stimuli used fell within the small limits of a retinal summation area. These results are important to have for understanding areal effects in vision, but I do not see that they argue for the validity of the Helmholtz theory. Small field studies do show, on the other hand, that a stimulus of any wavelength, if made sufficiently small at a moderate intensity is seen as either green or red in the fovea (small-field tritanopia); if made still smaller (or less intense) such spectral stimuli look white or achromatic. The paired loss of, first, blue and yellow, and second, red and green, is of course consistent with a theory of paired, opponent-color processes.

Dorothea Hurvich-Jameson (to U. Söderberg): 1. It is true that sensitivities vary in different parts of the retina but nevertheless homogeneous stimulus fields tend to be seen as uniform in appearance as if some sort of averaging process occurs. We would expect that surrounds of different sizes would yield different results both because of the sensitivity gradient and because of the effect of area per se. Thus we would consider surround size to be a relevant stimulus parameter. In the sense of “distorting” the results, however, this could occur only if we did not keep the surround image constant in comparisons of different surround chromaticities.

2. Eye movements certainly occurred in our experiments, and there is no question that different results are obtained when a “stopped-image” technique is used to compensate for involuntary eye movements and thus to keep the stimulus imaged on the same part of the retina. One of the major findings of the experiments utilizing stopped images is that there is a tendency for the test field to fade and eventually disappear. This artificial situation is more distorting with respect to normal vision than the one where involuntary eye movements do occur during fixation and where image clarity is maintained.

To W. Sickle: We agree with Dr. Sickle that the level of adaptation must be controlled in experiments that seek to determine the response vs. intensity relation whether the function is constructed from discrimination measures or measured directly. The relevance of adaptation level is seen in the work of Craik, Marshall and Talbot, and Hopkins, among others. Our own subjective magnitude scales show the importance of adaptation level and surrounding stimulation for the form of the subjective brightness function.

The finding of different b-wave slopes for different stimulus wavelengths in the excised frog’s eye provides an interesting lead, but to interpret the precise significance of this finding requires that we know more about the significance for vision of the various components of the ERG.

To R. Jung: The finding of decreasing neural response with increase in stimulation in the flicker studies on cat is an excellent example that illustrates two of the main points that we have sought to make about the response versus intensity relation. It makes clear that in physiological studies as well as in psychophysical ones, experimental determinations of this function will show wide differences in form depending on the particular stimulating conditions used. Since this is so, it also illustrates why correlations between physiological and psychological measures should properly be restricted to the results of experiments in which the stimulating conditions are as closely similar as possible.

The Origin of “on” and “off” Responses of Retinal Ganglion Cells

By


With 5 Figures

The complex train of neural events responsible for vision is initiated by the absorption of light in a photoreceptor cell, which in the vertebrate retina is but one

---

1 From the Physiology Division, Naval Medical Research Institute, National Naval Medical Center, Bethesda, Maryland, and Thomas C. Jenkins Department of Biophysics, Johns Hopkins University, Baltimore, Maryland.

2 The opinions or assertions contained herein are the private ones of the authors and are not to be construed as official or reflecting the views of the Navy Department or the naval service at large. The research was supported in part by National Science Foundation Grant G-7096.
unit of a highly organized structure containing many types of cells, nerve pathways and synaptic relationships. Very little is known regarding the role that each of the retinal structures plays in the transmission of information concerning the initial event of photoreception. We know that the various parameters such as intensity, hue, duration, shape, etc., must be encoded into the sequence of nerve impulses which leave the retina by way of the optic nerve. The ganglion cell is the final common pathway into the optic nerve through which the information regarding the stimulus must flow. In the complex pattern of the responses of this cell we can search for information on the controlling factors. Finding out the laws that govern the encoding of information by the retina is a basic step toward the understanding of the operation of the entire visual system.

It is well known from the work of Hartline (2), Kuffler (4), Granit (1), and others that all vertebrate retinal ganglion cell response patterns may be fairly well fitted into three types according to whether evoked spike discharges occur during illumination ("on" type); or they appear following extinction of illumination ("off" responses); or at both times ("on-off" type). In addition to the "on" and "off" components of the response patterns, an inhibitory aspect can often be detected in the discharge patterns either as a suppression of any preexisting spontaneous activity, or as the abrupt termination of a prolonged "off" discharge by re-illumination.

We consider that the response patterns and the presence of the three components can be explained on the basis of two independent processes acting on the ganglion cell. One is an excitatory influence tending to cause the ganglion cell to discharge spike potentials probably through a simple mechanism which depolarizes the cell membrane to the point of instability causing repetitive oscillations. The other process is an inhibitory influence which acts to prevent the ganglion cell from discharging spike potentials, perhaps by hyperpolarizing the cell membrane.

Since we assume that the membrane of the retinal ganglion cell is similar to those neural membranes whose electrochemical properties have been studied in detail, we would expect hyperpolarization of it by the inhibitory synapses to be followed by a post-inhibitory rebound or "off" discharge. This post-inhibitory rebound would be similar to the well known anodal break phenomenon and is consistent with the Hodgkin-Huxley model (3) of the nerve membrane. In this model, prolonged hyperpolarization decreases the potassium ion conductance and increases the rate of change of the sodium ion conductance when the membrane is subsequently depolarized. These changes in membrane conductance persist for some time after the hyperpolarizing current ends. Thus at the cessation of illumination when the hyperpolarizing influence is removed, the membrane potential of the ganglion cell falls toward the normal resting level. However, due to the decreased potassium ion conductance and the increased sodium ion conductance, the net ionic flux at the normal resting potential is inward. This results in still further depolarization of the membrane and the initiation of one or more impulses. Thus the inhibition and "off" components of the response are both the result of the same inhibitory process acting on the ganglion cell.

The evidence for the statement that the determinants of ganglion cell activity may largely if not exclusively depend upon the interaction of two simple opposed influences, one excitatory, the other inhibitory, is based on our studies on the iso-