Hormones and Behavior 84 (2016) 97–110

Contents lists available at ScienceDirect

Hormones and Behavior

journal homepage: www.elsevier.com/locate/yhbeh

Review article

Theoretical frameworks for human behavioral endocrinology

James R. Roney

Department of Psychological and Brain Sciences, University of California, Santa Barbara, CA 93106-9660, United States

ARTICLE INFO

Article history:
Received 25 October 2015
Revised 5 June 2016
Accepted 7 June 2016
Available online 16 June 2016

Keywords:
Human endocrinology
Testosterone
Oxytocin
Estradiol
Progesterone

ABSTRACT

How can we best discover the ultimate, evolved functions of endocrine signals within the field of human behavioral endocrinology? Two related premises will guide my proposed answer. First, hormones typically have multiple, simultaneous effects distributed throughout the brain and body, such that in an abstract sense their prototypical function is the coordination of diverse outcomes. Second, coordinated output effects are often evolved, functional responses to specific eliciting conditions that cause increases or decreases in the relevant hormones. If we accept these premises, then a natural way to study hormones is to hypothesize and test how multiple eliciting conditions are mapped into coordinated output effects via hormonal signals. I will call these input–output mappings "theoretical frameworks." As examples, partial theoretical frameworks for gonadal hormones will be proposed, focusing on the signaling roles of testosterone in men and on estradiol and progesterone in women. Recent research on oxytocin in humans will also be considered as an example in which application of the theoretical framework approach could be especially helpful in making functional sense of the diverse array of findings associated with this hormone. The theoretical framework approach is not especially common in the current literature, with many theories having eschewed explicit consideration of input–output mappings in favor of parsimony-based arguments that attempt to find the one main thing that a hormone does with respect to psychology or behavior. I will argue that these parsimony-based models have many shortcomings, and conclude that the construction and testing of theoretical frameworks provides a better means of discovering the evolved functions of human endocrine signals.

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E-mail address: roney@psych.ucsb.edu.

http://dx.doi.org/10.1016/j.yhbeh.2016.06.004
0018-506X/

1. Introduction

I once asked a ‘why’ question of a speaker who had just given a fascinating talk on human testosterone responses to competitive interactions. The speaker had reviewed evidence that testosterone may increase after status-promoting victories, which might then promote further status competition. The crux of my question was this: given that testosterone is known to have many effects throughout the brain and body—some of which, like immunosuppression, may be harmful—why use testosterone in particular as a signal that encourages further competition after competitive victories? Why not avoid the costs of testosterone by instead producing the same responses to social events via neurotransmitters within the relevant neural networks? The speaker paused, and then replied: “That, as they say, is a good question.”

In sketching possible answers to such why questions, it is likely important that hormones, unlike most neurotransmitters, are often released into the general circulation where they usually have effects on multiple downstream targets. Given this, hormones may be used as signals primarily when multiple outcomes are being produced in a coordinated way. Indeed, as described in the section below, coordination may be the prototypical function[1] of endocrine signals. If we accept this premise, then understanding the functions of hormones becomes an exercise in mapping, for each hormone, the coordinated outputs that it produces in response to the eliciting circumstances associated with release of the hormone.

Let us call the mapping between eliciting conditions and coordinated outputs a “theoretical framework” for a given hormone. Theoretical frameworks will essentially be lists of input conditions associated with increases or decreases in a hormone, combined with lists of output effects associated with such increases or decreases. Insofar as output effects appear to be functional responses to specific elements of the input conditions, a core functional logic for a given hormonal signal may emerge from the theoretical framework. That core logic may then facilitate interpretation of new findings, and may also generate novel hypotheses regarding linkages between variables that should co-occur given the functional logic of the theoretical framework. In what follows, I will first elaborate briefly on the idea of hormones as coordinators, before then proceeding to apply the theoretical framework approach to example endocrine signals that are being actively studied in human field and behavioral endocrinology.

2. Hormones as coordinators

The idea that the prototypical function of hormones is coordination is not an original one, and many scholars have previously emphasized this position. Beach (1974), for instance, described the endocrine system as “an integrated, finely tuned coordinating mechanism sensitive to changes in both the internal and external environment and adapted to promotion of the physiological and behavioral effectiveness of the total organism” (p. 15). Many textbooks on endocrinology open with descriptions of coordinating functions. Adkins-Regan (2005) wrote: “In general, hormones are coordinators: of reproduction, of suites of physiological and behavioral components, of different parts of the brain with body… They help adjust behavior to circumstances and contexts: physical, social, and developmental” (p. 3). Likewise, Ellison (2001) characterized endocrine systems as follows:

> …endocrine glands release specific molecules—hormones—into our general circulation. They are carried throughout the body by the circulatory system, potentially reaching a large majority of our cells. …This system is especially effective in communicating a given signal to lots of target cells, which may be located in many different places. The responses of those targets can be quite different as well, but they will be *coordinated* by their relationship to the common signal. … The endocrine system is the system that the body uses to achieve *integrated* responses among various cells, tissues, and systems, integration that is necessary to many critical biological processes, such as growth, metabolism, and reproduction (p. 13, emphasis added).

Central to the notion of coordination in the above quotes is that the multiple, diverse effects of hormones are *functional* responses to the “circumstances and contexts” associated with changes in hormone production. As a concrete example of functional coordination, consider the multiple effects of elevated circulating androgens in males of many seasonally breeding species during the breeding season (for reviews, see Andersson, 1994; Daly and Wilson, 1983; Folstad and Karter, 1992; Ketterson and Nolan, 1992). Androgens promote the growth of morphological ornaments and armaments involved in inter- or intrasexual competition, respectively, but often obtain energy for such growth in part via inhibitory effects of androgens on fat storage and immune function. These diverse effects in the soma occur simultaneous to androgen effects on brain structures that promote increased behavioral aggressiveness and sexual motivation, often concomitant with reduced time spent foraging or resting. More subtle physiological effects accompany these, such as changes in metabolic rate, sperm production, and levels of hemoglobin (e.g., Evans, 2010; Ketterson and Nolan, 1992). Here, a core functional logic to this coordination emerges, as all of the diverse effects of androgens align to promote effective mate competition precisely when the presence of fecund females means that such competition can promote reproductive success; the fall in androgens during the nonbreeding season then contributes to an alternative alignment of effects that address biological problems other than immediate mate competition. These diverse effects of androgens exemplify nicely Beach's point in the above quote regarding “promotion of the physiological and behavioral effectiveness of the total organism”—the suite of effects considered together promotes mate competition and reproductive success, even if individual effects (e.g., inhibition of some immune responses) may appear harmful.

The above example demonstrates the partial construction of a theoretical framework linking coordinated output responses to specific eliciting conditions in such a way that a basic functional logic of particular endocrine signals begins to emerge. The goal of the rest of the article is to apply this theoretical framework approach to example lines of research in human behavioral endocrinology.

3. Theoretical frameworks in human behavioral endocrinology

As defined earlier, theoretical frameworks map the eliciting conditions that affect hormone release to the output effects caused by changes in hormones. The phrase “eliciting conditions” is meant to be construed very broadly. Thus, it includes both immediate external triggers of hormone release, such as exposure to potential mates, but also internal signals representing dynamic variables such as energy balance. A variable like energy balance may ultimately be linked to ecological variables related to food availability, but may be indexed by internal endocrine messengers (e.g., insulin or leptin) that in turn act as inputs

[1] Throughout the article, function is used as in evolutionary biology: a phenotypic trait is functional if its effects promoted biological fitness on average during the evolution of the trait, and if those effects help explain the trait's origin and maintenance (see Tooby and Cosmides, 1992; Wakefield, 2016; Williams, 1966). On this definition, a trait may be functional even if it produces harmful effects in modern environments, as long as it promoted reproductive success in the environments in which it evolved. A hormone that reduced thresholds for physical aggression may have promoted reproductive success when released in specific circumstances in ancestral environments, for instance, even if those same effects would produce maladaptive outcomes in modern societies in which violence is legally proscribed. An overarching (but reasonable) assumption is that at least some of the signaling properties of human hormones evolved by natural selection because the specific effects of those signals promoted greater lifetime reproductive success relative to alternative phenotypes. Thus, although some properties of hormones may have resulted from selectively neutral evolutionary processes (such as genetic drift), or be by-products of other components of the phenotype, other properties should be functional, and articulating those functions is necessary to achieve a basic science of human behavioral endocrinology.