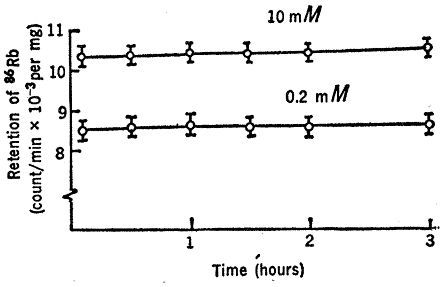

Fig. 3. Efflux of rubidium absorbed by *Chlorella* from 0.2 and 10 m*M* RbCl. *Chlorella* cells (500 mg dry weight equivalent) were allowed to absorb from ^{86}RbCl for 4 hours under light and were then transferred to 1 liter of unlabeled RbCl of equimolar concentrations. Samples were drawn at different times to measure the radioactivity retained in the cells.

RbCl, even at 3 hours (Fig. 3). Respiration of *Chlorella* is significantly enhanced by 10 and 30 m*M* RbCl (Table 2).

A dual isotherm for the absorption of a given ion points to two transport systems and raises the question of the location of each system, whether they operate in parallel at the same membrane or function consecutively across the plasmalemma and tonoplast. The evidence in support of the sequential transport through the two membranes is derived mainly from the absorption isotherms of nonvacuolate root tips and vacuolated segments of corn roots (*13*). Nonetheless, it has been admitted that the distinctions made on this basis cannot be absolute since the subapical cells differ from the apical ones for reasons other than vacuolation. Furthermore, the conclusion that the compartments into which the ions move are subcellular in origin is drawn from the kinetic analysis of ion absorption by multicellular systems (*3, 13*), which consist of cells differing morphologically and physiologically between themselves. The unicellular alga. *C. pyrenoidosa* is nonvacuolate (*9*) and hence devoid of an inner tonoplast membrane. The mechanisms for the dual pattern of rubidium absorption observed in this system therefore must reside in the plasmalemma. Chloroplasts are known to accumulate ions. However, these are functionally and anatomically different from the vacuoles. The occurrence of a dual pattern of absorption by *Chlorella* cells in the dark is evidence that the chloroplast is not implicated in the two ion-absorption mechanisms.

It has been contended that ions at high concentrations readily negotiate the plasmalemma by diffusion (*2*). However, sensitivity to metabolic inhibitors and nonexchangeability of the ion clearly support the view that the uptake, in the low and high concentration ranges, is energy-dependent. The energy for the operation of dual mechanisms in both the light and the dark (Figs. 1 and 2) is presumably derived from photosynthesis and respiration. The implication of respiration with rubidium absorption in the high concentration range (Table 2), which has been observed in higher plants (salt respiration) (*14, 15*), suggests that ion absorption by the second mechanism is not diffusive.

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Receptive Field Organization of Units in the First Optic Ganglion of Diptera

Abstract. Centripetal spike potentials were recorded from two classes of units (transient and sustained) in the intermediate chiasma of flies. On-off units were characterized by a transient discharge after the onset and cessation of a light spot presented within its elliptical receptive field. Receptive fields of sustaining units were composed of three roughly circular regions arranged adjacently along a line; stimulation of the center region elicited a sustained discharge, whereas stimulation of either adjacent region elicited an off discharge. Adjacent regions antagonized the central region, for stimulation of either inhibited the discharge resulting from stimulation of the central region.

The retina and first optic ganglion of flies have highly ordered structures. The retina is comprised of an array of several thousand ommatidia, each consisting of eight retinular cells; the first optic ganglion is composed of a corresponding array of synaptic compartments, called cartridges, each containing endings of six retinular cell axons and several second-order neurons (*1, 2*). Within each cartridge numerous synaptic contacts are made between the six retinular cell axons and two second-order neurons (type I monopolar cells) which send their axons to the second optic ganglion (*2*). Furthermore, the presence of elements conceivably capable of supporting interaction between neighboring cartridge elements (*2–4*) suggests that more than simple summation may occur within the first optic ganglion. Although slow potentials (*5, 6*) have been recorded from the cartridge region of flies, the fact that no spike potential has ever been observed raises the question of how neural signals are transmitted to the second optic ganglion. Experiments were performed which show that, indeed, spike potentials are carried by fibers en route to the second optic ganglion. Two types of fibers were identified whose spatial and temporal characteristics of discharge indicated complex integration mechanisms.

Several species of flies, principally *Phaenicia sericata*, were studied, and no species differences were observed. A specimen was prepared for an experiment by removal of a small triangular flap of exoskeleton from the posterior surface of the head capsule, which exposed one optic lobe. The preparation was placed at the center of a reflecting sphere (2 m in diameter) upon which stimulus patterns were projected. Tungsten microelectrodes (noise level 20 μv, peak-to-peak) were placed in the intermediate chiasma, and centripetal discharges representing two distinctly different classes of units were recorded (*7*).

One type is an on-off unit which responds to a diffuse light pulse with a transient discharge following the onset and cessation of stimulation. The other type is a sustaining unit which is quiescent in the dark, as is the on-off unit, but a diffuse light pulse elicits

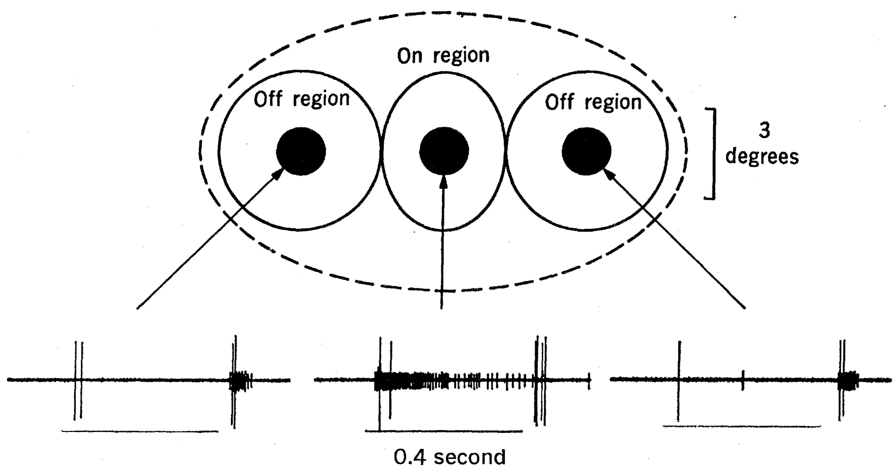

Fig. 1. Receptive field organization of the on-off and sustaining units. The three records of simultaneously recorded on-off and sustaining units correspond to different location of the 1.5° stimulus spot (dark spots) and characterize the receptive field organization of both units. Whereas the on-off unit responds in a transient fashion (on-off) regardless of the stimulus location within the receptive field, the sustaining unit responds with a maintained discharge upon stimulation of the on region and with a pure off discharge upon stimulation of either adjacent off region. In this case the receptive fields of both units were coincident and are schematically represented by the dashed (on-off unit) and solid (sustaining unit) lines.

an on discharge which slowly adapts to a steady rate dependent upon the light intensity. Frequently a unit of each type is recorded simultaneously with one electrode (Fig. 1), and in all cases the amplitude of the spike potential of the on-off unit exceeds that of the sustaining unit. Although 102 on-off and 74 sustaining units were studied, the relative number of each type does not reflect their true proportion, for on-off units were easier to observe and isolate. Another property which differentiates the two units is the threshold, for the sustaining unit is, on the average, 1.3 log units more sensitive to a small spot of light placed at its receptive field center.

The receptive field configuration of each unit was investigated by the presentation of a 1.5° light spot at each point of a 7 by 11 grid having a 1.5° spacing between grid points. Three representative records of the 77 taken during a typical experiment in mapping the receptive field are shown in Fig. 1.

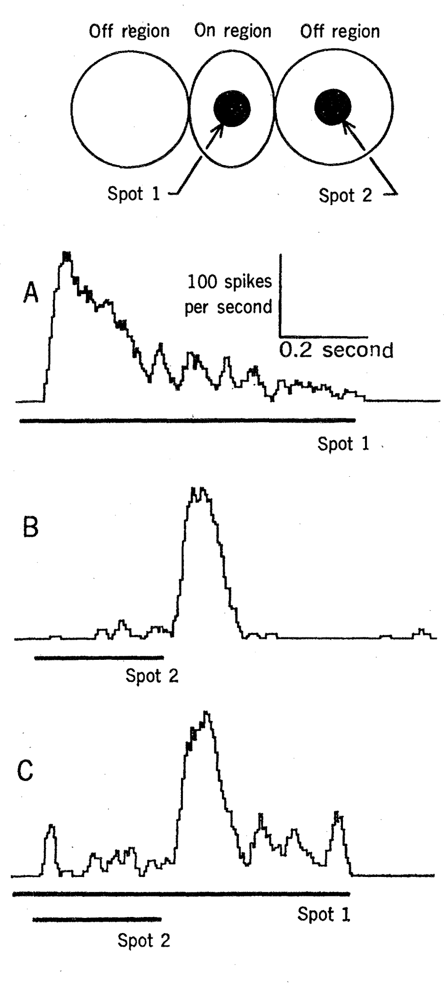

Fig. 2. Inhibitory influence exerted through the off regions of the sustaining unit. Poststimulus time histograms A and B represent the average discharge behavior resulting from stimulation of the on region (spot 1) and off region (spot 2), respectively. Note that some discharge occurred during the presentation of spot 2 and was presumably due to scattered light. Histogram C represents the average discharge behavior when both regions are stimulated in the temporal order indicated and reveals the inhibition resulting from stimulation of the off region. The histograms were computed from 12 trials, and the bin width was 4 msec. Both spots were 1.5°, and spot 2 was 0.9 log unit more intense.

An on-off and a sustaining unit were recorded simultaneously; the dark spots represent the approximate size and location of the three stimuli relative to the schematized outlines for the receptive fields (*8*) of both units. The on-off unit has an elliptical receptive field with average half-sensitivity angles (*9*) of 5.5° and 4.2° along the major and minor axes, respectively. Furthermore, the orientation of the major axis for all on-off units studied corresponds to the mediolateral axis (*10*) of the eye. The receptive field is homogeneous in that the discharge rate and not the discharge pattern is dependent upon the stimulus location.

In contrast, the receptive field of the sustaining unit is not homogeneous but, instead, consists of three functionally distinguishable regions each being roughly circular and arranged adjacently along a mediolateral axis line. Stimulation of the center on region elicits a sustained discharge characteristic of stimulation with diffuse light (Fig. 1); however, stimulation of either adjacent region elicits an off discharge. Consequently, the sustaining unit also possesses an elliptical receptive field which, like that of the on-off unit, is always oriented with its major axis roughly along the mediolateral axis of the eye. The average half-sensitivity angles of the on region along the major and minor axes are 2.4° and 2.7°, respectively, which compares favorably with the 3° average half-sensitivity angle for retinular cells in the frontal part of the eye (*11*).

On the basis of the discharge patterns evoked by stimulating the on and the off regions and on the basis of the pinched appearance of the on region along the major axis (*12*), antagonism between the on and off regions was suspected. Experiments were performed to test this possibility by the simultaneous presentation of 1.5° light spots to both the on and off regions. In Fig. 2 poststimulus time histograms A and B represent the average discharge elicited by stimulation of the on region (spot 1) and off region (spot 2), respectively; poststimulus time histogram C is the average discharge behavior when both stimuli are presented in the temporal order indicated. The inhibitory influence of stimulation of the off region is readily apparent, and both off regions are equally effective. However, to reveal such significant antagonism as this, it is necessary to make the intensity of spot 2 as much as 1 log unit greater than spot 1.

The sizes of receptive fields of both units reveal that they integrate the activity of several cartridges and that they do so more extensively along the mediolateral axis of the eye. However, the complex temporal characteristics of both units indicate that more than simple summation of the retinular cell signals occurs in the first optic ganglion. The spatial and temporal characteristics of the discharge of the sustaining unit suggest that the sustained discharge reflects the excitatory influence of the retinular cells converging on a single cartridge while the off discharge reflects a rebound from inhibition (*13*) resulting from the excitation of neighboring cartridges along the mediolateral axis. The discharge characteristics of the on-off unit are not so easily explained. The receptive field organization of sustaining units is similar to that of eccentric cells in *Limulus* and of certain retinal ganglion cells (on center) in the vertebrate eye, for, like both, lateral inhibition can be demonstrated and antagonistic discharge (off) can be elicited by stimulation of the surround region of the receptive field (*14*). However, in contrast to the concentric receptive field organization of the eccentric and retinal ganglion cells that of the sustaining unit is not circularly symmetric.

The existence of centripetal discharges in the intermediate chiasma establishes that spike potentials are a mode of neural communication between the first and second optic ganglia; however, only two different types of units have been identified on the basis of their discharge behavior to various stimuli (spatial, temporal, spectral, polarization) (*15*), and at least six centripetal fibers, associated with each cartridge, have been identified anatomically (*4, 16*). It would appear that either the units unaccounted for do not support impulse traffic, or they do and their discharge behaviors are either not sufficiently different from those of the on-off and sustaining units as to be distinguished with the types of stimuli available or their signals cannot be observed with the techniques used. The anatomical study of Trujillo-Cenóz (*16*) revealed two large fibers (3 to 4 μm) associated with each of the many bundles of fibers comprising the intermediate chiasma, and these fibers correspond to the axons of the type I monopolar cells of each cartridge. It is, therefore, possible that one large fiber of each pair is responsible for the on-off discharge while the other mediates the sustained discharge; however, it is difficult to account for the disparity in spike size between the two types of units. Furthermore, Autrum *et al.* (*6*) have recently recorded hyperpolarizing slow potentials without evidence of spikes from neurons in the first optic ganglion which they believe are monopolar cells. These observations are difficult to reconcile unless the micropipette renders the cell incapable of spike generation or unless spikes do not invade the cell body. The situation is further complicated by a recent report by Strausfeld and Braitenberg (*4*) that a type II monopolar cell associated with each cartridge sends collaterals to adjacent cartridges along the +Y and −X axes where they terminate on one of the type I monopolar cell processes, for the axis of interaction implied by this anatomical observation is roughly perpendicular to the axis of interaction manifested by the elliptical receptive fields of the on-off and sustaining units. Although the functional and structural correlates of the first optic ganglion remain unsettled, it is clear that profound transformations are made on the retinular cell signals.

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7. Stainless steel microelectrodes were also used, thereby making it possible to deposit a small amount of iron at the recording site which upon histological examination was found in the intermediate chiasma.
8. The outlines reflect only the relative shape and size of the receptive field of the on-off and sustaining units. A more absolute measure is given by the angular sensitivity which is the reciprocal of the stimulus intensity required to elicit a criterion response (one spike) as a function of the angular orientation of the stimulus relative to the receptive field center of the unit.
9. The separation, measured in degrees of arc, between points having half the maximum sensitivity and lying on an axis line of the receptive field is called the half-sensitivity angle along that axis. If the receptive field is circularly symmetric, then one half-sensitivity angle suffices.
10. This corresponds to the Z axis as defined in V. Braitenberg, *Kybernetik* **7**, 235 (1970).
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12. The pinched appearance of the on region is not particularly well reflected in the half-sensitivity angle values since these measurements were made at threshold. The effect is best observed in experiments to map the receptive field when the stimulus intensity is 2 to 3 log units above threshold.
13. Inhibition and off discharge are frequently associated; for example, see R. Granit, *Sensory Mechanisms of the Retina* (Oxford Univ. Press, London, 1947); C. A. G. Wiersma and T. Yamaguchi, *J. Exp. Biol.* **47**, 409 (1967); M. L. Wolbarsht, H. G. Wagner, E. F. MacNichol, Jr., in *The Visual System: Neurophysiology and Psychophysics*, R. Jung and H. Kornhuber, Eds. (Springer-Verlag, Berlin, 1961), p. 163; R. Granit, *Receptors and Sensory Perception* (Yale Univ. Press, New Haven, 1955). The strength of the off discharge or postinhibitory rebound depends greatly on the species and the level of the nervous system.
14. Special conditions must be employed to elicit an off discharge from eccentric cells. In this respect, the behavior of sustaining units more closely resembles that of on center units in the vertebrate retina. F. Ratlif and C. G. Mueller, *Science* **126**, 840 (1957).
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Serum Dopamine-β-Hydroxylase: Decrease after Chemical Sympathectomy

Abstract. *Dopamine-β-hydroxylase is an enzyme that is localized to catecholamine-containing vesicles in sympathetic nerves and the adrenal medulla, and is also found in the serum. Treatment of rats with 6-hydroxydopamine, a drug which destroys sympathetic nerve terminals, leads to a decrease in serum dopamine-β-hydroxylase activity. The decrease is not due to an effect on the adrenal medulla or to an increase in circulating inhibitor or inhibitors of enzyme. These data represent evidence that at least a portion of the circulating dopamine-β-hydroxylase activity arises from sympathetic nerve terminals.*

Dopamine-β-hydroxylase (DBH), the enzyme that catalyzes the conversion of dopamine to norepinephrine (*1*), is localized to the chromaffin granules in the adrenal medulla (*2*) and to the catecholamine-containing vesicles in