Introduction

Evolutionary Endocrinology: Integrating Proximate Mechanisms, Ontogeny, and Evolved Function

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Natural selection leads to the evolution of strategies that tend to optimize the allocation of resources to the competing somatic and reproductive demands faced by any organism. This theoretical approach, known as life history theory, is useful for understanding unavoidable trade-offs in resource allocation and the resulting variation in phenotypes (e.g., physical attributes, expressed behaviors, the number and size of offspring, etc.) (Charnov 1993; Stearns 1992). In recent years, life history theory has begun to influence research on the proximate mechanisms mediating ontogenetic strategies. The endocrine system plays a central role in coordinating ontogenetic processes and modulating cross-talk among different functional domains (e.g., hypothalamic–pituitary–gonadal and hypothalamic–pituitary–adrenal axes). These processes are integral to the evolution of phenotypic plasticity (a key feature of adaptive responses) in developmental schedules and other life-history traits.

From conception to death, hormones orchestrate growth, differentiation, maintenance, reproduction, and senescence. Pheromones may help parents-to-be to attract each other (Kohl et al., 2001; Hays, 2003). Androgen steroids increase libido encouraging them to mate (Hutchinson, 1995; Stern and McClintock, 1998). Gonadotrophins and gonadal steroids mediate gamete maturation and release. Endometrial steroids intervene in the capacitation of spermatozoa and chemotaxis, luring them towards the oocyte. Recognition, binding, and fusion between sperm and oocyte, and the consequent activation of the egg are mediated by a multitude of hormones (Sun et al., 2005). After fertilization, but before development of the endocrine system, chemical signals help guide cleavage, cell differentiation, migration, and growth. Once developed, the endocrine system transmits information between cells regarding internal and external conditions, coordinating a intricate dance between the epigenome and the genome, steering the organism through its ontogenetic road map.

All organisms of a given species follow a similar ontogenetic road map. Yet, as environmental opportunities, restrictions, and challenges are heterogeneously distributed between and within populations, each individual passes life-history mileposts at its own speed and according to its own strategy. The endocrine system is an integral part of the mechanisms that provide organisms with the plasticity and dynamism that are crucial for adapting to their individual contexts. The challenges to be met are broad in type and temporal scales. Some challenges involve almost all biologic systems and take place over long periods of time, such as coordinating proportionate growth or undergoing sexual maturation. Others involve fewer tissues but need to be achieved within minutes or hours, such as adjusting oxygen or blood glucose levels. Some challenges are predictable, such as the sequences of night and day, or the succession of changes that follow conception. Other challenges, such as a tornado or an aneurysm, may be less predictable. Organisms rely on the endocrine system to regulate responses to these challenges as well as to inform ontogenetic strategies based on them. When and how much to grow at each life stage, when to begin sexual maturation, when to stop growing, the timing of the first reproductive venture, the length of inter-birth intervals, and when to stop reproducing are just a few examples of critical life history "decisions" mediated by hormonal pathways.

Ontogenetic strategies are modified through neuroendocrine cues that trigger changes in gene expression. Phenotypic plasticity is ultimately achieved by changes in DNA methylation patterns and chromatin remodeling. These epigenetic changes provide great dynamism to genotypic expression. Recent research developments suggest that while some epigenetic DNA methylation patterns are preserved through multiple generations, others are not as stable as originally believed and can change in response to postnatal environmental stimuli at different times within an individual's life span (McGowan et al., 2008; Szyf et al., 2008). The epigenome, informed by neuro-endocrine cues, is critical for fine tuning the expression of the more static genotype in response to the demands that the environment places on the phenotype.

Given the dynamic and complex nature of the endocrine system, a holistic approach to its study should consider not only the longitudinal variation of hormones across days, seasons, and life stages, but also its interactions with the nervous system and the epigenome. Anthropologists are in the privileged position necessary for conducting the multidisciplinary research that will help to realize this admittedly daunting research agenda. The collection of high quality longitudinal data achieved through an intimate knowledge of study participants allows for the description of normal ranges of endocrine function and its variability in response to environmental challenges in nonclinical populations exposed to a broad range of social, economic, and physical contexts.

The 2008 Plenary Session of the Human Biology Association explored recent advances in the study of endocrine pathways approached from this holistic perspective. The

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Received 10 February 2009; Accepted 11 February 2009
DOI 10.1002/ajhb.20924
Published online 14 April 2009 in Wiley InterScience (www.interscience.wiley.com).

Plenary focused on the ontogenetic strategies that individuals use to navigate the endogenous and exogenous challenges they encounter throughout their lifespan. Drawing on empirical evidence from field and laboratory studies, presenters discussed the physiological processes mediating the trade-offs among somatic demands (e.g., development, growth, repair, immunological defense, etc.) and reproductive efforts (e.g., mate attraction, intrasexual competition, parental investment, etc.) from conception to death. Papers in this issue of the AJHB elaborate on these themes.

The Raymond Pearl Memorial speaker, Donna Baird, proposes a set of hypotheses to explain one of the most intriguing phenomena in human biology: the high levels of postimplantation first trimester pregnancy loss (PL) in our species. What proportion of those losses results from a deterioration of the maternal environment or from her nutritional, health or psychological condition, and what proportion is the result of poor quality of the offspring? Baird argues that failure of the corpus luteum to produce adequate levels of progesterone would be associated with maternal causes and that low or faltering hCG levels, a delay in the onset of progesterone production by the placenta, or a delay in the blocking of the spiral arteries to maintain a hypoxic environment for trophoblast development would be associated with poor fetal quality. Based on observations from the classic NC Early Pregnancy Study, the author proposes that the observed pattern of pregnancy losses is likely to be largely explained by maternal recognition and early elimination of suboptimal conceptuses rather than by a deterioration of maternal condition. Baird suggests that the high rate of late-pregnancy maternal morbidity and mortality may be the primary selective pressure behind the evolution of the proposed maternal screening mechanisms. Suzette Tardif and Corinna Ross examine the regulation of ovarian functioning, gestation, and development in callitrichids. They incorporate both life-history models and empirical evidence of energetic determinants into their evaluation. The authors use comparative data to discuss "unique" aspects of human reproduction such as the allomaternal provision of complementary food to weaning infants and its effect on female reproductive physiology and output.

Toni Ziegler and her colleagues examine neuro-endocrine mechanisms mediating male's attachment to mates and offspring in marmosets. According to their results males in this species present a plastic hormonal response to socially relevant odor cues. Their testosterone levels increase when exposed to the scent of the periovulatory female and decrease after exposure to the scent of their infants. This endocrine flexibility allows males to capture reproductive opportunities while also investing in paternal care, increasing the likelihood of their infant's survival. Using the common marmoset as a model, Julienne Rutherford explores the role of placental structure and function in the exchange of information that takes place between mother and fetus in terms of resource availability. Rutherford's evidence suggests that in marmosets litter size may affect placental architecture, IGF II production, fetal quality, and developmental trajectories. She argues that fetuses from larger litters may adjust their development to maintain pregnancy viable but that those adjustments may lead to poorer postnatal health.

Patricia Whitten and Trudy Turner discuss trade-offs between growth and reproduction in vervet monkeys in environments with different levels of resource availability and adult mortality. They assess the onset and cessation of growth in relation to sexual maturation in four populations through morphometric and hormonal measures and find interesting differences in the effects of resource availability, nutritional status, and adult mortality risk between males and females. After discussing their findings in the context of both the Adult Mortality and the Ecological Risk Aversion Models, they suggest new models and urge more in-depth research of the proximate mechanisms mediating growth-reproduction trade-offs, especially the biphasic actions of estradiol and its receptors. Trade-offs in adult human males in response to environmental challenges have often seemed more subtle and complex than those in human females (Bribiescus, 2001). Virginia Vitzthum and her colleagues present evidence of seasonal variation in testosterone (T) levels and circadian rhythms in rural Bolivian men. During late winter, when conditions in these communities are particularly severe, T fails to rise during the night to the level observed during other seasons, and over the course of a late winter day, mean T levels do not decline as they do during other seasons. Furthermore, regardless of season, there is substantial variation between men in circadian rhythms. The possibility that substantial variation in diurnality may be more common than previously recognized has clear implications in both clinical and basic research.

Mark Flinn presents data on the developmental stability of cortisol profiles among children from his 20-year study of a rural community on the island nation of Dominica. Results indicate that exposure to traumatic stressors during development can have variable effects on the HPA stress system. These findings suggest that links between early stress and subsequent pathology are complex and may involve adaptive neural remodeling. Carol Worthman presents a thorough review of theories on emotional regulation and integrates them as she explores their association with life history theory. She examines the influence that exogenous stimuli have on the development of emotion regulation, social cognition and behavior, and their dynamic inter-connection to the genetic, epigenetic, and endocrine mechanisms that respond to those stimuli. The author highlights the importance of understanding that the adaptive value of given alleles is context specific that gene–environment interactions vary between and within populations and epigenetic mechanisms provide dynamism to those interactions. To finalize, Worthman analyzes how those gene environment interactions affect neurologic and cognitive ontogenesis, the link between those interactions and the origin of health differences between individuals and populations.

Both the presentations in the Plenary Session and the contributions in this issue demonstrate the enormous and rewarding tasks that lay ahead. The integration of proximate mechanisms, ontogeny, and evolved function will advance our understanding of the endocrine system, help us explain its range of variation and uncover the ecological and evolutionary factors this account for this variation.

ACKNOWLEDGMENTS

The authors thank Peter Ellison for the opportunity to publish these papers in the American Journal of Human

Biology and for his encouragement and flexibility with the schedule; the members of the HBA Executive Committee, who provided the opportunity and assisted in the development of the plenary; and especially those who participated, often crossing disciplinary boundaries and helping us strive towards the multidisciplinary approach needed to explore human biology from multiple perspectives.

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