#### PHYSIOLOGY OF THE EYE

VOLUME 2



ARTHUR LINKSZ, M.D., F.A.C.S.

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VOLUME TWO

# Vision

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# **Preface**

HIS IS ACTUALLY the second, and much enlarged, edition of an essay I wrote quite some years ago, while practicing ophthalmology in Budapest, Hungary. This essay was never published. A professional organization of booksellers and printers (in Hungary, as in Great Britain, trade unions were the principal custodians of liberal thinking) approached me, and a number of my friends, in the year 1935, to prepare a series of lectures for its membership. The general topic of these lectures was to be rather broad, "The Weltanschauung of Our Era." There were two other physicians to participate, a psychiatrist and an endocrinologist; the others on the panel were jurists, economists, a historian and an artist. As the title of my contribution I chose "The Role of the Sensory Organs in the Evolution of a Weltanschauung." This was in good accord with the general topic and, at the same time, it indicated my belief that the very manner in which our senses convey information determines the way our mind works—not a new belief altogether. The actual content of the first of my two lectures was a kind of General Introduction to Sense Physiology, based especially on Thomas Young's and Johannes Müller's views—a shorter version of what constitutes the first three lectures of this volume. The second lecture consisted of some introductory remarks on space perception. I discussed Ramón y Cajal's and Köhler's views on retino-cortical and psycho-neural isomorphism, respectively. I couldn't, of course, miss the discussion of a problem which has occupied me all my life, the problem of the accessibility of events in other people's minds. This lecture then contained much of the material presented in the first lectures of Section III of this book.

These lectures were very well received and soon the editor of a magazine asked for my manuscript while the publisher of a series of science monographs even encouraged me to enlarge my manuscript into a book. I worked hard on my manuscripts, the magazine article was submitted and a great part of a book finished. This was in 1937, at a time when expression of opinion, at least in matters of science or psychology, was still rather free in Hungary. But then came 1938—Hitler to Vienna and Chamberlain to Munich—and even this relative freedom came to a sudden end. The editor stopped editing and escaped to South America. The publisher stopped publishing and was sent to a labor camp. My good fortune brought me to these blessed shores, but my manuscript got lost. And as to my friends, the other contributors? Only a few of them survived what was to come.

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There are great differences between this "second edition" and the original, which is to be expected. The first version was not written with an eye on readers trained in medicine, while my lectures in the Lancaster Course (which this book loosely follows) were given to eye doctors. Section IV of the present book, for example, was entirely missing in the "first edition." Very little was said about visual acuity and nothing at all about such topics as strabismus, anomalous correspondence, eye strain and aniseikonia. It is only Section I, structure and contents, which remained more or less the same (I have always been an adherent of the tetrachromatic theory of color vision), also the first two lectures of what now is Section II, and the first four or five lectures of what constitutes Section III of the present volume.

Of course, much new knowledge has come our way since—the contributions of Granit, Polyak, Chavasse, Wright, Ogle—and for this reason even the just mentioned parts of my book contain material which was missing in the original. The references to English-American literature naturally have multiplied. But what changed this author's outlook most was his good fortune in becoming acquainted with three men and their work: Adelbert Ames, Jr., of Dartmouth College; Rudolph Luneburg, of New York University; and Walter B. Lancaster. Ames, probably the greatest experimentalist in visual physiology of our generation, has provided entirely new insight into the role of retinal stimulus patterns for vision; Luneburg brought new life into the long petrified horopter theory\*; and as to the third of these three, Lancaster, there is no need to repeat what I said in the preface to the first volume of this series about the influence this friend and teacher has had upon me. Section IV, the new addition to this volume, could not have come into being without the author's association with Walter B. Lancaster.

But all these new impressions have not changed my approach, as inevitably shown in this text—whatever its merits and shortcomings. Being an eye doctor or a physiologist was not what turned my attention, secondarily, toward vision. It was my primarily philosophical interest in epistemology, in the problem of knowing, that turned me from a frustrated student of theology into a happy student of medicine, physiology, sense physiology, and made me finally choose ophthalmology as a career. But having once been a student of theology has left its indelible marks. What is Man to do?—How is Man to know?—are the two eternal questions of all theology and of all philosophy. They have always remained living issues for my thinking. This volume is as much an attempt at an answer to the second of these questions as an essay on the physiology of vision.

This, as finally printed here, is certainly a hybrid piece. It is the essay of a medical practitioner who, only after many harassed hours of daily practice, has found the time to work on it; the essay of a physician, although the clinical aspect receives secondary consideration throughout; an essay on vision, although its index contains many strange items and some authors' names seldom found in

\*It would have been impossible for me to find my way through Luneburg's intricate mathematics without the help of Doctor Albert Blank of New York and Professor M. Goodwald of Harper's Ferry. I want to express my thanks to both of them.

PREFACE

texts on visual physiology—Plato, St. Augustine or, for that matter, Ewald Hering, a name *not once* mentioned in some of the newer books on vision, notably those from Great Britain, of the last decade.

\* \*

This leads me to another point I cannot leave unmentioned in this introduction: The Prague background, the formative influence upon me of the Physiologisches Institut of the German University and of my first teacher, Ewald Hering's pupil and later successor, Armin von Tschermak. It was in the second year of my medical studies that I heard Tschermak's lectures on general and sensory physiology for the first time (what unforgettable lectures!) and for the first time heard the name of Johannes Müller, Purkinje (once too a professor in Prague), Thomas Young, Helmholtz, Mach, Cajal and Pavlov—all names which my up to then humanistic education had failed to reveal to me. But every corner of the institute breathed the memory of the great Hering. One still used some of his instruments in the laboratory and did research on problems which sprang from his work. One was even shown the window looking through which, legend held, he discovered his law of common visual directions.\* Ever since, Hering has remained the basic authority on visual physiology for this author and a kind of pater familias besides. Even the author's disagreements with some of Hering's teachings carry the air of a family quarrel, with basic loyalty untouched, while his homage to Helmholtz, Hering's great adversary, always has remained somewhat perfunctory, like the homage given an exotic prince a partibus infidelium. Perhaps I should have said "Prague bias," instead of "Prague background." I am not impartial in relating my subject—it would be hard to conceal this. And when I said "Prague background," I should have included the literary café, where, in endless discussions with friends over passages in Plato or Freud or Lao-Tse or the many others, many of the thoughts were first formulated which finally found entrance into this volume.

\* \*

Among my students, there have been many with whom my essentially humanistic approach to a chapter of medicine did not agree. Most of them grew up to see medicine as "pure" Science—having nothing in common with the Humanities. But most of them, I felt while lecturing, had a good time. And so had I. Teaching is a great satisfaction and more and more is a teacher to find out that teaching must be its own reward.

Looking back at my years of teaching, I find how much a reward in itself it has had to be. Had I been more interested in "practical" things, I probably would have found myself sponsored by funds, helped by technicians, promoted by

<sup>\*</sup>See fig. 2 in Professor Ogle's book, Researches on Binocular Vision, for a description of Hering's experiment. I have not referred to it in this text.

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superiors. But I have devoted myself to a subject which most students tend to admire only until they have passed their "exam," a subject those in our profession never fail to call important, even if few do anything appreciable to promote it. Had it not been for my great friend, Walter Lancaster, I would have indeed often despaired in following the path which now is mine. He heartily disagreed with much I present in this volume (there were seldom two people as different in their outlook), but he always encouraged me in presenting it. To grant the right to disagreement was part of his Harvard upbringing. This volume was to be given to him as a token of my appreciation. It is with sorrow that, after so many delays in publication, I can dedicate it only to his memory.

Written on borrowed time, before hours and after hours and between appointments; at home, in the office and in subway trains; and mostly at night; it took years to complete the text, to design the illustrations, to read the proofs, to prepare an index. It took me years, and still, this book is unfinished, I feel, uneven and harassed, I am afraid. Yet, at some stage a work must be considered finished—the law of diminishing returns operates even for the writing and rewriting of books.

Again I want to express my thanks to my wife, Magda, for her encouragement and help; to Mrs. Sylvia Bergman for her beautiful execution of the diagrams; and to my secretary, Mrs. Martha Weiss, for her cooperation in putting this manuscript into shape and for her help in reading the proofs and preparing the index.

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I. An Analysis of Sensations



Sensation, Modality, Spectral Quality-The Adequate Stimulus-The Range of Adequateness-Dominaand Modulators-Specific Energy-Fantastic Visual Nerve Apparitions—Sensory Reflexes-Radiation and Luminousnessand the All-or-None Threshold Parallelism Law-The between Physical Event and Physiologic Response

Y .

BEFORE STARTING our exposition on the sense of sight, on the physiology of vision, some general introductory remarks will be in order. No discussion of facts is planned in this and the coming two lectures and anyone not interested in general aspects of sense physiology might very well skip them. Some of what is said in this lecture is taken almost verbatim from the chapter "Sensory Functions" by Theodore C. Ruch, in Howell's Textbook of Physiology, edited by John F. Fulton, 1947. Most of it, however, was first formulated in one of a series of lectures to which reference was made in the Preface.

A "sense" is a modality of sensation. It is the subjective response to a stimulus (be the latter external or internal, that is, coming from the "outside" world or the organism itself), with a distinctive quality which defies description and can only be recognized by the sensing subject. Senses differ in modality, that is, in quality. They are incommensurable. Our mind might tell us that thunder and lightning are both caused by the same physical event; for our immediate experience, however, they are different sensations. Within the limit of a given sense, a given modality of sensation, a number of submodalities can be distinguished and they are usually designated by special names. We shall therefore speak not only of a light sense, but also of a color sense and even within the latter some differentiate a "red" sense, a "blue" sense, etc., all being submodalities of the sense of sight. But beside such modality as, say, color, every visual sensation carries a spatial quality, an awareness of the location of the stimulus in relation both to the sensing organism and to other sensed modalities. While easily being its most essential feature, the spatial quality is not peculiar to the sense of sight. Sounds, pressure, pain, muscle sensation, all have definite spatial quality. Due to this quality, some of the senses, like hearing or vision, serve to orient the body within its environment. Other senses, like the muscle or joint sense, the visceral sensations, and especially pain, orient the individual about conditions within his own body. As a matter of fact, every sensation, all the time, has its definite spatial quality and Sherrington's classification of the senses is actually based on their spatial quality. He divided the senses into (a) interoceptors, which transmit impulses from the visceral organs, (b) proprioceptors, which give information concerning the position and movements of the body, 4 VISION

(c) exteroceptors, which announce changes in the immediate environments, and (d) teleceptors, which make for the appreciation of conditions and changes in the more remote environments. Obviously, the sense of sight belongs in the last group.

We shall turn first to a short discussion of the adequate stimulus, a term we inherited from the great physiologist, Johannes Müller. The term denotes the fact that for each type of receptor there is a form of energy (whatever the actual meaning of this much misused term of physics) to which the receptor is especially sensitive. For the sense of hearing, for example, the adequate stimulus is the energy of the compression waves of air within certain frequencies. For the sense of sight, it is the radiant energy of the visible spectrum, that is, radiant flux of certain frequencies. When of sufficient intensity other forms of energy will also stimulate a certain receptor. Pressure on the eyeball, e.g., or the electric current applied to the eyeball will also stimulate the retinal receptors. Not only radiant energy. You see "stars" when hit in the eyeball; you "see." Pressure or electricity are non-adequate stimuli for the retinal receptors. The difference is quantitative. Much less energy of the radiant kind is needed to stimulate the retina than, e.g., of the pressure variety. The adaptation of the retinal receptors to the former is so great that according to Hecht's computations under favorable conditions a few quanta of light are sufficient to elicit a response.

One of Sherrington's most significant contributions to our understanding of sensation is the hypothesis that the role of sensory end organs actually consists in lowering the threshold for the discharge of sensory nerves by some specific type of energy.

The chief characteristic of sensory end organs is selective sensitivity to certain stimuli. And it is this selective sensitivity that determines a certain form of energy (even a certain range only of a certain type of it) as an adequate stimulus. "Adequateness" is not a peculiarity resting with the stimulus. There is nothing in a physical event itself to make it an adequate stimulus. For example, radiation of  $\lambda = 700 \text{ m}\mu$  is an adequate stimulus, radiation of  $\lambda = 1.400 \text{ m}\mu$  is not. In itself, most any physical event could be a stimulus as long as it is compatible with life. Temperatures of absolute zero or of 500°C are incompatible with life and therefore out of the race for adequateness. Electricity or magnetism are both important and ubiquitous forms of energy. Still, the first is a "non-adequate" stimulus. It does not act in minimal intensity, while the second is no stimulus whatsoever, because (1) there exist no special sensory end organs for electricity or magnetism through which to discharge sensory impulses and because (2) during its evolution the organism has created no specific subjective modality as its specific reaction to their impingement upon it. We became cognizant of electricity only late and only in a roundabout way, through other senses —the best proof, if any is needed, that our knowledge of the world around us is both limited and determined by the number and the kind of our sense modalities.

As in other realms of biologic or social evolution, greater selectivity is achieved by specialization, by narrowing of range as a price for better performance. A

sensory end organ might have a relatively large "range of adequateness," as we might call it. It might be a relatively wide spectrum of physical events for which a certain sensory end organ acts as a trigger, and in this case the sensory end organ will act as a useful signaler of a greater range of some kind of physical events. This type of sensory end organ will be the phylogenetically older and its response naturally less differentiating. On the other hand, the more selective the sensitivity of some sensory end organ, the shorter its "spectrum of adequateness," the greater will be its value for the recognition of some specific external or internal stimulus situation. Pain is a typical signaler, it only tells, that something is wrong and, due to its inherent spatial quality, tells where, but it does not tell, usually, what is wrong. The amazingly selective sensitivity of the ear of a bat or an insect to a certain frequency of air compression, on the other hand, tells the animal not only that there is "danger," but what kind of danger and where, and it tells this while the danger is far away. It would be too late to let the modality of pain convey the message. Pain is not a teleceptor and it is not too specific.

That sensory end organs for pain are not specific means that they answer all kinds of stimuli. Their range of adequateness is very large. Any narrowing of the range of adequateness naturally calls for a greater number of sensory end organs, the adequateness of each being maximum for a different band in the spectrum of physical events. The organism would not be served best if, in order to achieve greater selective sensitivity, the wider range of an already existing signaler became narrowed down without providing coverage for the rest of the stimulus spectrum. Facilitated recognition of an external situation would in this case be achieved for the price of "blindness" to the rest of the stimulus spectrum. In other words, the organism needs more than one of the more selective type of sensory end organs. Obviously, these cannot be overlapping in their range of adequateness, and by this very fact they have to become mutually exclusive. They cannot both be stimulated by the same stimulus. A priori, the organism has then two alternatives from which to choose: it can (1) replace a signaler, a sensory end organ of wide spectrum of adequateness by two (or more) mutually exclusive discriminators, as we shall call them, or it can (2) add one or two, or any number of pairs of the latter, while at the same time keeping the overall signaling system. We shall see that for the eye two fundamentally different sensory end organs have been found histologically and more sub-types have to be postulated theoretically. Some of wider range of adequateness (phylogenetically probably older) to act as signalers for a more general stimulus situation— Granit, to whom we owe most of our newer knowledge of the sensory mechanism of the retina, calls them dominators; some of shorter range, most likely younger and appearing in pairs, to occasion our refined recognition of external events-Granit calls them modulators.

As to the biologic significance of the adequate stimulus, we could do no better than quote from Ruch (p. 308):

"The sense organs collectively are not unlike a series of light filters. Collectively they analyze the complex energy pattern of the external world—just as

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color filters do in color photography—and translate the complex impressions into an intricate pattern of action currents which are recombined in the cerebral cortex—just as in color printing the various colors are recombined—to give a picture of the external world."

At Newton's time, human thinking was not yet ready for discriminating the subjective from the objective, the phenomenal from the physical. Pertaining to color, for example, it was taken for granted that particles of light are all in themselves different in color and that this gives rise to the differences in sensation. The first break came with the 18th century which replaced the happy duality of soul and body with the unfortunate antinomy, mind and matter. But the belief in the parallelism of physical event and sensation still prevailed. The occasionalist philosopher could not explain sensation without the interference of divine providence in every single instance. Still, even for him a rose was sensed red because a rose was red. The final break in the belief of identity of stimulus and sensation, even of a thoroughgoing parallelism between them, and the clear recognition that a third factor, the sensory receptor, has to be interpolated between the two, is the achievement of one of those great minds at the turn of the nineteenth century: Thomas Young. Analyzing the facts of color mixture as discovered by Newton, he stated (1801) that the presence of three different end organs (he actually spoke of nerve fibers) in the retina is sufficient to elicit all the variety of subjective color responses to the infinite variety of wave lengths of light.

Whether or not this statement is correct, whether or not there are actually three different end organs or more of them, has, as Granit emphasized, no bearing on the revolutionary character of this statement. The fact is that Thomas Young noted for the first time that there is a biological factor, a sampler mechanism, interpolated between stimulus and conscious response, and that there are a limited number of foreordained reactors which react only in a certain manner and react only to part of the total range, the total spectrum of oncoming physical energy. Young, one of the champions of the wave theory of light, knew of the great variety, the whole spectrum of wave lengths, impinging upon the eye. But the possible messages were—as he first realized—limited in number, whatever that number may be.

The concept of specific nerve energy, also originated by Johannes Müller, is closely related to his principle of the adequate stimulus and a logical step forward (1826, exactly a quarter century later) in the direction first pointed out by Young. We have already stated that a sensory organ like the retina can be stimulated by other than adequate stimuli. We know that from the presence of a subjective response. But of what kind is this subjective response? Müller pointed out that it is always of the same modality, whatever the stimulus. One "sees" stars when hit in the eye. The pressure on the retina elicits no other sensation but that of luminousness (the so-called pressure phosphen of Müller). Subjective light streaks are an early sign of diseases of the retina, like detachment, obviously elicited by some mechanical or chemical effect of the pathologic process on the retina. But the subjective sensation, the subjective response, is