THE EVOLUTION OF THE AMPHIBIAN AUDITORY SYSTEM

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R. Glenn Northcutt, *Editor*

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SERIES PREFACE

Neuroscience is a rapidly expanding interdisciplinary field that is yielding significant insights into the organization and function of nervous systems. An outgrowth of several more traditional disciplines—Animal Behavior, Comparative Biology, Cybernetics, Neuroanatomy, Neurochemistry, Neurophysiology, and Physiological Psychology—Neuroscience arose because of many reasons, but central to the focus of Neuroscience is the growing realization that no single approach or discipline can fully explain how nervous systems are organized; how they come into being ontogenetically, as well as phylogenetically; how a specific nervous system works and what operational principles are applicable to most, if not all, nervous systems.

From subcellular organelles and processes to entire networks mediating behavior, the complexity and diversity exhibited by nervous systems is staggering. The goal of Neuroscience is to understand how these complex and diverse systems work as devices for information processing, control, and communication. Unlike artificial devices that are man-made and thus specifically designed to solve limited, well-defined sets of problems, nervous systems are the result of a historical process called evolution. Thus their analysis is further confounded by the fact that they have arisen opportunistically and without optimal design. Understanding how they have arisen, how they have adapted to solve problems that are virtually unlimited, is a challenge that can not be met by a single discipline. Although individual neuroscientists will continue to focus on specific questions related to a particular facet of neural organization or a single species, achievement of the goals of Neuroscience demands an eclectic approach that is rapidly becoming its hallmark.

The Wiley Series in Neurobiology reflects this eclecticism, and the Series will present work ranging from subcellular to behavioral topics, from specialized monographs to contributions spanning several disciplines. As a

forum in which nervous systems are viewed and analyzed from widely different perspectives, it is hoped that these offerings will not only provide information to researchers in all disciplines of Neuroscience, but will also provide further stimulation for an eclectic approach to the evolution, organization, and function of nervous systems.

R. GLENN NORTHCUTT

Ann Arbor, Michigan
March 1983

PREFACE

An animal is a complex of synergistic biological systems. Furthermore, each system is composed of many interactive parts. However, as a matter of practical necessity, researchers usually concentrate on one part of a system, focusing on the anatomy or the physiology of one of its parts, or on its development or its evolution. They are rarely afforded the opportunity to interact at length with colleagues who study all the disparate parts constituting a whole system and gain a broader appreciation of the interconnections between the component parts. Those of us who work on the amphibian auditory system were provided that opportunity for interaction in March, 1986, through the generosity of the Volkswagen Foundation and the Zentrum für interdisziplinäre Forschung at the University of Bielefeld in the Federal Republic of Germany.

At that time, a workshop was held at the Z.i.F., bringing together researchers representing a wide range of fields from neuroanatomy to behavioral ecology, all of whom have focused their attention on the auditory system of amphibians. This book is the result of that workshop. The breadth of topics reflects the many levels at which the amphibian auditory system has been investigated. It is arguable that few other systems in a single vertebrate group have been subjected to the systematic scrutiny of researchers in so many fields of biology.

This book is organized as a progression of topics that lead the reader through the anatomy, physiology, and behavioral correlates of the auditory system in the vertebrate class Amphibia. At many points along this progression, the contributors stress the evolutionary implications of their findings. The first two chapters provide an introduction to the volume and an overview of amphibian phylogeny. Chapters 3 to 6 review the anatomy and physiology of the peripheral auditory system, and Chapters 7 to 12 provide the same for central auditory areas. Chapters 13 and 14 are discussions of one specialized, but critical, aspect of amphibian audition, sound

localization. Chapters 15 to 18 review the development of the amphibian auditory system, including changes that occur during metamorphosis. Chapters 19 to 24 explore the use of audition in the natural behavior of these vertebrates and concentrate on acoustic communication in anurans. The final four chapters, 25 to 28, address selected topics in the evolution of amphibian, and vertebrate, audition.

As the editors of this book, we would like to thank the Volkswagen Foundation and the Z.i.F. for the financial support that made the workshop and this book possible. We would also like to express our appreciation to the staff of the Z.i.F. for their help and hospitality. Finally, we would like to thank all the participants at the workshop for their contributions to the book and to the hours of discussion from which it arose. During those discussions, we began to see the ways in which investigation of anatomy, physiology, behavior, and evolutionary biology might be linked together to provide a deeper understanding of this biological system. We hope the readers of this book will, after comparing chapters from the various sections, be able to do the same.

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Austin, Texas
September, 1987

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CONTENTS

Chapter One

THE AMPHIBIAN AUDITORY SYSTEM AS A MODEL FOR NEUROBIOLOGY, BEHAVIOR, AND EVOLUTION

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I. INTRODUCTION

As anyone who has taken a high school or college biology class knows, amphibians have long been used as models to illustrate basic principles in the biological sciences. William Harvey's observations of frogs nearly 400 years ago led to his radical theory that blood actually circulated through the body. He described his results in *Anatomical Dissertation Concerning the Motion of the Heart and Blood in Animals* in 1628, and presumably under-

graduates have been forced to find the aortic arches in dissected frogs ever since. Harvey was not alone in his choice of frogs as model systems. Many of the pioneers in the fields of neurobiology and sensory physiology—people such as Galvani, Volta, Mueller, von Helmholtz, Sechenov, Yerkes, and Hodgkin—used amphibians at some time as model systems for extracting fundamental principles of neural and behavioral processes. This preference for amphibian models continues. Amphibians are used as experimental models in such diverse areas as the development and plasticity of the nervous system (Constantine-Paton and Capranica, 1975; Zakon, 1983), the cellular basis of sensory transduction (Hudspeth, 1985), the hormonal control of behavior (Kelley, 1986), the interaction of natural and sexual selection (Ryan, 1985), and the mechanisms of speciation and reproductive isolation (Blair, 1964; Littlejohn, 1981).

Each of those modern examples mentioned above has something in common: at some time researchers have used the amphibian auditory system to explore basic questions in these areas. Each of these topics, and several more, are covered by the contributors to this book, whose chapters provide discussions ranging from the anatomy, physiology, and development of the auditory system, through the behavioral context in which audition is used and its integration with systems for producing acoustic signals, to the evolutionary principles integrating these areas.

II. AMPHIBIANS AS MODELS

A. Emphasis on Anurans

The bulk of research on the amphibian auditory system has centered on the anurans (frogs and toads) for an obvious reason: they are the only amphibian group that engages in acoustic communication. For this reason, anuran auditory research encompasses not only anatomy and physiology, but acoustic communication and its attendant mechanisms and behaviors. Furthermore, because acoustic communication is used during reproductive behavior, the structure and function of the signals, and the manner in which the auditory system processes them, have important evolutionary implications in such areas as sexual selection, speciation, and reproductive isolation. This does not diminish the importance of research on the auditory system of the two other amphibian orders, the urodeles (newts and salamanders) and gymnophions (apodans). If anything, too little work on these other orders has been done. Nevertheless, anurans are especially attractive as research subjects because their auditory system allows integrative studies of neural, behavioral, and evolutionary biology in a way offered by very few other systems.

B. Advantages of Anurans

Anurans are not unique in their use of the auditory system during social behavior. Many insects, birds, fish, and mammals do the same. However,

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