Function of Insect Compound Eyes
Containing Crystalline Tracts

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ABSTRACT Image formation is studied in compound eyes of insects that contain crystalline tracts. In optical experiments the course of light is studied in fresh scalp of dark-adapted eyes using point and extended sources. In the tract region a point source gives a diffusely lighted area within which are punctate spots about 10 times brighter. Because the position of these spots does not change when the source is moved, and because their spacing agrees with estimates based on the known scalp depth, we conclude that these spots represent light radiating from the cut ends of tracts. An extended source gives a dim erect image in the tract region that may come from the pattern of illumination radiating from the cut ends of the tracts. In electrophysiological experiments intracellular microelectrode recordings of responses to illumination are made from single retinular cells of the skipper, Epargyreus clarus, an animal that lacks iris pigment. Measurements of visual fields of single retinular cells by three methods give half-power beam widths of about 2°. Though not conclusive, these experiments suggest that only the light contained in the tract is effective in stimulating the retinular cell. This agrees with the theoretical study of Allen (1968) and is inconsistent with the superposition theory of Exner (1891) as applied to certain moth and skipper eyes.

The classical theory of the function of the arthropod compound eye was proposed by Johannes Müller in 1826. Müller postulated that each ommatidium functions to monitor the intensity of the light from the direction that it faces. This mosaic theory was generally accepted for all compound eyes until 1891 when Sigmund Exner published a monograph on the physiology of the compound eyes of crustaceans and insects. He classified the compound eyes in two groups according to their function: the apposition and the superposition eyes. The superposition eyes are characterized by certain anatomical features, the most important of which is that the rhabdomeres are separated from the crystalline cones by considerable distances. The rhabdomeres and cones are, however, connected by crystalline tracts. When Exner examined these eyes to
study their function, he removed the rhabdomeres and the crystalline tracts and substituted glycerine solution. In such cleaned out *Lampros* eyes Exner observed a superposition image at the level of the rhabdomeres. He also observed a similar but poorer image in dark-adapted moth and crustacean eyes.

De Bruin and Crisp (1957) showed that the crystalline cones and tracts in some crustacean eyes form optically continuous strands with a higher refractive index than the surrounding medium and they suggested that these structures function as wave guides.

The superposition theory was also questioned by Nunnemacher (1959, 1960) and Kuiper (1962). They examined many crustacean eyes and failed to detect any superposition images. Kuiper did, however, confirm Exner's observations even to the finest details when he repeated the experiments on *Lampros*. Nunnemacher studied scalps of frozen eyes of *Lampros* and saw a superposition image, but it always fell behind the rhabdomeres. Recently, Horridge (1968) has found that the tracts in the firefly, *Photuris*, act as light pipes.

The previous studies have left a number of unresolved questions about the optical function of eyes with tracts. These include the problems of whether or not the crystalline tract actually is a light pipe in dark-adapted eyes, how much light, if any, is outside the tracts, and what is the path of light that stimulates the retinular cells. In an effort to resolve these problems we have been working with Bernard and Allen (Allen and Bernard, 1967; Allen, 1968; Miller, Bernard, and Allen, 1968) on theoretical, optical, anatomical, and physiological studies of various tract eyes. In a theoretical and experimental optical study of the tobacco hornworm moth compound eye Allen (1968) found that an image is focused at the distal end of the tract and that the tract is a light pipe. In the present investigation, optical and physiological experiments are reported that tend to support the light pipe theory.

**METHODS**

**Anatomy**

The anatomy of the compound eyes is studied with the light microscope. The eyes are fixed in 1% glutaraldehyde in phosphate buffer, pH 7.2, and embedded in Maraglass. Thick sections of these eyes are examined using the light microscope in order to measure the appropriate dimensions of the optical apparatus.

**Optical Experiments**

Completely dark-adapted living moths of the species *Hyalophora cecropia, Antheraea polyphemus*, and *Chaerocampa elpenor*, and the skipper, *Euphryus clarus*, are used. The animals are decapitated and scalps of the eyes are made with a razor blade. The scalps are transferred to a drop of 1% solution of glutaraldehyde in phosphate buffer at pH 7.2 on a cover glass. The cover glass is mounted in a moist chamber with the
eye looking down and positioned in the center of a universal stage. The universal stage is mounted on a Leitz compound microscope. The eye is illuminated with collimated light from a microscope lamp with a 15 W incandescent bulb (running at 5 V and 2 amp) mounted under the preparation at a distance of 70 cm.

The lamp together with its filter holder and diaphragm is attached to a pivot arm with its center of rotation at the preparation. A diagram of the experimental setup is shown in Fig. 1. Most observations are made with a 550 nm interference filter and a 2.0 log unit neutral density filter in the light beam. Scalps are also examined mounted on a front-surface mirror and under a dissecting microscope with the light coming from the same direction as viewing.

![Figure 1. Schematic diagram of experimental setup for optical experiments. Full explanation in text.](image)

**Electrophysiology**

All experiments reported here are on the silver spotted skipper *Epargyreus clarus*. The animal is decapitated and the head mounted with beeswax on a "jolter" (Tomita, 1965). A small hole is made in the cornea with a razor blade and then sealed with silicone grease. Cell penetrations are made with glass microelectrodes filled with 2 N KCl with a resistance between 100 and 200 Mohms. The potential changes in the cells following illumination are measured with a precision electrometer (M4, W-P Instruments, Hamden, Conn.) and displayed on an oscilloscope screen.

The light stimulus comes from a fiber optics bundle mounted on a perimeter at a distance of 33 cm. The light source subtends an angle of about 0.1°. A Xenon lamp
(Bausch and Lomb) serves as the light source. The light stimulus is controlled by a series of neutral density filters (Kodak) and a shutter and is monitored with a silicon photocell placed just under the eye.

The skippers are caught in the rural area around New Haven and used as soon as possible. However, satisfactory recordings can be made from animals kept for 2-3 days at +6°C. The animals are decapitated in dim light and prepared in red light. As soon as a successful penetration is made, we determine the center of the visual field and make recordings with the light in different positions, usually every 0.5° across the entire field. The size of the visual field is determined in two ways. One is to measure the size of the response at the center of the visual field and find the angular position off center that gives the same response at twice the intensity (half-power point). The other is to find the light intensity that gives a threshold response (2-3 mv) at the center of the visual field and to increase the intensity by small steps. At these increased intensities we determine the positions at which the increased light gives the threshold response. The angular positions can be determined with an accuracy of ±0.1°.

RESULTS

Exner’s Firefly Experiment

The interior soft parts of the firefly eye are carefully removed with a sharpened wooden toothpick, so that only the cornea with its attached crystalline cone remains. The hole is then filled with a 14% aqueous solution of glycerine, n = 1.35. We mount the eye as shown in Fig. 1 and described under Methods and with a 10× objective we observe and photograph the pattern of light at different distances from the cornea as indicated in Fig. 2. Our results confirm Exner’s and Kuiper’s observations. A superposition image of the light source is formed at the level of the rhabdomeres as seen in Fig. 3 E. When the focal plane is lifted above this level, the light rays from the crystalline cones diverge forming an hexagonal pattern (Fig. 3 F).

If the point source subtending an angle of 0.6° is replaced by an extended source which is a runic R subtending 4° lengthwise, we see small inverted images 30 μ distal to the tip of the crystalline cones (Fig. 4 A) and an erect superposition image at a distance of 340 μ from the front surface of the cornea (Fig. 4 B).
Optical Experiments on Scalps of Fresh and Fixed Eyes

We prepare scalps of the moth and skipper eyes as described under Methods. Using dim light to prevent light adaptation, we study the light from the point source. Proximal to the crystalline cones there is a diffuse area of light that converges toward the back of the eye. This diffuse spot of light is illustrated in Fig. 5 B. The microscope is focused on the plane of section of the eye; the
depth of the scalp is 630 μ. The depth of the scalp is measured by inverting the preparation and focusing first on the corneal surface and then on the cover slip. The diameter of the diffuse spot seems to be larger in eyes with greater radii of curvature and with larger sources of light.

![Figure 5](image1)

**Figure 5.** Scalp of compound eye of *elpenor*. A, spot of light presumably radiating from cut end of tract (arrow). B, same experiment as A but with 10 times the exposure length to show diffuse halo. Marker, 1 mm.

In *elpenor* and *polyphemus* this diffuse area of light is smallest in front of the rhabdomes within the tract region. By careful manipulation of the universal stage and by placing the light in different positions, small spots of light are seen at the level of the cover slip, i.e., at the plane of sectioning the eye. The alignment of all parts of the optical path is quite critical. The spots are approximately 1 log unit brighter than the immediate surround (Fig. 5 A). Occasionally by compromising, it is possible to illuminate two spots at once. It is also possible to walk the spot from one place to another, either by moving the light source or by rotating the universal stage.

![Figure 6](image2)

**Figure 6.** Scalp of compound eye of *elpenor*. A, illuminated with point source (see tract at arrow). B, illuminated by extended source with superimposed runic R. Marker, 1 mm.
**Table 1**

**Dimensions of the optical apparatus of some tract-containing eyes and their visual fields as determined by optical methods**

<table>
<thead>
<tr>
<th>Species</th>
<th>Corneal facet diameter</th>
<th>Cone length</th>
<th>Tract length</th>
<th>Rhabdom length</th>
<th>Radius of curvature</th>
<th>Incipient radius of curvature</th>
<th>Visual field</th>
</tr>
</thead>
<tbody>
<tr>
<td>Photuris</td>
<td>28</td>
<td>106</td>
<td>235</td>
<td>110</td>
<td>970</td>
<td>1.6</td>
<td>1.6</td>
</tr>
<tr>
<td>Antheraea polyphemus</td>
<td>32</td>
<td>46</td>
<td>570</td>
<td>138</td>
<td>1170</td>
<td>1.6</td>
<td>3.3</td>
</tr>
<tr>
<td>Hyalophora cecropia</td>
<td>31</td>
<td>100</td>
<td>600</td>
<td>160</td>
<td>1500</td>
<td>1.2</td>
<td>1.2</td>
</tr>
<tr>
<td>Manduca sexta</td>
<td>29</td>
<td>100</td>
<td>900</td>
<td>200</td>
<td>2000</td>
<td>0.8</td>
<td>~2.0</td>
</tr>
<tr>
<td>Epargyrus clarus</td>
<td>27</td>
<td>100</td>
<td>400</td>
<td>200</td>
<td>1200</td>
<td>1.3</td>
<td>4-5</td>
</tr>
</tbody>
</table>

**Figure 7.** Scalp of *elpenor* after optical experiment. Phase microscopy. Note accordion-like deformation of tracts (arrow) and pigment position corresponding to dark-adapted state. C, cornea. Marker, 25 μ.

When the depth of the scalp and the calculated intertract distance at this depth are taken into consideration, we conclude that these spots of light represent the appearance of the tracts viewed end on. The hexagonal pattern of the tracts can be brought out by changing the direction of the light.
When an extended source is substituted for the point source, we observe an erect image as shown in Fig. 6. This image, however, is very dim and varies in size according to the depth of the scalp; the shallower the scalp the bigger the image. Also, this image can be seen only at the plane of section of the eye. This indicates that the image is formed by light radiating from the ends of the crystalline tracts. Another indication that the spots we observe come from the tracts is that when the point source light position is changed, the spot position remains the same; but it grows brighter or dimmer until it disappears entirely. This experiment also allows one to estimate the total beam width for an ommatidium. By inspection we find visual fields of the order of 2–5° as shown in Table I.

The appearance of one of the preparations after an optical experiment as seen in a 1 μ thick and unstained section viewed by phase microscopy is shown in Fig. 7. This picture shows that the tracts tend to keep their normal relationships with the cones and surrounding material, although some of them tend to contract in the manner of a released spring (arrow). Most important, this section shows that the pigment has not moved and is in the fully dark-adapted state. Although the histology is not done routinely, we always float the scalp on a front-surface mirror after an experiment. When the eye shows a full glow (Fig. 8) viewed with light coming from the direction of viewing, we assume that the distal iris pigment is still in the dark-adapted condition. It has been shown that pigment migration towards the light-adapted position obliterates the glow (Högland, 1966).

**Electrophysiology**

For our purposes the skipper compound eye is a desirable physiological preparation because although the eye has crystalline tracts surrounded by "iris" cells, these iris cells do not contain pigment. This is illustrated by the phase
contrast light micrograph of Fig. 9. Note that pigment is located between the crystalline cones. This pigment does not appear to move when the eye is exposed to bright light and fixed in the light, but it is difficult to rule out the possibility of rapid pigment movements over short distances.

The penetration of single cells in the skipper eyes is facilitated by Tomita's (1965) jolter device. At the beginning of the downward movement of the electrode we frequently penetrate cells (presumably iris cells) that give negative potentials of the order of 30 mV when the eye is illuminated. The size of the potential varies with the position of the light, but responses can be evoked over large areas indicating that these potentials are merely pickup of the receptor potential in the penetrated cells.
Good penetrations of receptor cells are indicated by abrupt negative changes in DC potential of the order of 40 mv. When stimulated with light, these cells do not show any sign of hyperpolarization, but give a depolarizing response when light strikes the eye from the right direction. We usually search for the visual field of single retinular cells using a 3.0 v naked flashlight bulb that is run at 1.5 v. The sharp depolarization we observe when the light passes the visual field is dramatic. The responses resulting from waving the bare bulb back and forth across an active visual field are shown in Fig. 10. A rough calculation based on the estimated speed of the bulb movement gives about 5° for the total beam width as so measured. Although this is a crude measurement, it is important because it is made under circumstances that almost certainly rule out any effects of possible migration of the pigment around the crystalline cones that could result from light adaptation.

After this coarse determination of the position of the visual field in space, we position the fiber optics approximately and move the light back and forth carefully until we find the center of the visual field.

In some instances we take pictures of the responses with different light intensities. An example of an intensity series is shown in Fig. 11. When the light intensity increases above a certain level, an initial transient becomes evident as shown at 2.4 log units intensity. The graph of another intensity series is shown in Fig. 12. The amplitudes of the peak and the steady-state responses
are plotted against the light intensity. For the higher intensities the discrepancy in amplitude between the peak and the steady state becomes evident, and amplitude in the steady state reaches a maximum at around 3 log units for this particular case.

A coarse indication of the receptive field of an individual retinular cell can be obtained by stimulating the eye at different angles of incidence. Usually we start about 5° off-center and expose the eye for every 0.5° across the entire field to 5° off-center on the other side. The design of the perimeter makes it only possible to search the visual field in one direction, but since this direction would vary for the different cells under investigation and no great differences were found in visual fields, we assume that the visual fields are roughly symmetrical around the axes of the ommatidia. An example of the responses evoked by stimulating at different angles with the same intensity of light is shown in Fig. 13. In this case the initial peak is only evoked when the light is close to the center of the field. Outside ±3° no response can be observed. The amplitude of the responses is plotted against the angle of incidence for

![Figure 12](image)

**Figure 12.** Graph of initial transient (filled circles) and steady-state (open circles) intracellular response amplitudes as a function of intensity of stimulus for a skipper retinular cell.

![Figure 13](image)

**Figure 13.** Intracellular responses from skipper eye as a function of point source position. Stimulus duration, 0.2 sec; vertical marker, 20 mv.
another cell in Fig. 14. The initial peak reaches about 21 mv in this case while the maximum steady-state response is 12 mv. Since the half-power points are 70 % of the maximum response, the visual field between half-power points is 2.1° when using the initial peak as a criterion and 2.5° when using the amplitude of the steady state. Fig. 14 also demonstrates a frequently observed phenomenon, namely that at 3–5° off-center the light stimulus produces a hyperpolarization of the membrane potential. This is not observed in very good penetrations with high and stable membrane potentials, but it is seen when the cells start to depolarize or in penetrations which do not show a good membrane potential. If large depolarizations occur, we observe only hyperpolarization responses that have the same general appearance as the responses from the iris cells described above.

As mentioned above, threshold experiments give the most consistent results for determining the visual fields of single retinular cells. We also find this

![Figure 14](image)

**Figure 14.** Intracellular response as a function of light position for initial transient (filled circles) and steady state (open circles). Hyperpolarizing response is characteristic of deteriorating preparation.

![Figure 15](image)

**Figure 15.** Sensitivity of intracellular response as a function of light position.
method easier than any other way of describing the visual field. A definite advantage of this threshold measurement is that the particular cell under investigation is never strongly light-adapted. A threshold response of 2–3 mv is evoked in the center of the field. The illumination is increased stepwise and the position for a threshold response is determined at each step. In plotting the values of light intensity which evoke a threshold response we use the expression log sensitivity. This is the logarithm of the inverse of the light intensity actually used. An example of such a graph is given in Fig. 15. From such a graph the half-sensitivity angle is easily determined and in this case is found to be 1.9°.

For some units which could be held for a sufficient length of time both threshold determinations and the amplitude of the response with different angles of incidence for constant intensity are determined. An example of such an experiment is shown in Fig. 16. The half-sensitivity angle as determined by the threshold is 2.1°, compared to 1.5° which is the half-power beam width as determined by 70% of the maximum response.

**DISCUSSION**

The optical experiments show that it is possible to obtain a superposition image in the preparation used by Exner (1891) and Kuiper (1962) in which both the rhabdomeres and the crystalline tracts are removed. A similar but less well-defined picture of convergence at the retinal level is also obtained in the freshly cut eyes of moths and skippers. Simultaneously one observes small light spots at the calculated interommatidial distances corresponding to the depth of the scalp. We conclude that these light spots represent the appearance of the tracts as viewed end on. In dark-adapted moths, we see an erect image with the extended source; however, it is only seen at the level of the section and increases in size in shallower scalps. We therefore conclude that the image
is formed from the conduction of light in the tracts and observed as the light radiates from the tracts at the plane of the section.

In the original superposition theory formulated by Exner the eyes are postulated to form a superposition image only when dark-adapted. It is therefore imperative to keep the eyes of the moths in the dark-adapted stage and great care is taken to do this. A definite advantage of the skipper eye is that the distal pigment is confined to the area around the cones; we have not observed any changes in its position. There is no pigment migration as seen in the moths because the cells surrounding the tracts are devoid of pigment. The glow size and intensity of the skipper (Miller and Bernard, 1968) have not been observed to change upon exposure for many minutes to bright lights.

Our optical experiments show that much of the light is confined to the crystalline tracts, but part of it is more or less diffusely transmitted outside these structures. Our electrophysiological experiments show, however, that the light outside the tracts most probably does not enter the rhabdomeres and excite the retinular cells. These findings are in agreement with the theoretical study of light propagation in the moth eye conducted by Allen (1968). He measured the refractive index of all the optical apparatus in the tobacco hornworm moth, Manduca sexta, and on the basis of these experimental data calculated the light paths in the ommatidia. His results are in agreement with our conclusions in that he predicts that for light incident on a facet within 3°, about 80% of the light is transmitted in the crystalline tract. The half-power beam width was found to be about 2° which coincides with the experimental value found in the present physiological and optical study.

Electrophysiological experiments have been used to determine visual fields in many arthropods. In Calliphora Burkhardt et al. (1965) showed that the visual field half-power beam width varies between 3.3° and 5.2°. Vowles (1966) showed that the half-power beam widths in Musca eyes vary from 2.5° to 3.0° in light-adapted and from 4.5° to 8.5° in dark-adapted eyes. The first figures are horizontal field widths and the latter are vertical field widths. Kirschfeld (1965) found the half-power beam width in Musca to be 7.7°. In Limulus the half-power beam widths have been determined by Waterman (1954) and Kirschfeld and Reichardt (1964) and found to be 11.6°.

In Table II the visual field angles as observed with different methods in different animals are tabulated. In all the apposition eyes the half-power beam width (the angle at half the sensitivity) is much larger than that found in the skipper eye by electrophysiological means or in the moths and skipper by optical experiments. It is of special interest that in the skipper no responses whatsoever are observed electrophysiologically outside 2–4° off the center of the visual field. This is in contrast to the findings in Musca and Calliphora by Washizu et al. (1964), Kirschfeld (1965), and Vowles (1966) who observed responses (though small) as far as 20–40° off axis. A probable explanation of
these responses is that the screening pigment is transparent to red (Goldsmith, 1965). Since they used white light, some of the energy in the red part of the spectrum may reach the retinular cell through adjacent ommatidia.

We determine the visual field of the single retinular cells of the skipper eyes to be $2.1^\circ \pm 0.3^\circ$, and because of the symmetry of the optical apparatus there is no reason to believe that the visual field is different in different directions. The visual field of the skipper and also of the moth eyes seems to be smaller than that of any apposition eye studied so far. As pointed out in the Results,

<table>
<thead>
<tr>
<th>Animals</th>
<th>Interommatidial angle</th>
<th>Visual field</th>
<th>Author</th>
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<tr>
<td>Optimal</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Apis</em></td>
<td>Horizontal 2.8°</td>
<td>Horizontal 6.8°</td>
<td>Kuiper (1962)</td>
</tr>
<tr>
<td><em>Apis</em></td>
<td>Vertical 1.4°</td>
<td>Vertical 7.2°</td>
<td>Autrum and Wiedemann (1962)</td>
</tr>
<tr>
<td><em>Locusta</em></td>
<td>Horizontal 2.4°</td>
<td>Vertical 1.10°</td>
<td>Autrum and Wiedemann (1962)</td>
</tr>
<tr>
<td><em>Dixippus</em></td>
<td>7.5°</td>
<td>Vertical 9.8°</td>
<td>Autrum and Wiedemann (1962)</td>
</tr>
<tr>
<td><em>Calliphora</em></td>
<td>2.5°</td>
<td>Vertical 7.6°</td>
<td>Autrum and Wiedemann (1962)</td>
</tr>
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<td>Electrophysiological</td>
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<tr>
<td><em>Calliphora</em></td>
<td>Horizontal 2.0-4.6°</td>
<td>Frontal 3.3°</td>
<td>Burkhardt (1965)</td>
</tr>
<tr>
<td><em>Musca</em></td>
<td>Vertical 2.6-3.4°</td>
<td>Lateral 5.2°</td>
<td>Kirschfeld (1965)</td>
</tr>
<tr>
<td><em>Musca</em></td>
<td>Horizontal 3.9°</td>
<td>7.7°±2.1°</td>
<td>Vowles (1966)</td>
</tr>
<tr>
<td><em>Musca</em></td>
<td>Vertical 2.3°</td>
<td>Light-adapted, 2.5-3.0°</td>
<td>Vowles (1966)</td>
</tr>
<tr>
<td><em>Musca</em></td>
<td>Vertical 2.3°</td>
<td>Dark-adapted, 4.5-8.5°</td>
<td>Vowles (1966)</td>
</tr>
<tr>
<td><em>Limulus</em></td>
<td>4-15°</td>
<td>15°</td>
<td>Waterman (1954)</td>
</tr>
<tr>
<td><em>Epargyrus clarus</em></td>
<td>1.3°</td>
<td>2.1°±0.3°</td>
<td>Present study</td>
</tr>
</tbody>
</table>

* Quoted by Antrum and Wiedemann from various sources.

the interommatidial angle is also less for these eyes than for most apposition eyes.

In *Musca* the ommatidia have separate rhabdomeres and these tend to be differentially exposed to light from a point source (Kirschfeld, 1967). In both *Musca* and *Calliphora* the half-power beam width for a single retinular cell in dark-adapted eyes is 7.8°. The crystalline cones in fly eyes are 50 μ long or about one-third of the cone length in the skipper and in most moths. This might account for part of the difference in visual fields. The Airy disc formed by a point source would be expected to move a greater distance for increasing
angles of incidence in the moth and skipper than in the fly with the result that the image of the point source at the proximal end of the cone would only be located on the tract for angles of incidence very close to on-axis.

Although the explanation given above is plausible, there are other possibilities that could explain the narrow visual fields we find in eyes containing tracts. An ideal superposition image as defined by Exner should show such narrow fields. In the absence of other information, the physiological experiments reported here cannot be taken as proof of image formation by tract propagation. However, we know that the superposition image of Exner’s experiment in the firefly is far from ideal. It is coarse and covers many ommatidia. In addition, the medium between the cones and the rhabdom is not isotropic. When the theoretical and optical evidence (Allen, 1968; Miller et al., 1968) and the optical evidence presented here are taken into consideration, our physiological experiments are suggestive but not proof of tract propagation. Another unassessed factor which could contribute to the narrow fields in the skipper is the presence of pigment that optically isolates the sensory parts of the ommatidia.

The responses of the retinular cells in the skipper eye are similar in form and appearance to those observed in Musca and Calliphora (Washizu et al., 1964; Kirschfeld, 1965; Vowles, 1966; and Burkhardt, 1965). Although the rise time of the initial peak in the skipper is fast, we do not observe any spike-like activity such as Naka and Eguchi (1962) found in the eye of the drone of the honeybee. In many cells we find a negative response when the light is 2–4° outside the center of the visual field. These negative potentials of the retinular cells are only observed in cells which show a low membrane potential or depolarization after penetration. The negative responses could be seen when light hit the eye from 20° off-axis of the visual field. These negative responses from the obviously damaged cells looked very much like the responses from the iris cells, and we believe that these potentials are extracellular pickup of the activity from neighboring receptor cells. We do not know whether there is any neural interaction between the cells in different ommatidia, since we did not specifically look for it in this study.

The evidence for tract propagation reported in this study makes it necessary to reconsider the mechanism of dark adaptation in certain insect compound eyes. In the dark-adapted position the distal screening pigment is situated around the crystalline cones. During light adaptation the pigment migrates toward the rhabdoms (Bernhard and Ottoson, 1960a, b). During the adapting process the sensitivity of the eye is decreased by 6 log units. The pigment migration is responsible for about 3 decades of the total sensitivity decrease (Höglund, 1966).

Kuiper (1962) suggests that the pigment has a high refractive index and its presumed contact with the wall of the crystalline tract should frustrate total internal reflection. Allen (1968) suggests that since in a dielectric wave guide
some of the light energy extends outside of the tract boundary, lossy pigment surrounding the tract would absorb a portion of the energy outside the tract and reduce the amount of energy reaching the rhabdomeres. Theoretical calculations have shown that this mechanism could account for the reduction in sensitivity observed in the moth eye (Allen and Bernard, 1967).

Our optical experiments on moth and skipper eyes indicate that light is largely confined to the tracts and that these structures function as wave guides. The total estimated visual field of tract propagation as indicated by the measurement of moving the light is about 2–5°. In our electrophysiological experiments with the optical apparatus intact it could be ascertained that light enters the retinular cells only from the direction that the ommatidium faces. The visual field is much smaller than found for any other insects studied so far. This therefore seems to be additional evidence for tract propagation. Our findings are in agreement with the theoretical calculations of light paths based upon experimental studies of the refractive index of various parts of the optical apparatus (Allen, 1968; Miller et al., 1968). These calculations, together with the results of the present experiments, are in conflict with the superposition theory proposed by Exner (1891).

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