FLOYD RATLIFF
The Rockefeller Institute, New York

MACH BANDS: *Quantitative studies on neural networks in the retina*

HOLDEN-DAY, INC. 1965
San Francisco, London, Amsterdam

Ernst Mach

Preface

One hundred years ago Ernst Mach published the first of his several quantitative studies on the interdependence of neighboring elements in the retina. However, Mach's application of mathematical modes of thought to the study of the nervous system was so far ahead of the times that his papers attracted little attention when they first appeared.

Within recent years considerable interest has developed in the mathematical analysis of the properties of complex neural networks. The main reason for this seemingly belated development of interest is that only within the last quarter-century or so have the techniques of electrophysiology finally become sufficiently advanced to provide a sound empirical foundation for such studies. The interplay of the fundamental neural processes of excitation and inhibition, about which Mach could only speculate, can now be observed directly and with relative ease in practically all parts of the nervous system.

Of lesser importance, but nevertheless significant, is the recent development of a computer technology which has made the reduction of large amounts of neurophysiological data and the numerical solution of complex mathematical problems much less formidable than in years past. Furthermore, the ease with which mathematical models of neural processes can now be manipulated, both by means of computers and by special electrical analogs, makes these models useful as investigative tools in neurophysiology as well as mere descriptive devices. Once the fundamental properties of a neural network are known, exploratory work on more complex properties can be carried out on simulated networks prior to the technically more difficult physiological experiments on the real nervous system.

Finally, work in other fields has stimulated further interest in the properties of neural networks. The mathematical problems in the development of electro-mechanical sensing and pattern recognition devices, for example, are quite similar to those encountered in the quantitative study of neural networks; advances in each field are frequently relevant to the investigations being carried out in the other.

Nearly fifteen years ago I first became acquainted with Ernst Mach's psychophysical investigations in the field of vision, and saw their relevance to my own electrophysiological research on inhibitory interaction in the retina. Since that time a large number of experimental and theoretical papers by other investigators have appeared on this and closely related subjects. This recent upsurge of interest and activity in the investigation of the quantitative properties of neural networks further intensified my own interest in the subject. What started out to be a translation of a few of Mach's papers and a small collection of miscellaneous notes for my own use gradually evolved into an extensive and systematic study of a topic that cuts across the boundaries of many interrelated disciplines—including some aspects of history of science, theory of knowledge, psychophysics of vision, mathematical theories of inhibitory interaction, and neurophysiological investigations of the function and significance of inhibitory interaction in the retina. (The Introduction gives a brief summary of, and guide to, the material covered.)

It is my hope that the separate treatments of the diverse topics covered in this book will be of interest to students and investigators in each of the several special fields touched upon. But the book is not primarily intended for the specialist in any particular field, even though it includes some details that may be of interest to him only. I hope instead, in this age of increasing specialization and increasing difficulty of communication among different disciplines, that this attempt to integrate many diverse studies will help to break down some of the barriers that have been erected around the various special disciplines and, in some measure, to attain the genuine unity of science which Mach foresaw. To achieve this end, one of the major aims of the book is to examine some of the foundations of the empirical knowledge on which all of science is based.

The following brief account of how the book came into being illustrates the one aspect of the theory of knowledge with which the book is mainly concerned: the basis for, and meaning of, the common distinction that we make between the subjective and the objective.

The whole story begins with a star seen over Budapest, Hungary, in the year 1924. To the casual observer this was an ordinary star, but to an astronomer at the University of Budapest it appeared to be something out of the ordinary. An apparent doubling of lines in photographs of its spectrum indicated that it might be not one star, but two—a so-called *binary* star. Such double lines, previously observed in the single spectra of visibly separate binary stars, were attributed to the Doppler effect. As the two stars rotate about their common center of gravity the light waves emitted from the one approaching the earth appear to be shortened, while the light waves emitted from the one receding from the earth appear to be lengthened. Thus the spectral lines of any elements that the two stars have in common may be slightly displaced with respect to one another in the spectrogram. If the pair of stars is revolving in a plane that passes near the solar system, the Doppler effect may be so pronounced that, twice during each complete revolution of the pair, single spectral lines become clearly separated into two.

Using the Doppler effect as an indicator, astronomers had been able to detect many close binary stars which appeared to be single by ordinary telescopic means of observation. In this particular case, however, the evidence was inconclusive. Everyone who saw the spectrogram could clearly see two thin parallel lines at a certain spot, but physical measurements with a slit photometer showed only a single thick line. The astronomer who made these observations was very much disappointed because he could not prove the existence of the double lines—and thus the existence of a Doppler effect—by physical measurements, and he finally abandoned the work.

However, Georg von Békésy, a student at the University of Budapest who was among those to whom the astronomer had shown the photograph, was very much intrigued by the apparent contradiction between the visual appearance of the spectrum and its physical measurements, and he could not put the whole affair out of his mind. Von Békésy had long been interested in art and in the various optical and psychological techniques used by artists, and his familiarity with these techniques led him to believe that the effect observed in the spectrogram might be one of the optical illusions already known to artists and to sensory psychologists. But an examination of a large number of optical illusions described in the literature revealed none to explain the effect in question.

At that time von Békésy was using a Jamin interference refractometer in his research for his doctoral thesis. This instrument had been improved by Ludwig Mach, and the improvements had been described in the Proceedings of the Royal Academy, Vienna. While looking up this work von Békésy discovered quite by accident that in 1865 Ernst Mach (Ludwig Mach's father) had described in these same Proceedings "subjective" visual phenomena, which seemed to explain fully the apparent doubling of the single broad lines in the spectrogram. (These phenomena are now known as "Mach bands" and are the main subject of this book.) By that time, however, several years had gone by, the astronomer had moved to another laboratory, and the whole problem was forgotten for the time being.

In the years of inflation after World War I von Békésy was unable to continue his research in optics because of the high cost of the necessary instruments. He turned to the field of communications and through this work became interested in the function of the ear. Von Békésy's physical measurements of the mechanical properties of the basilar membrane (work for which he later won the Nobel prize) convinced him that some sort of neural "sharpening" mechanism must be required, in addition to the physical sound analyzing mechanisms of the ear, to account adequately for the remarkable sharpness of frequency discrimination by the auditory system. Remembering the incident described above, it occurred to him that some form of neural interaction similar to that which supposedly caused the Mach bands in vision might be the neural basis for a sharpening mechanism in the ear. He therefore advanced this hypothesis in a paper on the theory of hearing which he published in 1928.

In this paper he illustrated, by means of a visual analogy, how the sharpening mechanism might work; the mechanical displacement of the basilar membrane was represented by variations in photographic density —the lighter the region on the photograph, the greater the displacement represented. Using this visual analog of the auditory process he showed how a broad stimulus distribution along the basilar membrane, with a single flat maximum such as that produced by the combination of two resonance curves, could produce a sensation distribution with two fairly distinct and rather sharp maxima.

The bands in the photograph that von Békésy published were quite distinct. They were so distinct, in fact, that several of his colleagues reproached him for using the figure in his article, insinuating that the photograph might have been retouched in order to show the bands. Also, a few days after the article appeared, von Békésy received a letter from E. von Hornbostel who was an expert in the field of hearing and who regularly reviewed papers on sensory physiology for the *Berichte der allgemeinen Physiologie*. In this letter he stated that when he saw the published photograph he was immediately convinced that it had been retouched. Von Békésy was greatly disturbed by all this criticism and now began to doubt the validity of the phenomenon himself. Although he knew that *he* had not retouched the photograph, there was the possibility that the publisher had done so in order to make its appearance conform to that indicated in the accompanying graphs in the article.

After a sleepless night he gathered together all the leftover photographs and negatives to send to von Hornbostel in order to prove that the phenomenon was not an artifact—either intentional or unintentional. But it turned out not to be necessary. Von Békésy had neglected to read von Hornbostel's letter carefully in its entirety because of his great concern about the possibility that someone—unknown to him—might have actually retouched the photographs. On rereading the letter, he discovered that von Hornbostel himself had furnished the necessary proof. He had carefully scanned the published photograph under the microscope and found that the diameters of the black dots produced by the halftone process (the size of which determined the darkness of a given region) were uniform throughout the critical area. Evidently, as Mach had already concluded in 1865, the bands were produced by some process of interaction in the nervous system of the observer rather than by a physical process that occurred at some stage of the reproduction and publication of the photograph.

Following World War II, von Békésy was unable to continue his research under the conditions then prevailing, so he left Hungary, going first to The Royal Institute of Technology in Stockholm and later to Harvard University. It was there, in 1951, that our paths crossed and that my part in this story began. For some time previously I had been interested in the visual mechanisms that underlie the detection and enhancement of lines and contours. My initial work in this field, which was carried out under the direction of Lorrin A. Riggs at Brown University, had been to consider the possible role of minute involuntary eye movements in these mechanisms. Subsequently, I had worked under the direction of H. K. Hartline at the Johns Hopkins University on electrophysiological studies of inhibitory interaction in the retina of the marine arthropod, *Limulus*.

In our discussions of this and other work of mutual interest, von Békésy pointed out the formal similarity between the quantitative account of the inhibitory interaction in the eye of *Limulus* given by H. K. Hartline, Henry G. Wagner and myself, and Ernst Mach's quantitative theory of inhibitory interaction in the human retina. At the same time von Békésy introduced me to the other work of Mach—in particular, Mach's views on the theory of knowledge that were presented in his *Mechanics* and *The Analysis of Sensations*. My latent interest in the theory of knowledge, which had led me to the study of vision in the first place, was aroused once again, and I began a serious study of Mach and his work, mainly for my own entertainment and edification. But the study soon outgrew my original plans and gradually developed into this book.

In any attempt to integrate many diverse approaches to a particular problem, as in this book, one must cross the artificial boundaries that we have marked out around the various areas of knowledge and disciplines of science. The course of action is determined by the problem to be investigated rather than the particular discipline to which one belongs; where the problem leads one must follow. In following such a course one inevitably, and in most cases quickly, reaches the limits of his own knowledge and experience and must turn to others for help. I therefore wish to take this opportunity to express my gratitude to the many individuals who have been of assistance to me in the preparation of this book—in particular to my colleagues Alan R. Adolph, Frederick A. Dodge, Jr., Bruce Knight, Jr., G. David Lange, William H. Miller, Conrad G. Mueller, Jr., Richard L. Purple Robert L. Schoenfeld, and Charles F. Stevens—all of whom helped me with various and sundry problems which I could not solve alone and which are too numerous to mention here. It is inevitable, however, that there will be some errors of interpretation and errors of omission in this book. The responsibility for these, of course, is my own.

I am very grateful to many individuals and organizations for permission to reproduce figures and to quote passages from published material. (A specific acknowledgment appears in the text along with each figure reproduced and with each passage quoted.) I wish also to express my thanks to the American public at large for the continued and generous (if unknowing) support it has given to my experimental research and study in this area by means of grants and other aid from public funds administered by the Office of Naval Research and the National Institute of Neurological Diseases and Blindness.

Acknowledgments are due to Miss Jun Uramatsu who translated some articles from the French for me, and to Miss Christine Rosner and Mrs. Maria Lipski who translated some articles from the German. I should also like to express my gratitude to Mrs. Lipski for the typing of the manuscript. Finally, I am most grateful for the apparently unlimited patience and understanding exhibited by the editors and publishers and by my wife Orma and my daughter Merry during the several years that I worked on the translations of Mach's papers and the writing of this book.

Floyd Ratliff

The Rockefeller Institute
New York
January 1965