Springer Handbook of Auditory Research

Andrew H. Bass
Joseph A. Sisneros
Arthur N. Popper
Richard R. Fay *Editors*

# Hearing and Hormones

Springer

# Springer Handbook of Auditory Research

**Series Editors**

Richard R. Fay
Marine Biological Laboratory
Woods Hole, MA
USA

Arthur N. Popper
Department of Biology
University of Maryland
College Park, MD
USA

More information about this series at http://www.springer.com/series/2506

Andrew H. Bass • Joseph A. Sisneros
Arthur N. Popper • Richard R. Fay
Editors

# Hearing and Hormones

Springer

*Editors*
Andrew H. Bass
Department of Neurobiology and Behavior
Cornell University
Ithaca, NY, USA

Joseph A. Sisneros
Department of Psychology
University of Washington
Seattle, WA, USA

Arthur N. Popper
Department of Biology
University of Maryland
College Park, MD, USA

Richard R. Fay
Marine Biological Laboratory
Woods Hole, MA, USA

ISSN 0947-2657 ISSN 2197-1897 (electronic)
Springer Handbook of Auditory Research
ISBN 978-3-319-26595-7 ISBN 978-3-319-26597-1 (eBook)
DOI 10.1007/978-3-319-26597-1

Library of Congress Control Number: 2016933775

Springer Cham Heidelberg New York Dordrecht London


Printed on acid-free paper

Springer International Publishing AG Switzerland is part of Springer Science+Business Media (www.springer.com)

*We dedicate this volume to two comparative neuroanatomists extraordinaire:*
*Harvey Karten and R. Glenn Northcutt.*
*The studies of the nervous system of nonmammalian vertebrates generated by these two individuals for over four decades have provided, and continue to provide, essential guideposts to all investigators in the field of comparative vertebrate neurobiology. Their insights and unbridled passion for scientific inquiry have inspired many and have made an indelible imprint on generations of researchers. A heartfelt thanks to them both!*

# Series Preface

The following preface is the one that we published in Volume 1 of the *Springer Handbook of Auditory Research* back in 1992. As anyone reading the original preface, or the many users of the series, will note, we have far exceeded our original expectation of eight volumes. Indeed, with books published to date and those in the pipeline, we are now set for over 60 volumes in *SHAR*, and we are still open to new and exciting ideas for additional books.

We are very proud that there seems to be consensus, at least among our friends and colleagues, that *SHAR* has become an important and influential part of the auditory literature. While we have worked hard to develop and maintain the quality and value of *SHAR*, the real value of the books is very much because of the numerous authors who have given their time to write outstanding chapters and to our many coeditors who have provided the intellectual leadership to the individual volumes. We have worked with a remarkable and wonderful group of people, many of whom have become great personal friends of both of us. We also continue to work with a spectacular group of editors at Springer. Indeed, several of our past editors have moved on in the publishing world to become senior executives. To our delight, this includes the current president of Springer US, Dr. William Curtis.

But the truth is that the series would and could not be possible without the support of our families, and we want to take this opportunity to dedicate all of the *SHAR* books, past and future, to them. Our wives, Catherine Fay and Helen Popper, and our children, Michelle Popper Levit, Melissa Popper Levinsohn, Christian Fay, and Amanda Fay, have been immensely patient as we developed and worked on this series. We thank them and state, without doubt, that this series could not have happened without them. We also dedicate the future of *SHAR* to our next generation of (potential) auditory researchers—our grandchildren—Ethan and Sophie Levinsohn, Emma Levit, and Nathaniel, Evan, and Stella Fay.

## Preface 1992

The *Springer Handbook of Auditory Research* presents a series of comprehensive and synthetic reviews of the fundamental topics in modern auditory research. The volumes are aimed at all individuals with interests in hearing research including advanced graduate students, postdoctoral researchers, and clinical investigators. The volumes are intended to introduce new investigators to important aspects of hearing science and to help established investigators to better understand the fundamental theories and data in fields of hearing that they may not normally follow closely.

Each volume presents a particular topic comprehensively, and each serves as a synthetic overview and guide to the literature. As such, the chapters present neither exhaustive data reviews nor original research that has not yet appeared in peer-reviewed journals. The volumes focus on topics that have developed a solid data and conceptual foundation rather than on those for which a literature is only beginning to develop. New research areas will be covered on a timely basis in the series as they begin to mature.

Each volume in the series consists of a few substantial chapters on a particular topic. In some cases, the topics will be ones of traditional interest for which there is a substantial body of data and theory, such as auditory neuroanatomy (Vol. 1) and neurophysiology (Vol. 2). Other volumes in the series deal with topics that have begun to mature more recently, such as development, plasticity, and computational models of neural processing. In many cases, the series editors are joined by a coeditor having special expertise in the topic of the volume.

Richard R. Fay, Woods Hole, MA, USA
Arthur N. Popper, College Park, MD, USA

# Volume Preface

A fundamental goal of neuroscience is to understand how hormones modulate neural circuits and behavior. For example, steroids such as estrogens and androgens are well-known regulators of vocal motor behaviors used during social acoustic communication. Recent studies have shown that these same hormones can also greatly influence the reception of social acoustic signals, leading to the more efficient exchange of acoustic information. Understanding how hormones modulate auditory function has far-reaching implications for advancing our knowledge in the basic biomedical sciences and for understanding the evolution of acoustic communication systems.

The primary goal of this book is to review the growing literature that is consistent with the hypothesis that hormones can regulate auditory physiology and the perception of acoustic signals across a broad range of animal taxa, including humans. Chapter 1, by Andrew Bass, provides a historic overview of how we have learned about hormones and hearing, and he provides a guide to the rest of the chapters. In Chap. 2, Paul Forlano, Karen Maruska, Joseph Sisneros, and Andrew Bass review hearing-hormone relationships for teleosts, with sonic (or vocal) fishes as the focal point of research. Amphibians are the focus of Chap. 3 in which Walter Wilczynski and Sabrina Burmeister discuss the important influence of conspecific calling on circulating steroid levels and how changing steroid levels may influence the response properties of central auditory neurons.

Chapter 4 by Melissa Caras and Luke Remage-Healey takes the volume to studies of birds and focuses on how estrogen modulates auditory processing in both the peripheral and central auditory systems of songbirds. This is followed by Chap. 5, in which Donna Maney and Carlos Rodriguez-Saltos bring together many of the themes developed in Chaps. 2–4 and expand on estrogen mechanisms in songbirds with a perspective that draws us into the realm of social cognition with an emphasis on the *incentive salience* of song.

Then, in Chap. 6, Kelly Chong and Robert Liu return to a neurophysiological theme (as in Chaps. 2–4) but in this case with a focus on auditory perception and the learning and memory of vocal signals. In Chap. 7, Robert D. Frisina and D. Robert Frisina provide a timely review of experimental investigations of hormones and hearing in humans, much of which has focused (for good reason) on one steroid, estrogen. Finally, in Chap. 8, Douglas Forrest and Lily Ng address early developmental events in humans that are strongly shaped by hormone actions at a molecular and genetic level.

This volume in the *Springer Handbook of Auditory Research*, like so many others, benefits from volumes and chapters that have come earlier in the series. Indeed, the broad phylogenetic approach of this volume complements earlier volumes in the *SHAR* series: *Comparative Hearing: Fish and Amphibians* (Vol. 11, 1999, edited by Fay and Popper), *Comparative Hearing: Birds and Reptiles* (Vol. 13, 2001, edited by Dooling, Fay, and Popper), and *Evolution of the Vertebrate Auditory System* (Vol. 22, 2004, edited by Manley, Popper, and Fay). Given the subject matter, a number of chapters have an added focus on vocal communication. In this regard, the reviews provided in this volume further complement other volumes in this series: *Acoustic Communication* (Vol. 16, 2003, edited by Simmons, Popper, and Fay), *Hearing and Sound Communication in Amphibians* (Vol. 28, 2007, edited by Narins, Feng, Fay, and Popper), and *Fish Bioacoustics* (Vol. 32, 2008, edited by Webb, Popper, and Fay).

Andrew H. Bass, Ithaca, NY, USA<br>
Joseph A. Sisneros, Seattle, WA, USA<br>
Richard R. Fay, Woods Hole, MA, USA<br>
Arthur N. Popper, College Park, MD, USA

# Contents

# Contributors

**Andrew H. Bass** Department of Neurobiology and Behavior, Cornell University, Ithaca, NY, USA

**Sabrina S. Burmeister** Biology Department, University of North Carolina, Chapel Hill, NC, USA

**Melissa L. Caras** Center for Neural Science, New York University, New York, NY, USA

**Kelly K. Chong** Wallace H. Coulter Department of Biomedical Engineering, Georgia Institute of Technology and Emory University, Atlanta, GA, USA

**Paul M. Forlano** Department of Biology, Brooklyn College and Graduate Center, City University of New York, Brooklyn, NY, USA

**Douglas Forrest** Laboratory of Endocrinology and Receptor Biology, NIDDK, National Institutes of Health, Bethesda, MD, USA

**D. Robert Frisina** Department of Chemical & Biomedical Engineering and Communication Sciences & Disorders, Global Center for Hearing & Speech Research, University of South Florida, Tampa, FL, USA

**Robert D. Frisina** Department of Chemical & Biomedical Engineering and Communication Sciences & Disorders, Global Center for Hearing & Speech Research, University of South Florida, Tampa, FL, USA

**Robert C. Liu** Department of Biology, Emory University, Atlanta, GA, USA

**Donna L. Maney** Department of Psychology, Emory University, Atlanta, GA, USA

**Karen P. Maruska** Department of Biological Sciences, Louisiana State University, Baton Rouge, LA, USA

**Lily Ng** Laboratory of Endocrinology and Receptor Biology, NIDDK, National Institutes of Health, Bethesda, MD, USA

**Luke Remage-Healey** Department of Psychological and Brain Sciences, University of Massachusetts Amherst, Amherst, MA, USA

**Carlos A. Rodriguez-Saltos** Department of Psychology, Emory University, Atlanta, GA, USA

**Joseph A. Sisneros** Departments of Psychology and Biology and Virginia Merrill Bloedel Hearing Research, University of Washington, Seattle, WA, USA

**Walter Wilczynski** Neuroscience Institute, Georgia State University, Atlanta, GA, USA

# Chapter 1
# Hearing and Hormones: Paying Homage to the Comparative Approach

**Andrew H. Bass**

**Abstract** This volume on *Hearing and Hormones* for the Springer Handbook of Auditory Research (SHAR) series provides a broad comparative overview of hormonal influences on the behavioral and neural mechanisms of hearing in vertebrates. The chapters provide coverage for each of the major lineages of vocal vertebrates that have been foci of investigations of hearing and hormones, namely teleost fishes, amphibians, birds, and mammals, including humans. As reviewed in this chapter, a contemporary approach to asking how hormones affect the sense of hearing was triggered, in part, by the introduction of autoradiographic methods to map the location and abundance of steroid concentrating cells in the brain of fishes, amphibians, reptiles, birds, and mammals. Since that time, an armamentarium of other investigative tools ranging from underwater acoustics to single neuron recordings and in situ hybridization to identify patterns of gene expression have complemented these earlier methods to elucidate mechanisms that explain how hormones and other neuromodulators affect auditory processing in both the sensory periphery and the central nervous system. Comparative investigations of hearing and hormones have been, and will continue to be, enriched by researchers from the fields of animal bioacoustics, human audiology, neuroethology, behavioral and molecular neuroendocrinology, and genetics.

**Keywords** Androgen • Auditory • Autoradiography • Behavioral endocrinology • Estrogen • Genetics • Neuroethology • Song • Steroids • Vocalization

## 1.1 Introduction

A major goal of this volume on *Hearing and Hormones* for the Springer Handbook of Auditory Research (SHAR) series is to capture the richness of the comparative strategy in asking questions about the existence of biological traits, in this case hormonal influences on the sense of hearing. Toward this aim, the editors invited reviews from investigators who could offer perspectives on this topic for several of

A.H. Bass (✉)
Department of Neurobiology and Behavior, Cornell University, Ithaca, NY 14853, USA
e-mail: ahb3@cornell.edu

 
A.H. Bass et al. (eds.), *Hearing and Hormones*, Springer Handbook of Auditory Research 57, DOI 10.1007/978-3-319-26597-1_1

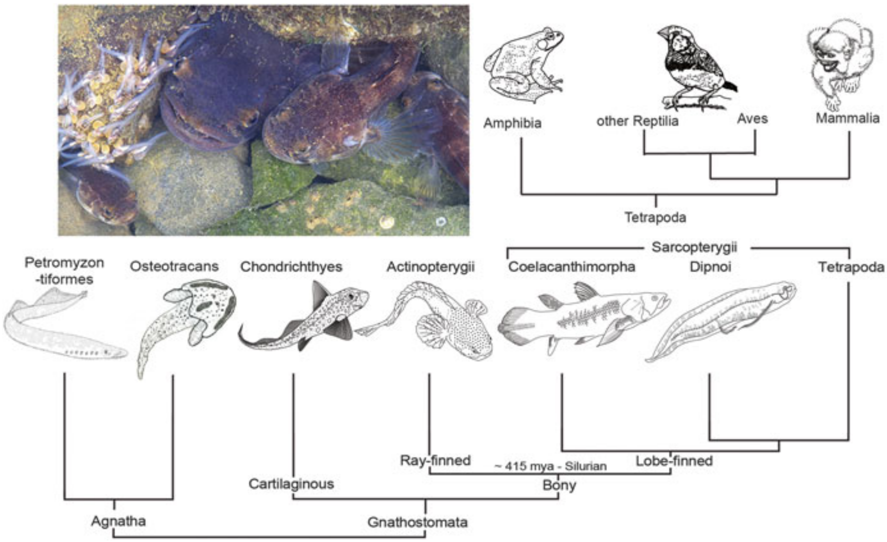


**Fig. 1.1** Cladogram of vertebrates illustrating the relationships among the lineages that include focal species in studies that are reviewed in this volume. Also shown is a photograph of a nest site in the intertidal zone along the northern California coast that is occupied by the plainfin midshipman fish, *Porichthys notatus*, a highly vocal teleost species that is one of the model systems used to investigate hormonal influences on hearing. As discussed in Chap. 2, midshipman fish have two male reproductive morphs: type I and type II males. Type I males build and guard nests, and produce long duration, multi-harmonic advertisement calls (known as hums) to attract females to their nest. Type II males neither build nests nor acoustically court females; instead they 'sneak spawn'. Shown here is a nest containing (*left* to *right*) a type II male, a type I male, a female and a type II male. Also shown to the far left are newly hatched larvae that are attached to a small rock inside the nest by an adhesive disk at the base of the yolk sac. Cladogram adapted from Bass and Chagnaud (2012)

the major lineages of jawed vertebrates (gnathostomes), namely ray-finned fishes (actinopterygians), amphibians, birds, and mammals (Fig. 1.1). Several of the chapters in this volume (Chaps. 2–6) provide an added focus on vocal communication in the context of social and reproductive behaviors. Given the salient role of coupling between auditory sensitivity and the spectral content of vocalizations in reproductive contexts (see Sect. 1.2), it is no surprise that sonic vertebrates often provide model systems for investigators interested in hormonal influences on hearing.

## 1.2 Turning Points in Hormonal Investigations: 1970s and 1980s

One hormonal theme throughout nearly all of the chapters in this book is the influence of steroids on hearing. The origin of such studies, which aim toward linking hormone actions to neural mechanisms, can be traced to 1849 when Arnold Berthold

**Fig. 1.2** Daguerrotype of Arnold Berthold by FE Ritmüller, courtesy of the National Library of Medicine

(Fig. 1.2) showed that malelike sexual behaviors in chickens, including crowing, could be restored in males castrated prior to reaching adulthood if one of their testes was reimplanted into their abdomen or if they received a testis from another male (Fig. 1.3) (Berthold 1849). About 100 years later, the use of a variety of methods, ranging from systemic elevations of steroids to lesions or steroid implants targeting specific brain regions in a variety of mammalian species, provided more direct evidence of the influence of the brain and steroids on reproductive mechanisms (for more complete reviews see Kelley and Pfaff 1978; Nelson 2011).

A turning point in neuroscience for investigations of hormonal mechanisms of behavior was the introduction of autoradiography in the 1970s and 1980s to map the location of populations of steroid-concentrating neurons, which are targets of steroid actions, in discrete regions of the central nervous system of mammals, including primates (Fig. 1.4) (Pfaff 1968; Pfaff and Keiner 1973; for more complete reviews see McEwen 1976; Morrell et al. 1978). This methodology opened a gateway for comparative studies among non-mammalian vertebrates (see Fig. 1.1 for phylogenetic relationships) that dovetailed especially well with new insights into forebrain organization that were emerging at that time for bony (Nieuwenhuys 1969) and cartilaginous (Ebbesson and Schroeder 1970) fishes, amphibians and reptiles (Northcutt 1966, 1969, 1981; Hall and Ebner 1970), and birds (Karten 1969) (for a more complete review see Northcutt 1981). This concurrence provided fertile ground for comparative brain studies using steroid autoradiography. As in mammals, autoradiographic studies showed estrogen- and androgen-concentrating neurons in

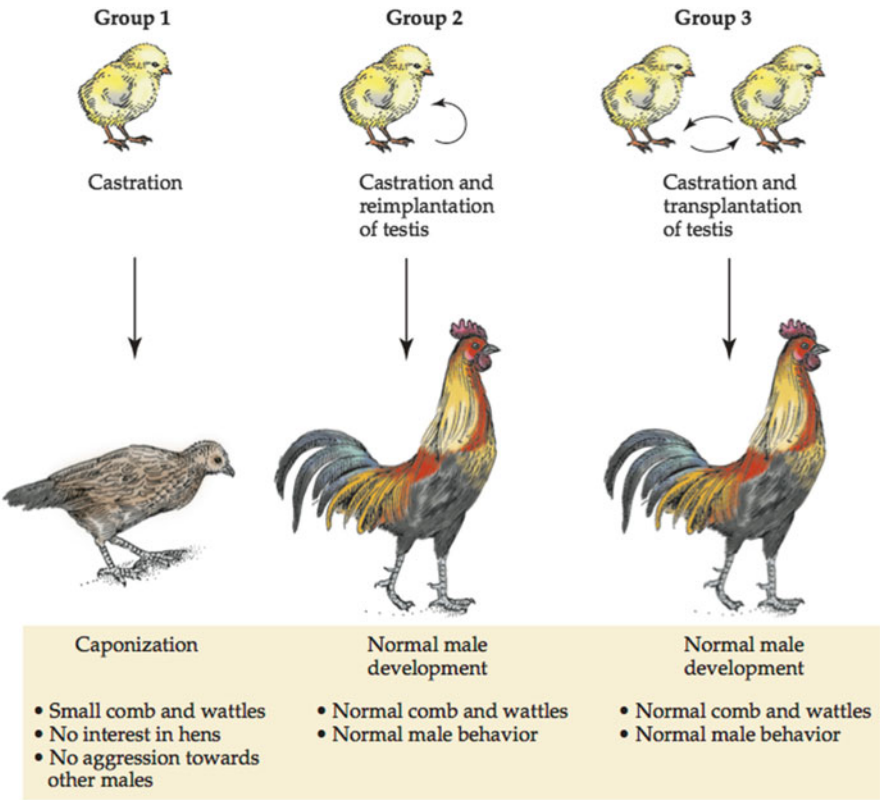


**Fig. 1.3** Schematic portraying experiments completed by Berthold (1849) using three groups of castrated chickens. Each experimental group included two males; see description at the bottom of each group depicted here for a summary of each group's outward appearance and behavior. Immature male chickens castrated prior to reaching adulthood are known as capons and do not display either a normal adult male appearance or sexual behaviors that are characteristic of intact adult male roosters (Group 1). Castrated male chicks displayed male-like behaviors following re-implantation of one of their own testes (Group 2) or transplantation of the testis from each male of a pair into the other male (Group 3) (Berthold 1849). Reproduced with permission from Nelson (2011)

the brains of representative species of amphibians, reptiles, birds, and fishes (Morrell et al. 1978; Morrell and Pfaff 1978). In particular, these studies, which largely came from the laboratory of Donald Pfaff and initially were focused on elucidating the behavioral control of reproduction, revealed surprisingly conserved patterns of steroid binding for the forebrain (preoptic area and hypothalamus) and the midbrain (central grey) as major hubs for reproductive behavior. All of the chapters in this volume benefited from these groundbreaking studies in comparative and evolutionary neurobiology.

Especially relevant to the vocal-auditory theme of this SHAR volume were reports during this time period of steroid-concentrating neurons in the central nervous system of songbirds, frogs, and lizards. Arthur Arnold, Fernando Nottebohm,

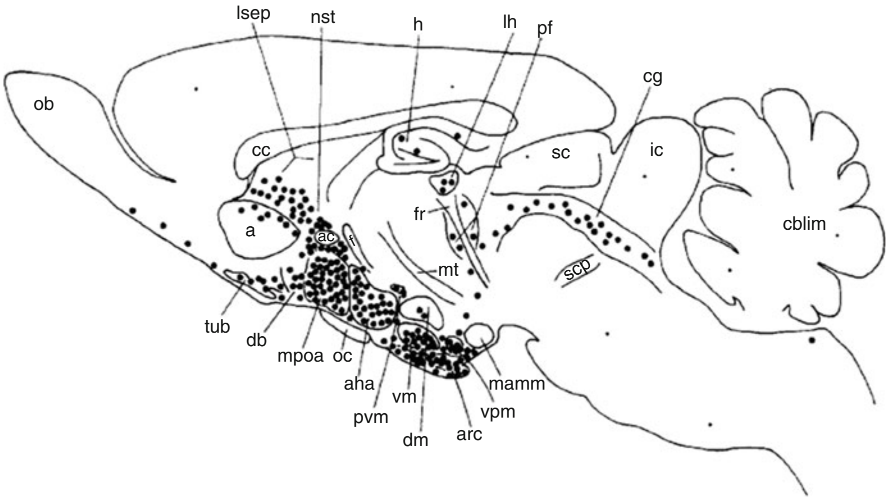


**Fig. 1.4** Sagittal view of a female rat brain showing the location of estrogen (E) concentrating neurons identified using steroid autoradiography. Dense clusters of E-neurons are found throughout the preoptic-hypothalamic axis including the anterior hypothalamic area (aha), arcuate nucleus (arc), dorsomedial nucleus of the hypothalamus (dm), medial preoptic area (mpoa), paraventricular nucleus (magnocellular) of the hypothalamus (pvm), ventromedial nucleus of the hypothalamus (vm), and ventral premammillary nucleus (vpm). Other areas with dense concentrations of E-neurons are the central gray of the midbrain (cg) and regions often included with the limbic system, namely the bed nucleus of the stria terminalis (nst), diagonal band of Broca (db), hippocampus (h), lateral septum (lsep), olfactory tubercle (ot), prepiriform cortex, entorhinal cortex (not shown), and medial and cortical nuclei of the amygdala (not shown). Other abbreviations: *a* nucleus accumbens, *ac* anterior commissure, *cc* corpus callosum, *cbllm* cerebellum, *f* fornix, *fr* fasciculus retroflexus, *ic* inferior colliculus, *lh* lateral habenula, *mamm* mammillary bodies, *mf* medial forebrain bundle, *mt* mamillothalamic tract, *oc* optic chiasm, *pf* nucleus parafascicularis, *sc* superior colliculus, *scp* superior cerebellar peduncle. Adapted with permission from Pfaff and Keiner (1973)

Richard Zigmond, and Pfaff identified androgen target sites in multiple nodes of the newly discovered vocal control system of songbirds (Zigmond et al. 1973; Arnold et al. 1976; Nottebohm et al. 1976). Explicit attention was directed to the sense of hearing as steroid targets were identified in the torus semicircularis, the main auditory nucleus of the midbrain in non-mammals that is a homologue of the inferior colliculus in mammals (see Butler and Hodos 2005). Androgen- and estrogen-concentrating neurons were mapped in the auditory midbrain of the South African clawed frog, *Xenopus laevis* (Kelley et al. 1975; Morrell et al. 1975; Kelley 1981) and the green anole lizard, *Anolis carolinensis* (Morrell et al. 1979).

Though not addressing hormonal mechanisms in hearing, several seminal neurophysiological studies using single-neuron recording methods published during this time period are worthy of note as a context for later experiments described in the chapters in this volume. Single neuron recordings by Nobuo Suga revealed the sensitivity of neurons in the auditory cortex of the insectivorous little brown bat, *Myotis lucifugus*, to frequency-modulated (FM) tones in the ultrasonic range of echolocation signals (Suga 1965). Masakazu (Mark) Konishi (1969) showed for the house sparrow (*Passer domesticus*) and the slate-colored junco (*Junco hyemalis*) that species variation in the best frequency of single neurons in the cochlear nucleus paralleled variation in the spectral peaks of species-typical vocalizations. The observations of Konishi and Suga were soon complemented by studies of eighth (VIIIth) nerve auditory afferents in frogs by Robert Capranica and colleagues (see Wilczynski and Ryan 2010; Megala Simmons 2013). Capranica et al. (1973) showed that population differences in VIIIth nerve frequency encoding by the cricket frog, *Acris crepitans*, could be explained by geographic variation in the spectral properties of the advertisement call (also see Frishkopf and Goldstein 1963 for earlier studies of VIIIth nerve in the American bullfrog, *Rana catesbeiana*). Soon thereafter, Narins and Capranica (1976) reported sex differences in VIIIth nerve frequency encoding in the neotropical tree frog, *Eleutherodactylus coqui,* that reflected sex-specific preferences for each note of the two note, "Co Qui" male advertisement call.

The demonstration of sensory-motor coupling between hearing sensitivity and the spectral features of vocalizations, which are often so prominent in reproductive contexts in both songbirds and frogs (Bradbury and Vehrencamp 2011), set the stage for neurophysiological investigations of steroid hormone influences on hearing. This included the influence of androgens in weakly electric fish on frequency encoding by the electrosensory lateral line periphery (Meyer and Zakon 1982; Bass and Hopkins 1984), a developmental relative of the inner ear (Northcutt 1997). Two decades later, estrogen and testosterone were shown to enhance frequency encoding in the inner ear of vocal fish, mimicking the seasonal switch from a non-reproductive to a reproductive peripheral auditory phenotype (Sisneros et al. 2004). The studies of fishes, amphibians, songbirds, and mammals that are reviewed in Chaps. 2–6 in this volume are direct beneficiaries of the collective findings discussed in this section.

## 1.3 Convergence of Neuroethology and Behavioral Neuroendocrinology

A focus on hearing and hormones brings together reviews by researchers that in some circles might refer to themselves as a neuroethologist and in others as a behavioral neuroendocrinologist (Chaps. 2–6). Jeffrey Camhi (1984) best summarized the neuroethology approach in the introductory chapter to his textbook *Neuroethology*: "The word *neuroethology* implies a blending of two scientific traditions that are about as different as one could imagine – that of the laboratory neurobiologist and that of the field ethologist (from the Greek *ethos*, meaning "manner" or "behavior"). … The key point is this: the reason that nervous systems evolve in the first place was to produce behavior, and to do so in the out-of-doors, under the full blare of natures' physical forces. Therefore, a true understanding either of the nervous system or of animal behavior cannot be had without a combination of neurobiological and ethological approaches" (Camhi 1984, pp. 3–4).

Neuroethology tends to be broad in its attention to a wide range of study species and physiological mechanisms (Camhi 1984), perhaps reflecting its zoological underpinnings (e.g., see Marler and Hamilton 1966). The major study species of behavioral neuroendocrinology are often mammals (especially rodents), and a few select avian species, with a focus on reproductive mechanisms. Broadly viewed, the behavioral neuroendocrinology research paradigm is not all that different from that of neuroethology given its interest in deciphering a translation between brain mechanisms and behavior—in the case of behavioral neuroendocrinology, the language is hormonal. Important for the disciplinary perspectives offered in this SHAR volume is that among the rich traditions of behavioral neuroendocrinology are its close attention to mechanisms of learning and memory and social behavior in support of reproduction (for a more complete review see Adkins-Regan 2005).

## 1.4 Hearing and Hormones: A Phylogenetic Perspective

As noted earlier, the editors invited reviews from authors who study fishes, amphibians, birds, and mammals (including humans) in order to capture the richness of a comparative, phylogenetic perspective. These authors further reference a wide range of disciplinary tools from bioacoustics and field studies of behavior to neuroanatomy, neurophysiology, and molecular endocrinology. Two of the chapters in this volume, 7 and 8, provide an essential human context. As Theodore Holmes (Ted) Bullock commented in a paper entitled *Comparative Neuroscience Holds Promise for Quiet Revolutions*: "The ancient question is still awaiting an answer: What features in our brain account for our humanity, our musical creativity, infinitely varied artifacts, subtlety of humor, sophisticated projections (in chess, politics, and business), our poetry, ecstasy, fervor, contorted morality, and elaborate rationalization?" (Bullock 1984, p. 473). To this list can be added hormonal influences on audition that are so central to perception of the world around us.

### *1.4.1 Hearing and Hormones in Teleost Fishes*

Inspired by earlier studies of hormonal mechanisms of seasonal changes in the neural substrates of avian song and fish electrocommunication (Sect. 1.2; for more complete reviews see Brenowitz 2004; Bass and Zakon 2005). Sisneros and Bass (2003) demonstrated a natural seasonal rhythmicity in the frequency sensitivity of eighth nerve afferents, in this case to the higher harmonics of male advertisement calls in the seasonally breeding plainfin midshipman fish, *Porichthys notatus*. Other studies soon followed showing androgen and estrogen regulation of seasonal variation in the midshipman fish's peripheral auditory phenotype (Sisneros et al. 2004). Midshipman fish are part of a large group of fishes, the toadfishes, that won the attention of comparative neurophysiologists in the 1960s and 1970s as models for