

## The Retinal Mechanism of Color Reception

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This paper is a review of the analysis of color reception with the aid of electrophysiological methods. Microelectrodes have been inserted into the retina to record the discharge of impulses from single or a restricted number of elements in response to illumination with a spectrum of known energy distribution. From the electrodes leads have been taken to amplifier, cathode ray, and loudspeaker. In this manner it has been possible to obtain curves showing the distribution of sensitivity to spectral light of active elements in the eyes of mammals, amphibians, and fishes. Thomas Young's conception, that the retina possesses elements sensitive to different regions of the spectrum, has been proved to be correct. A number of other results illustrate some fundamental properties of the mechanism of color reception.

THE key to the problem of color reception was given by Thomas Young in 1801 when he suggested that there were fibers in the retina carrying impulses elicited by different regions of the spectrum. When he, as well as von Helmholtz 50 years later, for well-known reasons chose a triple response and developed the trichromatic theory, this step was merely an elaboration of his first brilliant generalization. Today we are in a position to put Young's idea to an experimental test. The electrophysiological technique enables us to lead off directly from restricted areas in the retina, and this work has demonstrated the fundamental correctness of Thomas Young's conclusion. At the same time many unexpected facts have turned up and the full significance of them cannot yet be understood. Much remains to be done, but there are already a number of basic facts which deserve to be presented to those outside the domains of electrophysiology who are interested in color vision.

### FIRST ATTEMPTS WITH THE ELECTRORETINOGRAM

The electroretinogram, a relatively slow polyphasic potential elicited upon illumination of an eye, was discovered in 1865 by the Swedish physiologist Frithiof Holmgren and rediscovered in Scotland somewhat later by Dewar and McKendrick (1873). This discovery raised some hopes that the ancient problem of color vision would yield to the pressure of the new technique. Already in 1901 it was first shown by Himstedt and Nagel that light- and dark-adapted frogs' eyes reproduced the distribution of sensitivity

called for by the well-known Purkinje-shift. Other contributions confirmed this conclusion which, however, was not put on a strictly quantitative basis until 1937 by our own work [Granit and Wrede (1937); Granit and Munsterhjelm (1937); Granit (1937)]. It has also been shown that the size of the electroretinogram of dark-adapted eyes was distributed in the spectrum much as the absorption curve for visual purple (see author's review (1938)).

But these facts, after all, did not offer color theory anything that was radically new. Some authors [Kohlrausch (1914), (1918); Brossa and Kohlrausch (1913)] concluded that different wave-lengths gave different types of electroretinogram. And if this had been so there would have been, so to speak, a natural opening for an attack on the physiology of color reception, but these results have been disputed and remain unconfirmed [Graham, Kemp and Riggs (1935); Granit *et al.* (1937)]. They have failed to convince chiefly because many such effects could be imitated by intensity variations, others could be explained on the idea of a difference in the relative contribution of rods and cones to the total response. It is clear that a mixture of photopic (daylight) and scotopic (dim light) spectra can be made to simulate a mixture of, for example, green and yellow.

New hopes were raised by the idea that selective fatigue to one wave-length, by removing its own elements, would leave the electroretinogram with the more or less isolated response to other wave-lengths. Waller (1903) was the first