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Hormonal Mechanisms in Acoustic Communication

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1. Introduction

Hormones have profound effects on behavior, bridging the external and internal environments. Certain external events, such as changes in photoperiod or the social environment, are perceived by an animal and are transduced into adaptive behavioral changes via effects on hormone secretion. Hormones modulate behavior by altering cellular physiology in a global and coordinated fashion. In this chapter, we will review how hormones modulate behaviors involved in acoustic communication.

Social communication is integral to animal survival and reproduction. In many species, communication takes the form of vocal production and acoustic perception. In acoustic communication, endocrine state is an important determinant of what signal is transmitted and how it is perceived. Gonadal steroids, for example, have profound effects both on male courtship vocalizations and on the responses of females to male calls. Our aim in this chapter is to examine the physiological mechanisms whereby hormones affect acoustic signaling and perception. Most of the information available concentrates on a few species: birds, frogs, rodents, and fish. Although it is phylogenetically narrow in scope, we are beginning to form an in-depth picture of some aspects of endocrine modulation, even at the molecular level.

Hormonal influences on acoustic communication can be studied at a variety of levels. The first and critical step is to identify which, if any, hormones are involved in vocal production and acoustic perception. Establishing correlations between signal production/perception and plasma levels of hormones, and demonstration of the causal relation between a particular hormone and a communicative behavior, is required before the physiological substrates can be further studied. The next step is to identify the neural and somatic substrates for the production and perception of acoustic signals. We can then determine whether the hormone exerts its effects directly by binding to the cells that mediate the behavior and, if so, how. Current technology permits us to examine a large number of

dependent variables (i.e., molecular, cellular, or systemic properties) that can change in response to changes in hormone levels. Determining which of these physiological changes is critically responsible for behavioral change is a steep challenge. Problems include identification of all of the neural and somatic cells involved in vocal production and perception and the difficulty of relating hormonally induced changes at one level of biological organization to another, higher level of organization (e.g., cellular to systems, systems to behavioral levels). Some vocal communication systems, those of frogs for example, appear less complex in this regard, especially in terms of vocal production. In this chapter, we will first review the cellular changes induced by different types of hormones and then extend our study to the endocrine basis of behavior. Abbreviations used throughout the text are listed in Table 6.1.

2. The Biological Effect of Hormones

2.1. Source of Hormones

Hormones are chemical messengers released from cells in a variety of secretory glands and the central nervous system. The types of hormones discussed in this chapter are restricted to gonadal steroids and a few neurohypophysial hormones released from the pituitary gland (Fig. 6.1). Gonadal steroids such as androgens and estrogens are primarily released from the male testis and female ovary, respectively (Fig. 6.1A). The synthesis and release of these gonadal steroids are regulated by the plasma levels of luetenizing hormone (LH) released from the adenohypophysis (anterior pituitary; Fig. 6.1B). LH synthesis and secretion, in turn, are regulated by gonadotrophin-releasing hormones (GnRH) released from the hypothalamus. Thus, the neuronal activity of GnRH-synthesizing neurons in the hypothalamus determines the levels of LH released from the pituitary and eventually controls plasma levels of gonadal steroids.

Neuropeptides such as arginine vasopressin (AVP) or its nonmammalian homolog, arginine vasotocin (AVT in birds, reptiles, amphibians, and fishes), and oxytocin (OXT) are released from the neurohypophysis of the pituitary gland (posterior pituitary; Fig. 6.1C). These hormones are synthesized by neurons whose cell bodies lie in two hypothalamic nuclei—the supraoptic and the paraventricular—and released from the axon terminals of these cells in the neurohypophysis (Fig. 6.1C). The primary function of systemic AVT/AVP is to regulate osmolarity and blood pressure, and that of OXT is to regulate milk release and uterine contraction. Recent studies reveal that OXT- and AVT/AVP-synthesizing neurons project to a variety of brain regions aside from the pituitary. Neurohormones secreted directly in the brain may affect neuronal function to modify behavior in addition to their more classical, systemic effects.

TABLE 6.1. Abbreviations used throughout the text.

11-ketoT	11-ketotestosterone
AChE	acetylcholinesterase
APOA	anterior preoptic area
AVP	arginine vasopressine
AVT	arginine vasotocin
cAMP	cyclic adenosine monophosphate
CAT	choline acetyltransferase
CNS	central nervous system
DBD	DNA-binding domain
DHT	dihydrotestosterone
DIC	diacylglycerol
DLM	medial dorsolateral nucleus of the thalamus
DTAM	pretrigeminal nucleus of the dorsal tegmental area of the medulla
E_2	estradiol
GnRH	gonadotropin-releasing hormone
G-protein	guanine nucleotide binding proteins
HRE	hormone response element
HVc	higher vocal center
IP	inositol phospholipid
IP3	inositol triphosphate
LBD	ligand binding domain
LH	leutenizing hormone
LM	myosin heavy-chain isoform
MAN	magnocellular nucleus
MPOA	medial preoptic area
n.IX-X	laryngeal motor nucleus
nXIIts	tracheosyringeal portion of hypoglossal nerve nucleus
OXT	oxytocin
P	progesterone
PG	prostaglandin
PGE_2	prostaglandin E_2
PIP2	phosphatidyl inositol phosphate
PKC	protein kinase C
PLC	phospholipase C
POA	preoptic area
RA	robustus archistriatalis
SDA	sexually dimorphic area
SDApc	sexually dimorphic area pars compacta
T	testosterone
TS	torus semicircularis
VH	ventral hypothalamus

2.2. *Cellular Response to Hormones*

Secreted hormones can be transported by the bloodstream throughout the body and modify the biological function of target cells distant from the site of secretion. Target cells express receptors that have a selective affinity for a particular hormone. The receptor–hormone complex in target cells triggers a cascade of intracellular biochemical reactions.