

Some neural mechanisms of visual perception

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Some experiments dealing with the comparative neuropsychology of vision were reviewed. The experiments dealt with the anatomical structure and function of the peripheral receptor, the mechanism for the conversion of energy by the peripheral receptor, the nature of the peripheral neural code for the representation of peripheral phenomena, the nature of the central relay mechanisms, and the nature of the cortical representation of peripheral visual phenomena. The classic experiments of Hecht, Wald, Hartline, Dowling, DeValois, and Hubel and Wiesel were reviewed.

The purpose of the present paper is to review some experimental approaches to the comparative neuropsychology of vision. Studies to be reviewed will include experiments with such diverse organisms as horseshoe crabs, dragonflies, rats, cats, primates, and humans. The studies that have been selected for review provide information from a comparative point of view. The outcome of such a review will be a composite model of a visual system based upon data from mammalian and invertebrate sources.

Hecht's (1929) work on dark adaptation in humans provides a starting point and lends some insight into the functioning of the mammalian visual receptor. Hecht found that the visual threshold varied in a systematic manner with time in the dark.

The most noteworthy feature of the experiment was the finding that the dark adaptation curve consisted of two functions, a slowly adapting one and a more rapidly adapting portion. The rapidly adapting portion presumably represented cone vision, and the slowly adapting portion represented rod vision. Such an interpretation is supported by anatomical findings of two distinct types of visual receptors on the mammalian retina. Hecht's (1929) conclusions concerning the nature of the visual receptor were inferential and were based upon observations of two different rates of adaptation reflected in the dark adaptation curve (Detwiler, 1941). Wald (1959) determined that the biochemical basis for the dark adaptation process could be found in the rhodopsin cycle. The breakdown and regeneration of rhodopsin was shown to correspond to the more molar reversible dark adaptation process. Wald has extended his research to the visual pigments of such diverse organisms as fish and chickens. In a subsequent study, Hillman, Hochstein, and Mercks (1972) inferred the existence of a visual pigment in the barnacle from intracellular recordings of the animal's photoreceptors.

The question of the number of types of receptors in the visual system has been explored with the horseshoe crab (Riggs & Graham, 1945), the dragonfly (Ruck, 1965), and the rat (Dowling, 1963). Riggs and Graham recorded from the optic nerve of the limulus eye while

varying the amount of illumination. The brightness threshold, as measured by an increase in the number of nerve impulses from the optic nerve, was found to vary with intensity of illumination. The experiment yielded a single unbroken curve and suggested, therefore, that the limulus photoreceptor consisted of only one element, and not two, that was sensitive to brightness changes rather than to color. Such a functional interpretation is reasonable, since limulus is a crab of the insect family that crawls along the bottom of the sea and is, most of the time, sheltered from bright sunlight. It is an evolutionarily old organism and, therefore, probably has no color vision.

Ruck (1965), working with the electroretinograms of dragonflies, identified five classes of color receptors in the insect eye. The identification of the color receptors was based upon measurement of the peak sensitivities of spectral sensitivity curves that were taken from the dorsal ocelli and the ventral ommatidia of the compound eye.

Dowling (1963) measured the effects of dark adaptation on the electrogram threshold of the albino rat's eye. An unbroken, slowly adapting function was found that was analogous to the unbroken function found for limulus. Dowling showed that there was a correspondence between the time course of dark adaptation and the rhodopsin content of the rat's eye. The rhodopsin content increased as the visual threshold decreased. The rat's eye, therefore, acts physiologically primarily like an all-rod eye, although there are a few cones present.

The functioning of the optic nerve has been explored electrophysiologically in classic experiments with limulus by Hartline (1934). Hartline recorded from a single fiber of limulus optic nerve and varied the brightness, or intensity, of the peripheral stimulus. He found that the frequency of neural firing of the optic nerve varied directly with the logarithm of the intensity of the peripheral stimulus. The function relating frequency of firing to stimulus intensity was an S-shaped function.

Brightness is coded as the logarithm of the frequency of neural firing in the peripheral visual system. It is a

sinusoidal function rather than a step function, suggesting that the nerve may function as if it were an analog computer rather than a digital computer.

The nature of the central relay mechanisms in the visual system has been investigated extensively by DeValois (1960, 1965, DeValois & Jones, 1961). DeValois (1960) recorded from the six layers of the lateral geniculate body (LGN) of the primate while varying the brightness and wavelength of the peripheral stimulus. The LGN lies deep within the central nervous system and can be reached, in the primate, by stereotaxically placed microelectrodes. DeValois (1960) identified three functionally distinct portions of the LGN, based upon intracellular microelectrode recordings, that corresponded well with the anatomical laminations of the structure. The "on" cells were shown to regulate brightness and color vision, the "on-off" cells were shown to regulate color vision, and the "off" cells were shown to regulate brightness vision.

The Purkinje shift (i.e., the loss of red-green color vision as brightness decreases in the twilight) can also be accounted for by one of DeValois' (1960, 1965; DeValois & Jones, 1961) experiments. There is a shift in peak sensitivity of a red-on cell as brightness is decreased. The shift in color sensitivity, as brightness decreases, is toward the violet end of the spectrum.

Interest in the cortical representation of peripheral visual phenomena dates from the Gestalt-oriented experiments of Lashley, Chow, and Semmes (1951). Those investigators attempted to short-circuit the hypothetical cortical visual fields of the primate by inserting strips of gold foil into the cortex. The operation had no effect on tests of visual discrimination, suggesting that an electrical field theory of cortical functioning in perception was not tenable.

More recently, Hubel and Wiesel (1959), using cats, have correlated cortical visual receptive fields with

perception of simple objects and contours in the cat's peripheral visual field.

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