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*A great work of lasting interest.*

—H.-T. CHANG, Journal of Neurophysiology

The aims, means, and results of electrophysiological research on the processes of reception are discussed and interpreted by one of the greatest experts in the field, who draws on a lifetime's study of the nervous system and special senses. Dr. Granit also analyzes new knowledge in specific fields, such as muscular end organs, skin receptors, the retina, and the long distance control of sense organs. In discussing postural reflexes and brain control he provides the first complete description of the system of feedback controls running the ventral horn cells, and deals extensively with the motor role of the gamma system and the physiology of the spinal cord. This comprehensive study is of first importance to physiologists, neurologists, psychologists, ophthalmologists, and color physicists. It should interest the general biologist as a first attempt toward a synthetic view incorporating both peripheral and central principles in the organization of the sensory message.

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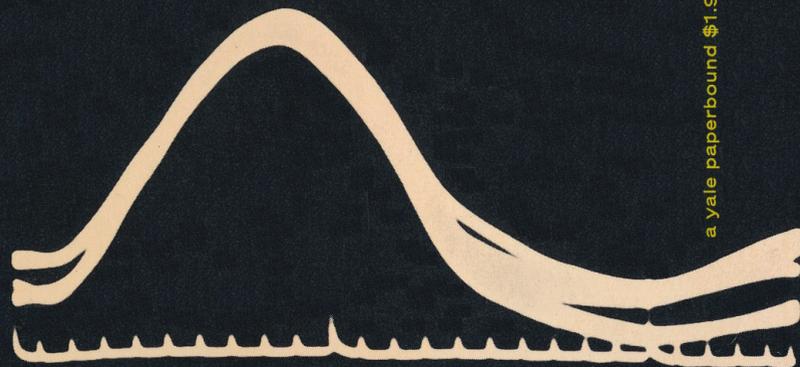
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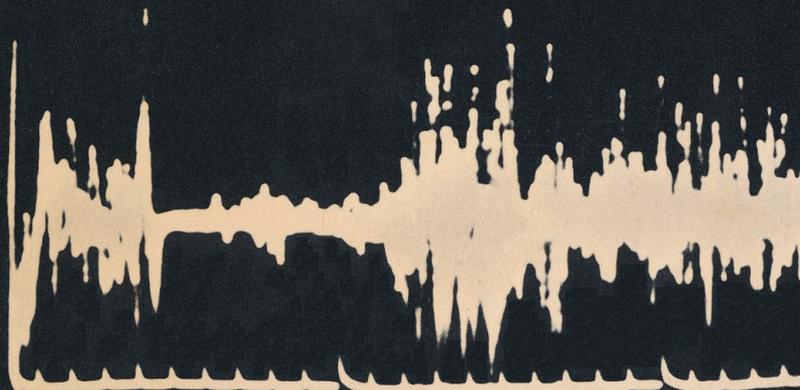
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RAGNAR GRANIT



# Receptors and Sensory Perception



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RECEPTORS AND SENSORY PERCEPTION

Based on the Silliman Lectures delivered at Yale University

RECEPTORS AND  
SENSORY PERCEPTION

*A Discussion of Aims, Means, and Results of*

*Electrophysiological Research into the Process of Reception*

BY RAGNAR GRANIT

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## Preface

THE title and with it the theme of these lectures was suggested by my friend and colleague John Fulton and tempted me immediately because I thought it might be of interest at this particular moment to comment on the achievements of a quarter century of work by electronic methods on the special senses. It was clear that there was no need for an annual-review type of book, or for one expanded to deal with the results text-book fashion. Again, a complete general physiology of the special senses, apart from the danger of being too pretentious for the present age, might easily turn out to be too general for the specialist, yet too special for the general scientific reader.

Thus I felt I had good excuse for following my natural inclination to go into detail only in the fields where I felt I had mastered the details, to extract general principles from them, and to look for applications in adjacent fields. It seemed to me also that what we as experimenters individually pay a price for is laboratory experience and that therefore my innumerable omissions might be more generously forgiven if, as a counterpoise, I inserted chapters based on first-hand knowledge acquired by experimentation. The sections on the eye, on the muscle receptors with their reflexes, and on centrifugal control of sense organs serve this purpose.

My major omissions concern audition, which as a subject of electrophysiological research has been so beautifully developed by several workers in the United States. I try to follow the work on the ear but am not expert enough in the field to include a separate chapter on it.

Now, why is this an appropriate moment for commenting on the aims, means, and results of research by electrical methods on various aspects of perception? Clearly, the main reason is that we have actually arrived at principles which ought to be formulated and held to a mirror in order to prevent them from becoming immersed in the steady stream of annual contributions from many different points of view. Such principles concern, among others, "receptive fields," "generator potentials," "centrifugal control," "specific and unspecific afferents," and "organization of the frequency code." These and many others will be dealt with below.

Much as I speak about results obtained by electrical methods, my

secret plea between the lines—I emphasize it now—is really for this kind of work *combined* with adequate stimulation of sense organs. I see no other way to a real understanding of the principles of organization of the central nervous system. This, in a different way, was emphasized very long ago by John Locke (see below, introductory quotation). The brain, after all, is the great interpreter of the senses.

While preparing these lectures I occasionally felt some apprehension that the time required was being spent less profitably than for laboratory work. I then derived some solace from the thought that the generation of postgraduate students about to enter this field may find the book useful as an introduction to the principles involved. At other times, in other moods, I have greatly enjoyed both the excuse for writing and the writing itself, feeling stimulated by the hope of, perhaps, gathering something of what, with Walter B. Cannon, one might refer to as the “durable results of the perishable years.”

In the preparation of the manuscript my secretary, Gunvor Larsson, has given freely of her spare hours in order to make it possible to finish the book in time for the lectures. Evi Reigo and Anne-Marie Bengtson took charge of the illustrations and legends. At Yale John F. Fulton and Mary P. Wheeler devoted a great deal of unselfish care and labor to the perusal of the manuscript, suggesting improvements and corrections. The book and its author owe a great deal to these collaborators.

Several members of the staff of the Nobel Institute for Neurophysiology, as well as guest workers, have read parts of the manuscript and made valuable suggestions. Friends in Stockholm, London, and Cambridge have read sections of the book and given me the benefit of their criticism. Many more in different parts of the world have liberally lent me originals of illustrations from their papers and given me access to data in the course of publication. Though no one is specifically mentioned, none is forgotten, and I thank them all.

It is seldom that one has an opportunity of expressing one's gratitude to the foundations which have supported the Nobel Institute and made its work possible. This seems such an occasion, and I therefore wish to put on record my great indebtedness to the Knut och Alice Wallenbergs Stiftelse, the Royal Caroline Institute, the Nobel Foundation, the Rockefeller Foundation, and the Swedish Medical Research Council. Originally my Institute was set up in 1940 by a generous combined gift from the Wallenberg and the Rockefeller Foundations.

Finally, to the officers of Yale University and the members of the

Silliman Committee I wish to convey my sincere thanks for the invitation to deliver the Silliman Lectures. The great care taken by the Yale University Press in publishing this book is gratefully acknowledged.

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