Auditory Neuroscience

Making Sense of Sound

Jan Schnupp, Israel Nelken, and Andrew King

The MIT Press
Cambridge, Massachusetts
London, England

For information about special quantity discounts, please email special_sales@mitpress.mit.edu

This book was set in Stone Sans and Stone Serif by Toppan Best-set Premedia Limited. Printed and bound in the United States of America.

Library of Congress Cataloging-in-Publication Data

Schnupp, Jan, 1966–
Auditory neuroscience : making sense of sound / Jan Schnupp, Israel Nelken, and Andrew King.
p. cm.
Includes bibliographical references and index.
ISBN 978-0-262-11318-2 (hardcover : alk. paper) 1. Auditory perception. 2. Auditory pathways. 3. Hearing. I. Nelken, Israel, 1961– II. King, Andrew, 1959– III. Title.
QP461.S36 2011
612.8′5—dc22

2010011991

10 9 8 7 6 5 4 3 2 1

Preface

What This Book Is About

As I write these lines, a shiver is running down my back. Not that writing usually has that effect on me. But on this occasion, I am allowing myself a little moment of indulgence. As I am writing, I am also listening to one of my favorite pieces of music, the aria "Vorrei spiegarvi, oh dio!" composed by Mozart and masterfully performed by the soprano Kathleen Battle. A digital audio player sits in my pocket. It is smaller than a matchbox and outwardly serene; yet inside the little device is immensely busy, extracting 88,200 numerical values every second from computer files stored in its digital memory, which it converts into electrical currents. The currents, in turn, generate electric fields that incessantly push and tug ever so gently on a pair of delicate membranes in the ear buds of my in-ear headphones. And, voilà, there she is, Kathleen, hypnotizing me with her beautiful voice and dragging me through a brief but intense emotional journey that begins with a timid sadness, grows in intensity to plumb the depths of despair only to resolve into powerful and determined, almost uplifting defiance.

But Kathleen is not alone. She brought a small orchestra with her, prominently featuring a number of string instruments and an oboe. They were all hidden in the immaterial stream of 88,200 numbers a second. Pour these numbers into a pair of ears, and together they make music. Their sounds overlap and weave together, yet my brain easily distinguishes the different instruments from each other and from Kathleen's voice, hears some on the left, others on the right, and effortlessly follows the melodic line each plays. The violins sing, too, but not like Kathleen. Kathleen sings in Italian. My knowledge of Italian is not as good as I would like it to be, and when I first heard this piece of music I spoke no Italian at all, but even on my first hearing it was obvious to me, as it would be to anyone, that this was a song with words, even if I couldn't understand the words. Now I am learning Italian, and each time I hear this song, I understand a little bit more. In other words, each time, this by now so familiar song is engaging new parts of my brain that were previously deaf to some small aspect of

it. The title of the song, "Vorrei spiegarvi, oh dio!," by the way, means "I would like to explain to you, oh Lord!" It seems a curiously appropriate title for the purpose at hand.

Every time we listen, not just to music, but to anything at all, our auditory perception is the result of a long chain of diverse and fascinating processes and phenomena that unfold within the sound sources themselves, in the air that surrounds us, in our ears, and, most of all, in our brains. Clearly you are interested in these phenomena, otherwise you would not have picked up this book, and as you learn more about hearing, you will increasingly appreciate that the sense of hearing is truly miraculous. But it is an "everyday miracle," one which, most of the time, despite its rich intricacy and staggering complexity, works so reliably that it is easily amenable to scientific inquiry. In fact, it is usually so reliable and effortless that we come to overlook what a stunning achievement it is for our ears and brains to be able to hear, and we risk taking auditory perception for granted, until it starts to go wrong.

"Vorremo spiegarvi, caro lettore!" we would like to try and explain to you how it all works. Why do instruments and voices make sounds in the first place, and why and in what ways do these sounds differ from one another? How is it possible that our ears can capture these sounds even though the vibrations of sound waves are often almost unimaginably tiny? How can the hundreds of thousands of nerve impulses traveling every second from your ears through your auditory nerves to your brain convey the nature of the incoming sounds? How does your brain conclude from these barrages of nerve impulses that the sounds make up a particular melody? How does it decide which sounds are words, and which are not, and what the words might mean? How does your brain manage to separate the singer's voice from the many other sounds that may be present at the same time, such as those of the accompanying instruments, and decide that one sound comes from the left, the other from the right, or that one sound contains speech, and the other does not? In the pages that follow, we try to answer these questions, insofar as the answers are known.

Thus, in this book we are trying to explain auditory perception in terms of the neural processes that take place in different parts of the auditory system. In doing so, we present selected highlights from a very long and large research project: It started more than 400 years ago and it may not be completed for another 400 years. As you will see, some of the questions we raised above can already be answered very clearly, while for others our answers are still tentative, with many important details unresolved. Neurophysiologists are not yet in a position to give a complete account of how the stream of numbers in the digital audio player is turned into the experience of music. Nevertheless, progress in this area is rapid, and many of the deep questions of auditory perception are being addressed today in terms of the responses of nerve cells and the brain circuits they make up. These are exciting times for auditory neuroscientists, and we hope that at least some of our readers will be inspired by this book

to join the auditory neuroscience community and help complete the picture that is currently emerging. We, the authors, are passionate about science: We believe that miracles become more miraculous, not less, if we try to lift the lid to understand their inner workings. Perhaps you will come to share our point of view.

How to Use This Book

People are interested in sound and hearing for many reasons, and they come to the subject from very diverse backgrounds. Because hearing results from the interplay of so many physical, biological, and psychological processes, a student of hearing needs at least a sprinkling of knowledge from many disciplines. A little physical acoustics, at least an intuitive and superficial understanding of certain mathematical ideas, such as Fourier spectra, and a fairly generous helping of neurophysiology and anatomy are absolute requirements. Furthermore, some knowledge of phonetics and linguistics or a little music theory are highly desirable extras. We have been teaching hearing for many years, and have always lamented that, although one can find good books on acoustics, or on the mathematics of signal processing, the physiology of the ear, psychoacoustics, speech, or on music, so far no single book pulls all of these different aspects of hearing together into a single, integrated introductory text. We hope that this book will help fill this important gap.

We wrote this book with an advanced undergraduate readership in mind, aiming mostly at students in biological or medical sciences, audiology, psychology, neuroscience, or speech science. We assumed that our readers may have little or no prior knowledge of physical acoustics, mathematics, linguistics, or speech science, and any relevant background from these fields will therefore be explained as we go along. However, this is first and foremost a book about brain function, and we have assumed that our readers will be familiar with some basic concepts of neurophysiology and neuroanatomy, perhaps because they have taken a first-year university course on the subject. If you are uncertain about what action potentials, synapses, and dendrites are, or where in your head you might reasonably expect to find the cerebral cortex or the thalamus, then you should read a concise introductory neuroscience text before reading this book. At the very least, you might want to look through a copy of "Brain Facts," a very concise and highly accessible neuroscience primer available free of charge on the Web site of the Society for Neuroscience (www.sfn.org).

The book is divided into eight chapters. The first two provide essential background on physical acoustics and the physiology of the ear. In the chapters that follow, we have consciously avoided trying to "work our way up the ascending auditory pathway" structure by structure. Instead, in chapters 3 to 6, we explore the neurobiology behind four aspects of hearing—namely, the perception of pitch, the processing of speech, the localization of sound sources, and the perceptual separation of sound mixtures.

The final two chapters delve into the development and plasticity of the auditory system, and briefly discuss contemporary technologies aimed at treating hearing loss, such as hearing aids and cochlear implants.

The book is designed as an entirely self-contained text, and could be used either for self-study or as the basis of a short course, with each chapter providing enough material for approximately two lectures. An accompanying Web site with additional materials can be found at www.auditoryneuroscience.com. These supplementary materials include sound samples and demonstrations, animations and movie clips, color versions of some of our illustrations, a discussion forum, links, and other materials, which students and instructors in auditory neuroscience may find instructive, entertaining, or both.