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PART III

The Visual Pathway

A confrontation of physiology with anatomy

by

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Introduction

In view of the amount of space allotted to this part of the book—ample in itself but modest considering the enormous literature on the anatomy and physiology of the visual pathway—some indication of what can be aimed at is needed. A major sacrifice is the omission of historical background. The anatomical aspects will be found detailed in Polyak's (1957) comprehensive historical summary. The history of the neurophysiology of the retina, reasonably complete up to 1945, has been described in the author's (1947) "Sensory Mechanisms of the Retina." In terms of neurophysiological experimentation the rest of the visual pathway has a fairly brief history. The first steps were summarized by Bartley in 1941, later developments by Albe-Fessard in 1957. Recently Müller-Limmroth (1959) has published a book on the retina and the visual pathways aiming at completeness with regard to references from the electrophysiological field; to this work the reader is referred for the literature on a large number of special questions such as, for instance, effects of cold, pressure, and drugs on the electroretinogram. Below it has been found necessary to introduce descriptive material of this kind in a manner wholly determined by the relevance of such facts to knowledge of a more coherent type. Albeit deficient, there exists at the moment neurophysiological knowledge with some structure to it and the author's aim is to explain, for beginners, the aims of the experimenters, what has been achieved and also to mention some major deficiencies in our knowledge. Some examples should make clear why this attitude has been adopted.

To the beginner too many loosely connected facts merely would be confusing. Actually they fall into two categories: on the one hand we have facts at the moment really confusing, or facts insignificant, striking, stimulating, as the case may be, on the other hand we have facts that have been assembled in order to illuminate a piece of structural knowledge. This structure may not always be easily discernible. Thus, for instance, the beginner, who is bewildered by the large number of purely descriptive papers dealing with the electroretinogram (ERG) of different animals including man, may not realize that much of this material has served to test the generalization (Granit, 1935) that there are two main types of ERG, those of rod and cone systems respectively—originally called E- and I-retinograms—and that in mixed eyes both types co-exist and can be separated by measures such as light-adaptation, flicker-frequency, and choice of wavelength. This is the kind of organized knowledge that can be built up only by extensive team work on a variety of animals. Today one is entitled to state that we

know the main features of rod and cone electroretinograms and can predict fairly well what will happen in mixed eyes when experimental conditions are varied in certain directions so as to replace scotopic with photopic vision. This means that the results of a very large number of papers now can be briefly summarized in support of a single, broad generalization. Many neurophysiological problems run through such a phase of "accumulation" of facts.

On the other hand there are neurophysiological questions which from the very beginning can be stated with considerable precision and which require a few decisive experiments to exclude some alternatives in favour of others. Thus Himstedt and Nagel in 1902 raised the question of whether the region of maximum spectral sensitivity of the frog's eye—as in man—shifted towards the short wavelengths in dark-adaptation (an effect that in honour of its discoverer we call the Purkinje shift (Purkinje, 1823)) and the reply was "yes", even though, at the time, it was not qualified by precise energy calibrations of the spectrum used. A related problem (Granit *et al.*, 1938, 1939) was whether the amplitude of the ERG in rod vision simply reflected the available amount of visual purple or rhodopsin—the photochemical pigment of the rods—and the answer was "no," as was established by parallel measurements of the two.

Two major aims have animated physiological research on the visual system. In one group stand the biochemical or biophysical questions which to some extent are independent even of the kind of organ that happens to be their subject, and which generally in the last instance lead to the cellular or molecular stage. The aim of the other line of research is to understand the organization of the sensory message in order to elucidate principles of information and control. This is often called integrative physiology. There is no hard and fast boundary between the two modes of approach. But "organization" and "information" touch upon a host of interesting epistemological problems. Constant interchange between the organism and its environment has created biological structures which from this point of view are manifestations of certain aims. Thus the eyes of night animals and day animals are very different and in biology it is just as legitimate to describe the "meaningful" adaptations for these two extreme conditions as to determine, say, the quantum efficiency of rhodopsin. Another example is the mechanism of colour reception. If colour had not been perceived by man, the problem might never have occurred to us and, when studying electrophysiologically the effects of variations of wavelength on the eye, our own world of colour and light remains in the background as a secret frame of reference, guiding or misguiding—as the case may be—by preconceived notions our research, and again secretly introducing questions of purpose and meaning, the general problem of how something is organized to perform certain tasks.

References

- Albe-Fessard, D. (1957). Activités de projection et d'association du néocortex cérébral des mammifères. *J. Physiol. Path. gén.* **49**, 521-588.
- Bartley, S. H. (1941). "Vision. A Study of its Basis". Macmillan & Co., London.
- Granit, R. (1935). Two types of retinae and their electrical responses to intermittent stimuli in light- and dark-adaptation. *J. Physiol.* **85**, 421-438.
- Granit, R. (1947). "Sensory Mechanisms of the Retina". Oxford University Press, London.
- Granit, R., Holmberg, T., and Zewi, M. (1938). On the mode of action of visual purple on the rod cell. *J. Physiol.* **94**, 430-440.
- Granit, R., Munsterhjelm, A., and Zewi, M. (1939). The relation between concentration of visual purple and retinal sensitivity to light during dark-adaptation. *J. Physiol.* **96**, 31-44.
- Himstedt, F., and Nagel, W. A. (1902). Versuche über die Reizwirkung verschiedener Strahlenarten auf Menschen- und Tieraugen. *Festschrift der Universität in Freiburg*, 259-274.
- Müller-Limmroth, H.-W. (1959). "Elektrophysiologie des Gesichtssinns. Theorie und Praxis der Elektroretinographie". Springer Verlag, Heidelberg.
- Polyak, S. (1957). "The Vertebrate Visual System". University of Chicago Press, Chicago.
- Purkinje, J. E. (1823). "Beobachtungen und Versuche zur Physiologie der Sinne. Beiträge zur Kenntnis des Sehens in subjektiver Hinsicht", II. J. G. Calve, Prague.

ADDENDUM

This review was completed in January 1960. Since then the following major summaries have appeared:

- Brindley, G. S. (1960). "Physiology of the Retina and Visual Pathway". Edward Arnold, London.
- Galifret Y. (Ed.) (1960). "Mechanisms of Colour Discrimination". Pergamon Press, London.
- Jacobson, J. H. (1961). "Clinical Electroretinography". Charles C. Thomas, Springfield.
- Jung, R., and Kornhuber, H., (Eds.) (1961). "The Visual System: Neurophysiology and Psychophysics". Springer Verlag, Berlin, Göttingen, Heidelberg.