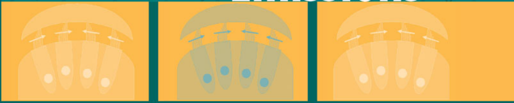
SPRINGER HANDBOOK OF AUDITORY RESEARCH
Series Editors: Richard R. Fay and Arthur N. Popper

Geoffrey A. Manley
Richard R. Fay
Arthur N. Popper

Active Processes and Otoacoustic Emissions



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Springer Handbook of Auditory Research

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Active Processes and Otoacoustic Emissions in Hearing

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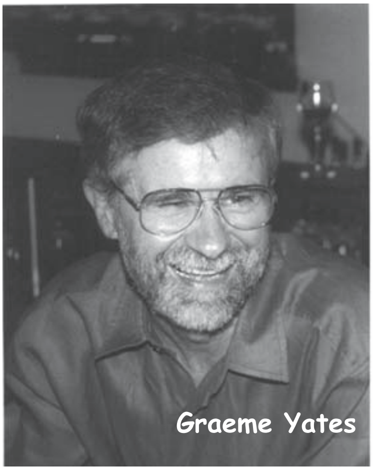
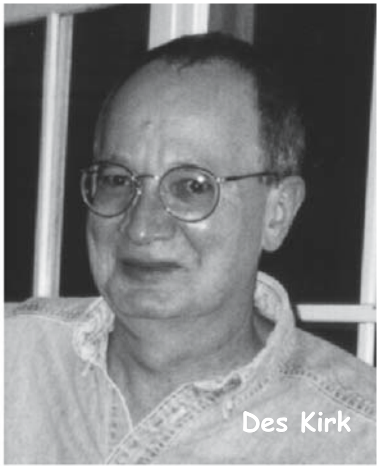
Dedication





This book is dedicated to two colleagues of Geoff Manley: Graeme Yates and Des Kirk, who worked in the Auditory Laboratory of the Department of Physiology of the University of Western Australia. Their untimely deaths within two years of one another robbed this research field of a dedicated and clever research team. Their publications over many years represent very significant contributions to the fields covered by this book, and their intellect, humanity, and humor are sorely missed by those who loved and respected them.

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Series Preface

Springer Handbook of Auditory Research

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, Chicago, IL
Arthur N. Popper, College Park, MD

Volume Preface

Most sciences undergo occasional smaller or greater revolutions, such as the Darwinian revolution in biology. In most cases, these revolutions are conceptual in nature, providing a new framework for understanding a host of data, and this new concept plays a dominant role in later discourse in that field. In the early 1980s, hearing science went through a revolution that was at the same time both conceptual and technical and that dramatically changed the face of auditory neuroscience. It is the aim of this book to summarize what is currently known about the remarkable phenomenon of active processes and their manifestations and provide a comprehensive resource for readers to understand and implement this phenomenon in their work.

There is no doubt that in the early 1980s, auditory science was ripe for a revolution. There was a veritable mountain of anatomical and physiological findings that were not clearly reconcilable and with no adequate models to describe them. Physiological studies showed that the movement of the organ of Corti and the behavior of auditory nerve fibers were clearly nonlinear and physiologically sensitive. Anatomically, inner and outer hair cells were very different. What did all this mean, and how could these findings be reconciled? Within the first five years of the 1980s, technical advances permitted studies of outer hair cells and of the newly discovered otoacoustic emissions that together clearly demonstrated that hair cells were not just passive receivers of sound stimuli but that they are able to produce mechanical energy themselves. These technical breakthroughs permitted the development of a new conceptual framework of the function of the hearing organ as an active, highly nonlinear system that modifies the responses to sound such that very sensitive, highly frequency-selective hearing becomes possible. Later studies showed that the active ear originated early in evolution and thus has a long history. We now know that it is based on not just one but several interlocking mechanisms.

For research purposes, one great advantage of the active processes in the inner ear is that some of the energy produced by hair cells is lost out of the hearing organ, passes the middle ear, and produces measurable sounds in the ear canal. These otoacoustic emissions can be spontaneous or induced by different sounds or combinations of sounds. Their study has opened up extremely useful new methods not only for "remote sensing" of how the ear works, but also for more direct comparisons of hearing in animals and humans and, importantly, very useful new clinical procedures in audiology and otolaryngology. Also importantly, the techniques are both noninvasive and objective.

The finding that vertebrate hearing depends on active processes in the inner ear has increasingly dominated and revolutionized hearing research over the last 25 years. The time is now ripe to bring together all of these ideas. This book begins with a discussion of the history of the discovery of otoacoustic emissions by David Kemp (Chapter 1), and a companion chapter by Cooper et al. (Chapter 2) traces the history of research findings and ideas that provided the historical framework that led to the discovery of the active cochlea. These chapters make it easier to understand the origin of this research field and especially the context in which important discoveries were made.

These introductory and historical chapters are followed by three chapters that deal with the concepts and the probable cellular mechanisms underlying active processes of hair cells. Duke and Jülicher (Chapter 3) discuss the theories underlying the concept of active processes, how these may be integrated into a sensory system, and how they are controlled—without knowing necessarily what the actual cellular mechanisms are. Martin (Chapter 4) and Hallworth and Jensen-Smith (Chapter 5) then discuss the main types of motor systems that drive active processes at the hair-cell level. Martin discusses the evidence for an involvement of the hair-cell bundle in both nonmammalian and mammalian ears and reveals mechanisms that are both ancient (clearly also present in vestibular hair cells) and complex. Their complexity rests on the fact that there is good evidence for the involvement both of myosins that control sensory adaptation and of the transduction channels themselves. Hallworth and Jensen-Smith present the evidence for a unique additional molecular motor in the lateral walls of mammalian outer hair cells, based on the protein prestin, and discuss how this system might work.

There follow three chapters that describe the evidence for active processes in three groups of animals. Göpfert and Robert (Chapter 6) describe the active movements of the auditory organ (the antennae) of flies and mosquitoes and reveal a system of sensitivity enhancement with similar functional principles as those seen in vertebrates and that are possibly even evolutionarily related at the level of the sensory cells. Manley and van Dijk (Chapter 7) give a broad overview of nonmammalian land vertebrates, such as amphibians, lizards, and birds, that lack the prestin motor but from which there is a plethora of data that clearly show that their hearing is also driven partly by active processes. Interestingly, amphibians and especially lizards are particularly reliable producers of spontaneous otoacoustic emissions, and this makes them very useful animals for studying these phenomena. Clearly, the performance of many of these ears rivals that of mammals and makes one wonder what advantage mammals gain from also having prestin-driven motility. Lonsbury-Martin and Martin (Chapter 8) then give an overview of otoacoustic emission measurements from laboratory mammals. Although these species tend not to show spontaneous emissions, their sound-induced emissions provide the most directly comparable data to measurements on humans and are therefore of clear interest for the interpretation of human data and of clinical studies.

Shera and Guinan (Chapter 9) discuss the problem as to why otoacoustic emissions in mammals, which are based on the activity of all hair cells, manifest themselves as distinct spectral patterns with energy peaks only at certain frequencies and offer a conceptual model to expain these patterns. Russell and Lukashkin (Chapter 10) then discuss the centrifugal control exerted on the ear by the efferent system and its effects as seen in otoacoustic emissions. Clearly, active systems of hair cells will also be under the influence of efferent fibers, and it is of especial interest for clinical studies to understand the extent to which this occurs and what characteristic activity patterns are produced.

Neely and Kim (Chapter 11) describe the mathematical modeling of active processes and otoacoustic emissions in the historical context. The predictive value of modeling has benefited enormously from the concept of active processes, and the authors show how some features that were incorporated into early models as necessary to explain the phenomena can now be given names and even identified at the cellular level.

Two chapters then discuss the relevance and importance of active processes and otoacoustic emissions for the study of human hearing. Johnson et al. (Chapter 12) bring together the results of previous techniques (such as psychoacoustical methods) used to study the human ear with those recently gained using otoacoustic emissions. Janssen and Müller (Chapter 13) then provide an overview of the use of the measurement of otoacoustic emissions in a clinical context: Which techniques have been applied, what have we learned from them, and what are appropriate protocols for examining different kinds of hearing problems?

Finally, Manley and Brownell (Chapter 14) summarize the main questions that have arisen out of all of these studies and still remain to be answered. Hearing researchers now have an unprecedented array of methodologies at their fingertips, backed up by the fastest and most sensitive equipment ever available. Future work will no doubt solve most of these problems and reveal new and fascinating details about the functions of this quite remarkable sensory system.

We trust that this book will be of interest to a very wide audience of auditory researchers but also clinicians, sensory physiologists, and teachers of neurobiology.

As is frequently the case, there are other chapters and volumes in the Springer Handbook of Auditory Research that provide additional insight into the issues raised in this volume. A discussion of the structure, function, and physiology of sensory hair cells is found in volume 27, *Vertebrate Hair Cells* (edited by Eatock, Fay, and Popper). The mechanics of the mammalian cochlea, particularly as related to active processes, can be found in a chapter by Patuzzi in volume 8, *The Cochlea* (edited by Dallos, Popper, and Fay), while other chapters in that volume provide further insight into the structure and function of the mammalian cochlea. An earlier discussion of otoacoustic emissions was presented by Whitehead et al. in volume 7, *Clinical Aspects of Hearing* (edited by Van De Water, Popper, and Fay)

September, 2007
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