memory tasks (Voyer, Postma, Brake, & Imperato-McGinley, 2007), whereas men tend to excel at mental rotation tasks (Voyer, Voyer, & Bryden, 1995), among other sex differences (see, e.g., Kimura, 2004). These sex differences often appear or increase around puberty when sex hormone levels increase (e.g., Hyde, Mezulis, & Abramson, 2008), lending support to the proposed organizing (and later activating) role of sex steroids in behavior. Similarly, the influence of estrogens in activating aspects of learning and memory has received a great deal of attention in recent years (reviewed in Ervin & Choleris, this volume; see also Duarte-Guterman, Yagi, Chow, & Galea, 2015), although most work has been done with rodents (e.g., Kim, Szinte, Boulware, & Frick, 2016; Luine, 2015).

Together, this work highlights how underlying hormonal mechanisms can evolve to influence multiple domains. Sex differences in play behavior and adult cognition appear to develop under the influence of sex steroids (e.g., Hampson & Rovet, 2015; Hines, 2003; Puts et al., 2008; Williams et al., 1990) and likely reflect different selection pressures on males and females (see Cashdan & Gaulin, 2016). For instance, travel over large ranges may have been more important for males due to different reproductive interests (Miner, Gurven, Kaplan, & Gaulin, 2014), which would lead to greater selection for visuospatial abilities in males compared to females (e.g., Halpern, 2013). Others have hypothesized that the female advantage in object location memory reflects a sex-linked division of labor in our ancestral past, with females engaging in comparatively more gathering than males (e.g., Neave, Hamilton, Hutton, Tildesley, & Pickering, 2005; Silverman, Choi, & Peters, 2007). Thus, differences in hormonal profile are related to evolved differences in behavior, although it is worth noting that evolved hormonal mechanisms can be affected by modern pollutants called *endocrine-disrupting chemicals* (reviewed in Vandenberg, this volume), which may alter important hormonal functions, including those associated with reproductive behavior (e.g., Colborn, vom Saal, & Soto, 1993). These mechanisms work between individuals (e.g., sex differences) but also within individuals as levels of endogenous hormones fluctuate. Next, we review how changes in these hormones within an individual functionally influence changes in behavior that promote reproduction and parenting.

Reproductive Behavior

Sexual selection involves members of one sex choosing members of the other sex to mate with and competing with members of the same sex for access to potential mates. Over the last few decades, increasing evidence suggests that women's fertile status is not entirely concealed, as had been previously supposed (see, e.g., Gangestad & Thornhill, 2008; Gilldersleeve, Haselton, & Fales, 2014a, 2014b). Rather, hormonal fluctuations associated with ovulation are related to shifts in attractiveness (e.g., Miller & Maner, 2011; Pipitone & Gallup, 2008; Puts et al., 2013; Roberts et al., 2004), (p. 4) sexual motivation (e.g., Gangestad, Thornhill, & Garver, 2002; Haselton & Gangestad, 2006; Roney & Simmons, 2013), and preferences for male traits putatively associated with underlying genetic quality (e.g., Gangestad, Simpson, Cousins, Garver-Apgar, & Christensen, 2004; Havlíček, Roberts, & Flegr, 2005; Little & Jones, 2012; Welling et al., 2007). Within-subject changes in measured or estimated sex hormones associated with the fertile phase of the menstrual cycle may underlie physical, psychological, and behavioral changes that increase conception probability and the likelihood of reproducing with high-quality mates (reviewed in Welling & Burriss, this volume). Relatedly, women report greater jealousy (Buunk & Van Brummen-Girigori, 2016; Cobey et al., 2012) and engage in more intrasexual competition (e.g., Fisher, 2004; Lucas, Koff, & Skeath, 2007; Piccoli, Foroni, & Carnaghi, 2013) when maximally fertile (for an in-depth review of the hormonal correlates of jealousy and intrasexual competition, see Buunk, Massar, Dijkstra, & Fernandez, this volume). Because jealousy and intrasexual competition facilitate securing and retaining a mate (e.g., Buss, 2005), these findings lend support to the premise that within-woman variation in sex steroid hormones influences mating psychology and behavior. Moreover, synthetic hormones such as those found in the hormonal contraceptive pill may alter aspects of mate choice (e.g., Roberts et al., 2014) and behavior (e.g., Welling et al., 2012), indicating that exogenous hormones also impact behavior and may disrupt evolved functions of endogenous hormones (reviewed in Hahn & Cobey, this volume).

Sex steroids can serve similar functions in men (reviewed in Goetz, Weisfeld, & Zilioli, this volume); testosterone in men amplifies risk-taking behaviors in the service of mating effort (Ronay & von Hippel, 2010), increases mate-seeking behavior (van der Meij, Almela, Buunk, Fawcett, & Salvador, 2012), and decreases interest in infants (Zilioli et al., 2016). Likewise, men's testosterone is negatively correlated with relationship length (Gray et al., 2004), relationship commitment (Edelstein, van Anders, Chopik, Goldey, &

Wardecker, 2014), marriage and fatherhood (Gettler, McDade, Agustin, Feranil, & Kuzawa, 2013; Gettler, McDade, Feranil, & Kuzawa, 2011; Gray, Ellison, & Campbell, 2007; Gray, Kahlenberg, Barrett, Lipson, & Ellison, 2002; see also Boyette & Gettler, this volume, for a review on fatherhood), and involvement in parenting (e.g., Gettler, McDade, Agustin, Feranil, & Kuzawa, 2015; Gettler, McKenna, Agustin, McDade, & Kuzawa, 2012). Given the association between testosterone and aggression (e.g., Archer, 2006), this research suggests that testosterone functionally decreases across a long-term relationship and in response to fatherhood in order to decrease aggressive and mate-seeking behaviors and, in turn, to increase resource allocation toward parenting effort (i.e., investment in one's mate and children; see also, e.g., Bribiescas, 2001).

Mate preferences in both sexes likely evolved to facilitate reproduction with individuals possessing "good" genes and other traits (e.g., kindness) indicative of fecundity and good parenting potential (reviewed in, e.g., Little, 2015). To be sure, stress during gestation and poor parenting can have a severely negative impact on offspring well-being and survival (e.g., Gilbert et al., 2015; Pratchett & Yehuda, 2011; Taylor, Guterman, Lee, & Rathouz, 2009; for a review, see Deer, Bernard, & Hostinar, this volume), making mate choice an important component of reproductive outcomes. Preferences for these traits emerge very early; newborn infants spend longer looking at faces judged as attractive by adults compared to faces judged as relatively unattractive (Slater et al., 1998; Slater, Quinn, Hayes, & Brown, 2000), although childhood preferences do not become fully mature until around age 14 years (e.g., Boothroyd, Meins, Vukovic, & Burt, 2014; for a review of mate preferences across the lifespan, see Boothroyd & Vukovic, this volume). The onset of adult mate preferences peripubertally implicates a hormonal component, such as dehydroepiandrosterone (e.g., Boothroyd et al., 2014; Saxton, DeBruine, Jones, Little, & Roberts, 2009), and further evinces the connection between hormones and reproductive behavior (e.g., Jones et al., 2005; Welling et al., 2008). Yet, sex steroids and other hormones serve a multitude of other social and affective functions. Next, we briefly review some findings on the bidirectional relationships between hormones, affect, and social behavior.

Social and Affective Behavior

The relationships between hormones and affect are among the most well established of the many research areas within behavioral endocrinology. For example, when someone colloquially refers to a person as "hormonal," they are often referencing sudden changes in mood or general negative affect. This pejorative use aside, hormones do influence multiple aspects of affect and social behavior, both positive (e.g., affiliation; Brown et al., 2009) and negative (e.g., aggression; Carré, Putnam, & McCormick, 2009). (p. 5) Affiliation, which consists of close interpersonal relationships (e.g., parent–child, romantic partners) and the behaviors necessary to establish and maintain those relationships (e.g., caregiving, trustworthiness; Feldman, 2012), is a commonly studied element of social behavior (reviewed by Anderl, Saphire-Bernstein, & Chen, this volume). Social/affiliative behaviors are related to steroid concentrations, such as cortisol level (e.g., higher salivary cortisol levels are associated with less social networking;

Koernienko, Clemans, Out, & Granger, 2014), but the majority of research has focused on the mediating influence of the peptide hormone oxytocin. Oxytocin increases in response to affectionate contact with infants (e.g., Apter-Levi, Zagoory-Sharon, & Feldman, 2014) and romantic partner empathy (Schneiderman, Kanat-Maymon, Ebstein, & Feldman, 2014) and is positively correlated with reports of relationship quality (e.g., Holt-Lunstad, Birmingham, & Light, 2015). Some findings are somewhat contradictory, however. For example, oxytocin has been found to both increase (Kosfeld, Heinrichs, Zak, Fischbacher, & Fehr, 2005) and decrease (Bartz et al., 2011) trust during an economic game. This contradictory evidence suggests that hormones can be co-opted across social contexts to accomplish specific behavioral goals under specific conditions (e.g., nurturing behavior characterized by high oxytocin and low testosterone vs. sexual behavior characterized by high oxytocin and high testosterone; van Anders, Goldey, & Kuo, 2011; see also Witczak, Simmons, & Bales, this volume, for a discussion of social bond paradoxes). Oxytocin may function more broadly as a component of a threat management system, whereby it enhances the salience of social cues in response to perceived threats to important social relationships and motivates the individual to repair possible damage (see Grebe & Gangestad, this volume). In this way, oxytocin would serve a prosocial function, but may be expressed differently depending on the circumstances.

Other hormones, particularly testosterone and cortisol, influence antisocial behaviors. Circulating testosterone influences status-seeking (e.g., Eisenegger, Haushofer, & Fehr, 2011), competitive (e.g., Carré et al., 2009), and aggressive (e.g., Klinesmith, Kasser, & McAndrew, 2006) behaviors (reviewed in Geniole & Carré, this volume). These behaviors help define social hierarchies within primates, and placement within these hierarchies is reflected in an individual member's circulating testosterone and cortisol levels (e.g., Kornienko, Schaefer, Weren, Hill, & Granger, 2016; reviewed in Casto & Mehta, this volume). Specifically, in primate species in which hierarchical rank is maintained with aggression, dominant individuals are under more stress and have higher cortisol levels (e.g., Muehlenbein & Watts, 2010), whereas in primate species in which the subordinates are suppressed with intimidation, the subordinates are under more stress and have higher cortisol levels (e.g., Sapolsky, 2005). Although acute stress can be functional in that it fuels survival-related behaviors and motivates relationship reparation, chronic stress and the associated hormones can have detrimental long-term impacts on health and well-being, including decreased physical and mental health (reviewed in Mogilski et al., this volume). Indeed, hormonal changes may precede or accompany several mental health disorders, such as depressive disorders (reviewed in Ellenbogen, Tsekova, & Serravalle, this volume) and anxiety disorders (reviewed in Pigott et al., this volume). For example, chronic dysregulation of the hypothalamic-pituitary-adrenal (HPA) axis resulting in abnormally high cortisol concentrations is commonly found in individuals with depressive disorders (e.g., Carroll et al., 2007). Dysregulation of diurnal hormone levels can have a similar impact on mental health (reviewed in Cissé, Borniger, & Nelson, this volume). This research demonstrates that mental health issues can manifest physiologically as a downstream consequence of hormonal mechanisms being out of balance.

Conclusion

Behavioral endocrinology and evolutionary psychology encompass the topics covered in this chapter and many more. Evolutionary psychology, in particular, has at times been mischaracterized as supporting or justifying negative behaviors (e.g., rape, aggression; discussed in Nicolas & Welling, 2015). These critiques are often based in the naturalistic fallacy—the idea that what is ought to be (i.e., what is natural is good; see Hagen, 2005). Such criticisms are unfounded, however, because studying or postulating *why* something exists does not mean something *ought* to exist. Put another way, because a trait or behavior is natural does not make it morally defensible. Similarly, evolutionary psychology and behavioral endocrinology have at times been mistakenly assumed to support genetic determinism (i.e., the view that human behavior is entirely controlled by genes/biology). For example, the cross-cultural finding that men are, on average, (p. 6) more aggressive than women and that testosterone is associated with aggression can be misinterpreted as claiming that men are biologically incapable of controlling their aggression (reviewed in Campbell, 2012). But genetically determined mechanisms do not necessarily translate into specific behaviors (see Hagen, 2005); for instance, the extent to which men engage in intimate partner violence varies greatly depending on the gender equality of their culture (Archer, 2006), showing that environment plays a role in shaping behavioral responses. By the same token, although feelings of pathogen disgust likely evolved to facilitate contagion avoidance (Tybur, Lieberman, Kurzban, & DeScioli, 2013), people (e.g., healthcare professionals, sanitation workers) can and do purposefully come into contact with disease-causing agents. Thus, mechanisms such as hormones may predispose individuals to behave in certain ways given a particular environment, but that does not mean biology is destiny.

The human brain and body consist of adaptations that evolved in ancestral environments, but to understand why they work, it helps to understand how they work. In addition to their more basic biological functions, hormones influence our behavior in many domains, including our developmental, survival-related, reproductive, social, and affective behaviors. Viewing human behavior through an evolutionary lens informs our understanding of the selection pressures faced by our species in our ancestral past. Incorporating hormonal mechanisms into that evolutionary perspective allows researchers to integrate proximate explanations into ultimate causal reasoning. More fundamentally, understanding both the proximate and ultimate causes of behavior helps us to understand why traits change over time.

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