

Spectral Sensitivity Studies on the Visual System of the Praying Mantis, *Tenodera sinensis*

CHARLES SONTAG

From the Department of Zoology, University of Wisconsin, Madison, Wisconsin 53706, and the College of Human Biology, University of Wisconsin-Green Bay, Manitowoc County Campus, Manitowoc, Wisconsin 54220

ABSTRACT In these studies a constant ERG response was used as a measure of visual sensitivity to different wavelengths of light. The dark-adapted compound eye of *Tenodera sinensis* is dominated by a single class of photoreceptors, with a major peak of sensitivity at about 510–520 nm, and with a minor peak of sensitivity in the near-ultraviolet region at about 370 nm. The dark-adapted dorsal ocellus does not contain a homogeneous population of sensory receptors. The sensitivity function of the dark-adapted ocellus to longer wavelength light (yellow and red) is determined by a single receptor with a major peak of sensitivity in the green at 510–520 nm with some sensitivity in the near-ultraviolet. Sensitivity at shorter wavelengths (near-ultraviolet and blue), however, involves the stimulation of both this and a near-ultraviolet-sensitive receptor with a maximum sensitivity at about 370 nm. Anatomically, the sensory cells of the dorsal ocellus of *Tenodera* were determined histologically to be grouped into two distinct regions, each group making its own separate contribution to the ocellar nerve. This may represent the separation of two different photoreceptor types in the ocellus of the mantis.

INTRODUCTION

Although the praying mantis has been the subject of behavioral studies (Crane, 1952; Mittelstaedt, 1957; J. Ruck, 1960; and Roeder, 1963), it has received little attention from the visual physiologists. A few years ago Michiele (1966) and Montel et al. (1966) in search of a Purkinje phenomenon determined the spectral sensitivity and spectral efficiency functions of the compound eye of the praying mantis, *Mantis religiosa*, at different levels of luminance using the electroretinogram (ERG) as a criterion of responsiveness. In some mammalian eyes different populations of receptors are revealed as the luminance is decreased. This is accompanied by a corresponding shift in spectral sensitivity of the eye toward shorter wavelengths (the Purkinje shift

from cone vision to rod vision at twilight). If a similar shift were evinced in the compound eye of *Mantis*, the existence of a heterogeneous population of receptor types would be demonstrated.

Michiele (1966) studied the spectral sensitivity of *Mantis* using six interference filters over the range 405 to 658 nm. Both spectral sensitivity and spectral efficiency curves showed a maximum at about 546 nm. Since there were no measurements taken between 493 and 546 nm, one could argue that the maximum sensitivity might actually be between 493 and 546 nm (or around 510–520 nm). The spectral sensitivity curves determined at three quantal ranges were very similar which suggests that no Purkinje shift phenomenon exists in the *Mantis* compound eye.

The spectral efficiency of the compound eyes of *Mantis* of various color forms was determined by Montel and his coworkers (1966). They used 16 metallic interference filters over the range 375 to 750 nm. The spectral efficiency functions reported by Montel et al. show a broad maximum from 480 to 550 nm. With the increasing intensity of illumination, the broad maximum from 500 to 550 nm was not greatly affected, but the sensitivity to the blue end (less than 450 nm) of the spectrum was enhanced. Montel et al. concluded that the location of maximum sensitivity varied as a function of intensity and thus a Purkinje shift might exist. All color forms of mantids gave essentially the same qualitative results.

It is difficult to interpret the significance of the work of Michiele (1966) and Montel et al. (1966) on *Mantis* and correlate it with the present studies on *Tenodera sinensis*. The results and the procedures used are not adequately discussed, and therefore it is impossible to discern the number of classes of photoreceptors present in the compound eye.

This paper reports (a) the spectral sensitivity functions of the various parts of the visual system of the praying mantis, *Tenodera*, and (b) the possible receptor types which contribute to these sensitivities. Since the mantis is an active predator, using visual cues to localize its prey, it is of interest to know what kind of visual information is used and how it is processed by the mantid's integrating centers. Electrophysiological studies such as this one should serve to sharpen the focus for critical behavioral experiments which are designed to study these processing mechanisms.

MATERIALS AND METHODS

Mantis Culture Methods The praying mantids were raised in the laboratory using a modification of a method described by Rilling et al. (1959). The cages were kept in a temperature-controlled room at about 23°C. The photoperiod was regulated by a time clock-controlled bank of fluorescent bulbs located above the cages which provided illumination for 13 hr per 24 hr period (lights on at 0800, lights off at 2100 hours).

Adult mantids were maintained on blowflies (*Calliphora*) from a laboratory stock culture. Because mantids resort to cannibalism if there is inadequate food or conditions become too crowded, the number of mantids per cage was reduced to six or less in the later instars.

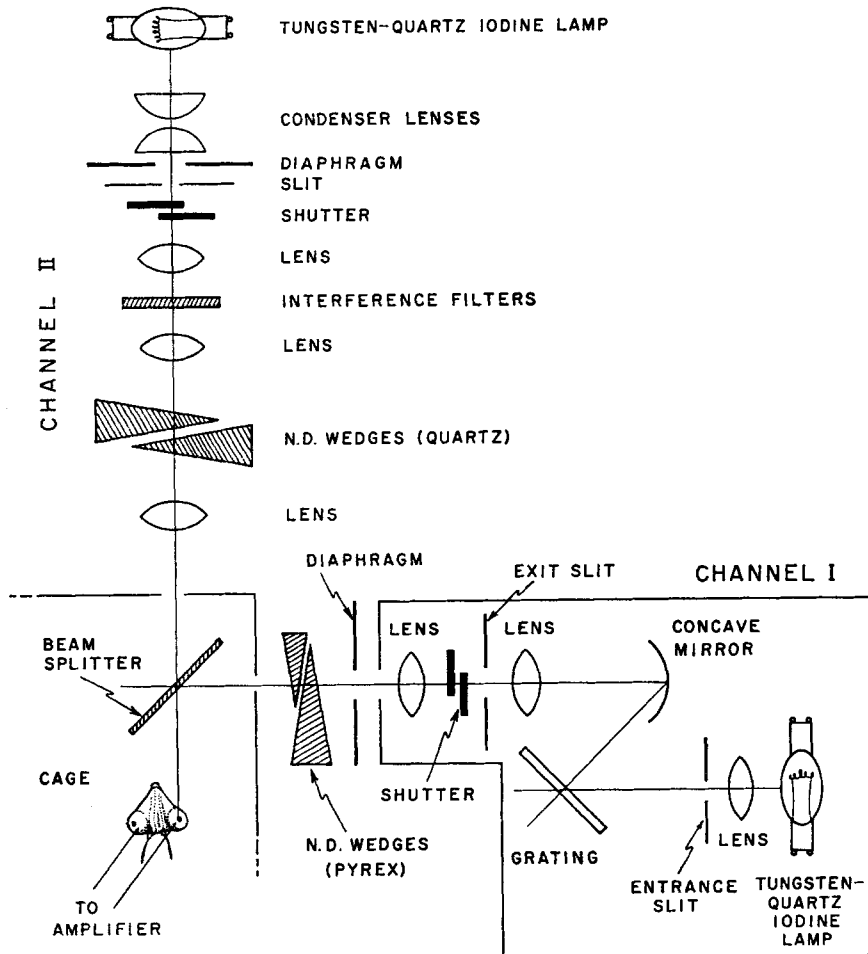


FIGURE 1. Diagram of the optical apparatus. Light from each channel was combined so that the stimulating (test) and adapting lights (from channels I and II) arrived at the eye along the same optical path by suitable positioning of the beam splitter (a half-silvered quartz neutral density filter, 0.7 OD).

Optical Stimulator Monochromatic lights from two channels were used (see Fig. 1). The light source in each channel was a tungsten-quartz iodine lamp powered by a Sorensen constant voltage source. Channel I included a Bausch and Lomb ultra-violet-visible "high intensity" grating monochromator. Collimated light from the monochromator was interrupted by a shutter located next to the exit slit. The shutter was a rotary solenoid coupled with two vanes which served as leaves for the shutter.

The light was collected by an achromatic condenser which was constructed of quartz and fluorite lens elements. The light intensity was controlled by a diaphragm and a compensated neutral density wedge, and provided a variation in intensity of approximately 4 OD units. The optical density wedge was calibrated in optical density units for every wavelength used.

Channel II included a series of mounted interference filters which served as the source of monochromatic light. White light was collected and collimated with a quartz condenser lens system. It then passed through an exit slit and a shutter. This shutter, like that described previously, was positioned immediately behind the slit. One of 15 narrow-band Balzer interference filters was positioned in the collimated light emerging from the slit. The intensity of monochromatic light from channel II was controlled by a diaphragm and by two quartz neutral density wedges mounted in such a way as to rotate in opposite directions. A variation in intensity with a range of approximately 5 OD units was available with this wedge. The wedge was calibrated in optical density units for every wavelength used.

The light from channel I was combined with that from channel II by a beam splitter (half-silvered quartz neutral density filter, OD of 0.7). The light from the two channels, therefore, arrived superimposed upon the eye. The shutters which interrupted the light from channels I and II were triggered with a rack-mounted American Electronic Laboratories (Lansdale, Pa.) stimulator through a transistorized relay circuit which eliminated the stimulus artifact, and also triggered the oscilloscope trace.

The relative energies of the incident monochromatic light sources were periodically determined with the beam splitter in place (neutral density wedges were removed for this calibration procedure) using a calibrated General Electric photocell.¹ The photocell had previously been calibrated by the late Dr. Phillip Ruck using a calibrated Epply thermopile and a controlled monochromatic light source.

Animal Preparation and Recording Methods Only adult male and female mantids whose eyes and ocelli were free from injury (due to age deterioration or tears on the cornea from the cage screening) were used in experiments. The mantids were anesthetized with CO₂ and secured with Tackiwax to a small platform which provided flexibility in positioning the animal. The ocelli and eyes were shielded with aluminum foil except for the area of the eye or ocellus being investigated. All animals were dark-adapted for a minimum of 1 hr.

The ERG was recorded by leading off from a punctured illuminated cornea with an uninsulated stainless steel electrode. The reference electrode was positioned in the opposite eye which was maintained in constant darkness. The tips of both electrodes probably came to rest at the proximal end of the crystalline cones. It was impossible to determine whether this reference point in *Tenodera* was electrically indifferent to potential changes occurring in the illuminated eye. This, however, has been established for several other insect preparations (see Goldsmith, 1960; Ruck, 1965; and Bennett, 1967). Monochromatic light stimulated the eye as single flashes with a duration of 100 msec. The response was fed into the cathode follower stage of a Grass P6

¹ Model No. 8PVICAB with a quartz window.

preamplifier which was AC-coupled and operated push-pull. The low frequency response was operated at 1 cps (half-amplitude frequency). The high frequency cutoff was positioned at 0.1 kc. A Tektronix 502A dual-beam oscilloscope was used for displaying the amplified signal.

Following the experiments, the mantids were removed from the Tackiwax and marked with India ink. They then had their mandibles moistened with water and were returned to the culture cages. If the animals were to be used for another series of experiments, they were given a week's rest and recuperation period. The same ocellus or part of the compound eye was never used twice.

The Form of the ERG The ERG of the dark-adapted mantis compound eye consists of a simple monophasic negative-going potential that is dominated almost entirely by the generator potential or component 1 (Ruck, 1961 *a, b, c, d*). ERG components 2, 3, and 4 are not usually present in the compound eye mass response. The ocellar ERG shows in addition to the generator potential, a transitory rapid positive deflection at "on" (component 2 or axonal response). Component 4 (discharge of ocellar nerve) is also seen occasionally in the ERG of the light-adapted ocellus.

The generator potential (component 1) of the ERG was used throughout the study as the criterion of responsiveness. Its shape as recorded from the compound eye and ocellus was determined to be independent of the wavelength and intensity of light used, and it was not influenced by the presence of an adapting or fatiguing light. These parameters therefore did not introduce complexities which would obscure the generator potential of the mantis ERG and influence the interpretation of the sensitivity functions.

EXPERIMENTAL PROCEDURE

1. *Spectral Sensitivity* Spectral sensitivity is defined as the reciprocal of the relative number of quanta necessary to elicit a constant response at every wavelength. Mantids were prepared as previously described. The animals were dark-adapted 1 hr prior to each determination. The intensity of the test illumination at each wavelength was varied with the neutral density wedge until it produced a generator potential (ERG) equal to 200 μv . The part of the visual system under study was stimulated with single flashes of 100 msec duration at 10 sec intervals. This allowed the eye to remain in the dark-adapted state without significantly light-adapting the eye during the determination. During the course of individual determinations the response of the eye to a standard light flash of 520 nm was used as an "anchor" point. Throughout each determination and at the end of each determination the reading at 520 nm was checked. If the reading at 520 nm did not check with previous readings, that determination was discarded and the run repeated.

(The magnitude of the generator potential of the ERG was recorded over 4 log units at test wavelengths of 371, 431, 526, and 577 nm for each part of the mantid's visual system. The resulting response-energy curves were all determined to be approximately parallel. The choice of the criterion amplitude of the generator potential therefore does not influence the shape of the spectral sensitivity functions. The 200 μv generator

potential amplitude was chosen in these studies because it was clearly defined and maximized the useable UV light energies which were relatively feeble.)

2. *Selective Adaptation* Spectral sensitivity of the various parts of the visual system was determined under constant (fatiguing) illumination. The eye was dark-adapted at least 1 hr prior to light adaptation. The intensity of the adapting light was adjusted so as to reduce the sensitivity at 520 nm to one-tenth that of the dark-adapted level. The eye was stimulated with the test light at 520 nm until a constant level of adaptation was obtained over a 5 min period. The spectral sensitivity was determined as before using a 200 μv generator potential as response criterion. The response at 520 or 526 nm was again used as an "anchor" point as described above.

3. *Increment Threshold* Channel I was the adapting channel and channel II was the test channel. The logarithm of the relative number of quanta ($\log N$) required to evoke 200 μv generator potential amplitudes was determined with test wavelengths of 371, 431, 526, and 577 nm under increasing intensities of background illumination (light adaptation). The adapting lights were monochromatic lights of either 370 or 580 nm. In one case an adapting light of 500 nm was used on the ventral anterior part of the compound eye. At each level of light adaptation, threshold was determined by adjusting the intensity of the test stimulus in order to obtain a 200 μv generator potential response. The reading at 526 nm was used as an "anchor" point. If this reading was not obtained following the determination of threshold for the other test lights, the thresholds were redetermined at that particular level of light adaptation. Before determinations were made with a new adapting light, the part of the visual system being studied was dark-adapted for a minimum of 2 hr.

RESULTS AND DISCUSSION

The visual system of the mantis, *Tenodera*, consists of two very prominent compound eyes (apposition type) and three ocelli. Since the data are different for the compound eye and the ocellus, each part will be considered separately.

Dorsal Ocellus The ocelli or simple eyes of the praying mantis are located on the dorsum of the head between the two antennae and are three in number; two ocelli have their optical axis directed laterally while the third median ocellus is directed anteriorly. Since the antennae lie close to the optical axis of the lateral ocelli, the median dorsal ocellus was chosen for this study.

The spectral sensitivity function of the dark-adapted ocellus, using a criterion amplitude of 200 μv , shows a single broad maximum sensitivity in the green region of the spectrum at about 510 nm and a secondary rise in sensitivity in the near-ultraviolet at about 370 nm (Fig. 2). A high valley occurs at about 420 nm between the two maxima. The sensitivity decreases monotonically from 520 to 650 nm. This type of sensitivity function is fairly typical for insect ocelli. (See Goldsmith and Ruck, 1958; and Ruck, 1965.)

In order to test whether the spectral sensitivity function for the ocellus

was obtained from a homogeneous population of receptors or whether more than one receptor type contributed to the spectral response, the ocellus was tested under various background fatiguing lights. In the first study, the intensity of background fatiguing illumination remained constant, whereas in the second the intensity of background illumination was varied (increment threshold). The purpose of these experimental procedures is to selectively change the sensitivity of the responding receptors so that the different populations of receptors will individually reveal their sensitivity, should different kinds of receptors exist.

In this study, the spectral sensitivity of the dorsal ocellus was determined under the influence of constant fatiguing illumination of near ultraviolet and yellow light. Adaptation with near-ultraviolet adapting light (346.5 nm) reduced the sensitivity about equally throughout the spectrum which revealed no selective suppression of sensitivity in any part of the spectrum (Fig. 2). Yellow light (577 nm) adaptation, however, enhanced the near-ultraviolet maximum at 370 nm relative to the 510 nm maximum in some mantids (Fig. 2). Yellow light is absorbed more efficiently by the receptor responsible for the green sensitivity than by receptor(s) with maximum sensitivity at shorter wavelengths. This differentially suppresses the sensitivity of the "green" receptor and reveals a receptor type whose maximum sensitivity lies in the near-ultraviolet. The results are not consistent from mantis to mantis (Fig. 2). In some mantids, yellow light adaptation (574 nm) only slightly enhanced the near-ultraviolet sensitivity relative to the 510 nm maximum. In other mantids (577 nm light adaptation) the change was considerably greater. This variation in near-ultraviolet sensitivity is most perplexing and extremely difficult to explain.

The results of the selective light adaptation studies suggest that there is more than one type of receptor in the ocellus which contributes to the spectral sensitivity function. One receptor type is maximally sensitive to light of 370 nm. A second receptor type is maximally sensitive to light of 510 nm with some sensitivity in the near-ultraviolet. The inability to selectively change the sensitivity function with near-ultraviolet adaptation may be explained by the absorption of near-ultraviolet light by at least two receptor types. Similar results have been reported for the ocelli of other arthropods. Goldsmith and Ruck (1958) reported that the bee ocellus possesses receptors sensitive to ultraviolet illumination. Lall and Chapman (1964) also reported an UV receptor for the ocellus of the horseshoe crab, *Limulus*. Lall and Chapman were, however, able to suppress the near-ultraviolet maximum in the *Limulus* median ocellus with an ultraviolet adapting light.

In order to test the extent of overlap of sensitivity of the receptors, the sensitivity of the ocellus was determined at different levels of background or adapting illumination. This procedure was developed by Stiles (1946, 1949,

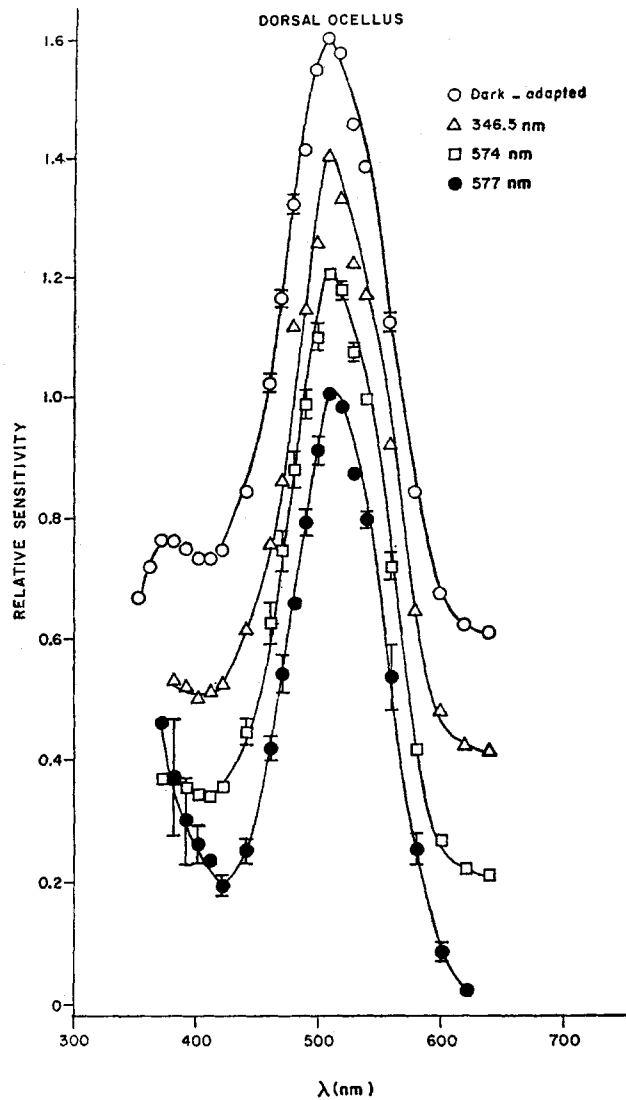


FIGURE 2. Spectral sensitivity curves of dark-adapted and light-adapted mantis dorsal ocellus. The relative sensitivity using a $200 \mu\text{v}$ criterion of responsiveness is plotted as a function of the wavelength of light. The three lower curves show the effects of yellow (577 and 574 nm, lower two curves) and near-ultraviolet (346.5 nm, second curve from the top) adapting lights on the sensitivity of the dorsal ocellus (upper curve). Data for the three lower curves were obtained by superimposing 100 msec test flashes on the adapting lights. During each light adaptation experiment, the sensitivity of the eye was reduced to 10% of its dark-adapted value at 510 nm. Since the sensitivity of each curve is expressed as a per cent of the maximum at 510 nm, the light adaptation curves appear to have the same relative sensitivity for each condition. This was done to facilitate comparison between light- and dark-adapted eyes for positions of maximum sensitivity and for changes in maxima relative to one another. The curves have been shifted vertically

1959) for investigating color types and properties of human cones. Goldsmith (1960) modified the procedure and applied the technique to the study of receptor systems in the compound eye of the worker honeybee. The results can be correlated with selective adaptation studies.

Operationally, the procedure measures the threshold of an eye to monochromatic test lights of different wavelengths, presented as flashes on an adapting field of fixed wavelength. The properties of the receptor are then revealed by varying the intensity of the adapting background light and determining the threshold for visual perception of the test flash.

Two assumptions are basic to the technique: The different receptor types must behave independently of one another (or a point must be found where a minimum of interaction between the two systems exists). By choosing a suitable monochromatic background adapting light, one can depress the sensitivity of one receptor type more than the other and thus isolate the second type. This is very difficult when two types have nearly the same spectral sensitivities. The second assumption requires that the threshold-intensity curve of the receptor will approximate Weber's law (i.e., increases in a predictable manner). Weber originally described the relationship as a method establishing a quantitative scale of sensation. He found that if (I) was the intensity of the stimulus applied at the moment, then in order to produce a perceptible change (ΔI), the extra intensity was always a constant fraction of (I), or, $\Delta I/I = \text{constant}$. To restate Weber's law in this context: There exists a linear relationship between the threshold intensity of the test stimulus ($\log N_{\text{test}}$) and the intensity of the background illumination ($\log N_{\text{adapt}}$). This assumption is important in evaluating the results of increment threshold tests in which more than one receptor type is present.

The resulting families of curves for this experimental procedure resemble typical energy-response functions. The exact shape of the function and displacement along the X and Y axis is dependent upon the sensitivity(ies) and kind(s) of responding receptors.

The effects of a yellow-green (580 nm) adapting light on the ocellus are shown in Fig. 3. With increasing intensity of the yellow-green adapting light (580 nm), the sensitivity of the ocellus to 526 and 577 nm test lights was suppressed more than the sensitivity to the 371 nm test light. The curves ($\log N_{\text{test}}$ vs. $\log N_{\text{adapt}}$) for the test lights, 526 and 577 nm, rise in a parallel fashion with a continually increasing slope. The response to the 371 nm test light, however,

by arbitrary amounts to further facilitate this comparison. The vertical lines represent the standard error of the mean. In the dark-adapted eye, each point represents the mean of 14 different determinations. In the light-adapted eye (near-ultraviolet, 346.5 nm and yellow, 574 nm), data are from single preparations. In the yellow-adapted (577 nm) eye, each point represents the mean of two different determinations.

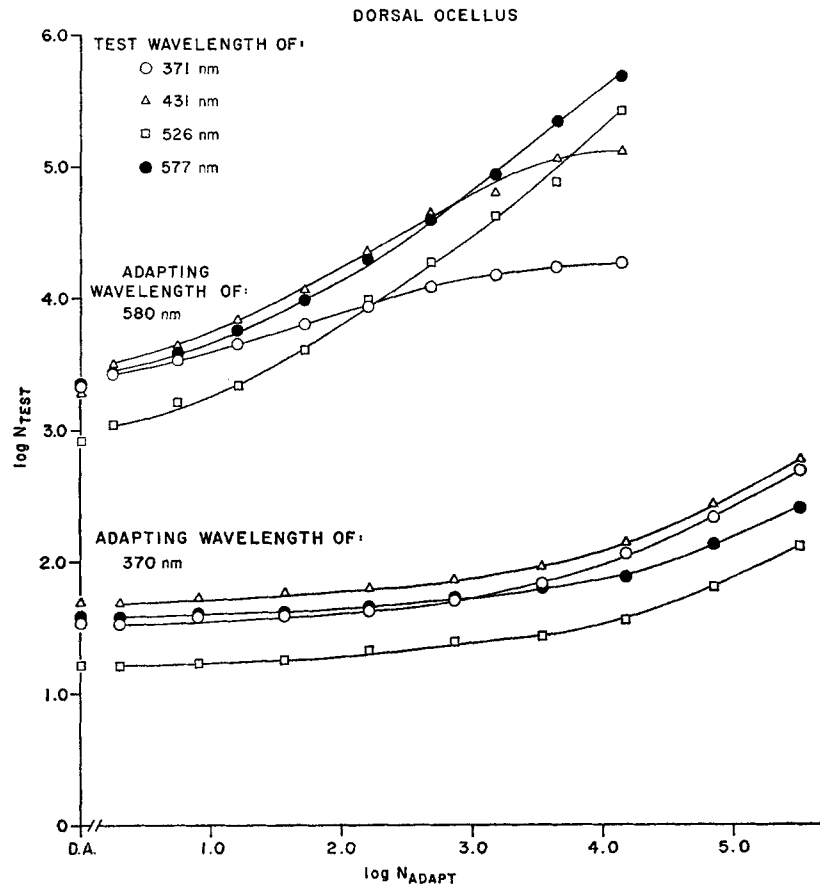


FIGURE 3. Threshold-intensity curves for the dorsal ocellus. The log relative number of quanta required for a constant 200 μv generator response ($\log N_{\text{test}}$) is plotted as a function of the log relative number of quanta of the adapting light ($\log N_{\text{adapt}}$). The dark-adapted threshold sensitivities are represented on the ordinate. The uppermost family of curves was obtained under the influence of a 580 nm adapting light. The lower family of curves was obtained under the influence of a 370 nm adapting light, as labeled. Note that the ordinate ($\log N_{\text{test}}$) and abscissa ($\log N_{\text{adapt}}$) are expressed in relative light energies. The families of curves for 580 nm adaptation and for 370 nm adaptation are positioned relative to each other. The vertical displacement is used to separate the families of curves. The horizontal displacement of families of curves is a consequence of the experimental design. The absolute flux for $\log N_{\text{adapt}}$ is impossible to define because different diaphragm settings were used for each adapting light. This was done to maximize the usable ultraviolet light energies in both the test and adapting channels. Unfortunately, even under these conditions the energy of the fully attenuated near-ultraviolet adapting light (370 nm) was so feeble as to be completely ineffective in influencing the response of the receptor cells ($\log N_{\text{adapt}}$ from 0 to 2). It was not until the intensity of the adapting light was increased ($\log N_{\text{adapt}}$ from 2 to 3) that the influence of the ultraviolet light became apparent. See text for further details. Data are from a single preparation.

becomes more independent of the intensity of the long wavelength adapting light and its function ($\log N_{\text{test}}$ vs. $\log N_{\text{adapt}}$) continually decreases in slope as the threshold becomes more independent of the intensity of the background illumination. The curve at 431 nm displays a behavior intermediate between the others. As the adapting light becomes more intense, sensitivity at 431 nm is suppressed, but less so than that at 526 and 577 nm. There are several ways to explain these data:

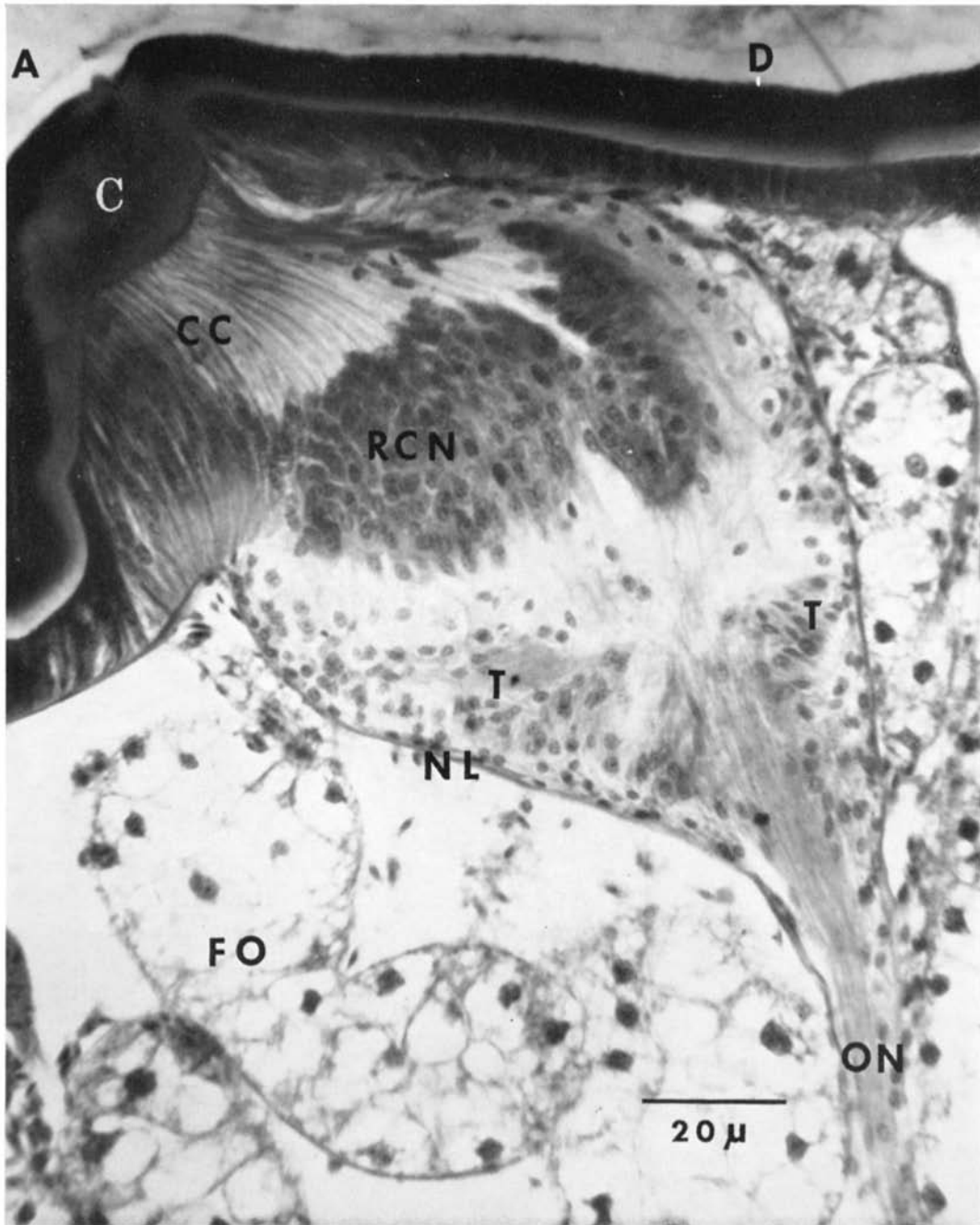
1. There are two receptor types which have overlapping curves, one with a maximum sensitivity in the ultraviolet, and one with maximum sensitivity in the green (wavelength maximum 520 nm) with sensitivity in the near-ultraviolet. In this case, as the yellow adapting light becomes more intense, the ultraviolet receptor will determine the response at 431 nm rather than the receptor with the sensitivity maximum at 510 nm.

2. Another possibility is that there are three receptors, the third being maximally sensitive in the blue. This seems improbable in the light of the previous selective adaptation studies.

The effects of an ultraviolet adapting light on the ocellus are shown in Fig. 3. At low intensities of near-ultraviolet light adaptation, the curves are essentially parallel. With increasing intensity of $\log N_{\text{adapt}}$, however, the sensitivity of the ocellus to test wavelengths of 371 and 431 nm is more effectively suppressed than it is to test wavelengths of 526 and 577 nm. The slopes of the curves for 371 and 431 nm are, therefore, steeper after being initially parallel. It is probable that if high intensity ultraviolet adapting and test light had been available, the function for 371 nm would have ultimately crossed the curve for 431 nm. It is difficult, therefore, to determine from these data how much each receptor type contributes to the changing sensitivity of the dorsal ocellus to shorter wavelengths.

To summarize, the results of these experiments suggest that there are at least two receptor types in the mantis ocellus. In the dark-adapted ocellus the sensitivity to longer wavelength light (green and red) is determined by a single pigment with a maximum absorption at 510–520 nm. Sensitivity to ultraviolet light is determined by two pigments, one with a wavelength maximum at 370 nm, the other with a wavelength maximum at 510–520 nm. Since the ultraviolet adapting light does not completely spare the green receptor (Fig. 3), the green receptor is also sensitive in the ultraviolet which exists either as a “shoulder” or as a secondary maximum. The possibility that one kind of receptor cell contains both pigments in various proportions is not excluded.

It is interesting to note that the retinula cells of the dorsal ocellus of *Tenodera* appear to be morphologically grouped into two distinct regions (see Fig. 4). The two groups of retinula cells also contribute separate groups of fibers to the ocellar nerve. One could question whether this represents the anatomical isolation of the two receptor types found by the light adaptation studies.



Perhaps this question could best be answered by microspectrophotometric studies in which the absorption spectrum of the individual rhabdomere is determined.

Compound Eye The ommatidia of the mantis compound eye are characteristically colored so that the eye appears to be divided into distinct regions. The parts of the compound eye that are readily identified are the dorsal anterior and ventral anterior. The ventral anterior region of the compound eye is identified by its morphological position and a larger pseudopupil as compared to the dorsal region. The ommatidia of the ventral region appear as light aqua, whereas the dorsal ommatidia appear to be a darker shade of aqua. During the experiments on the compound eye each region was tested separately by suitable shielding procedures.

The spectral sensitivity functions for each part of the mantis compound eye (both dorsal and ventral parts) were found to have two maximum sensitivities using an ERG constant response criterion of 200 μv (see Fig. 5). One maximum lies in the near-ultraviolet at about 370 nm. The second maximum (major sensitivity) lies in the range 510 to 520 nm. These two sensitivity maxima have been found in compound eyes of several insects representing at least six different orders in which detailed spectral sensitivity studies have been performed; the fly, *Calliphora* (Walther and Dodt, 1959); the cockroach, *Periplaneta* (Walther and Dodt, 1959); the worker bee, *Apis* (Goldsmith, 1960); the ground beetle, *Carabus* (Hasselmann, 1962); the sphingid moth, *Macroglossum* (Hasselmann, 1962); the dragonfly, *Libellula* and *Sympetrum* (Ruck, 1965), and the whirligig beetle, *Dineutes* (Bennett, 1967).

The compound eye was also subjected to the light-adapting procedures reported for the ocellus. The different parts of the compound eye, however, did not behave like the ocellus. Fig. 5 shows that neither 346.5 nor 574 or 577 nm adapting lights exerted qualitatively different effects on the mantid compound

FIGURE 4. Midsagittal section through the median dorsal ocellus of *Tenodera*. Picture orientation is in the proper perspective if the mantis is standing on a horizontal surface facing left. The retinula cells are divided into two distinct groups. The axons originating in each group can be seen making separate contributions to the ocellar nerve. The ocellar nerve fibers penetrate the tapetum (cup-shaped ring of widely separated nuclei surrounding the retinula cells) and emerge as the ocellar nerve. Because of the thickness of the section (20 μ) the exact position of the rhabdomes is obscured by the retinula cell nuclei. $\times 1000$.

Abbreviations

<i>A</i> ,	anterior	<i>T</i> ,	tapetum
<i>D</i> ,	dorsal	<i>NL</i> ,	neurilemma
<i>C</i> ,	cornea	<i>ON</i> ,	ocellar nerve
<i>CC</i> ,	corneal (matrix) cell	<i>FO</i> ,	fat organ
<i>RCN</i> ,	retinula cell nuclei		

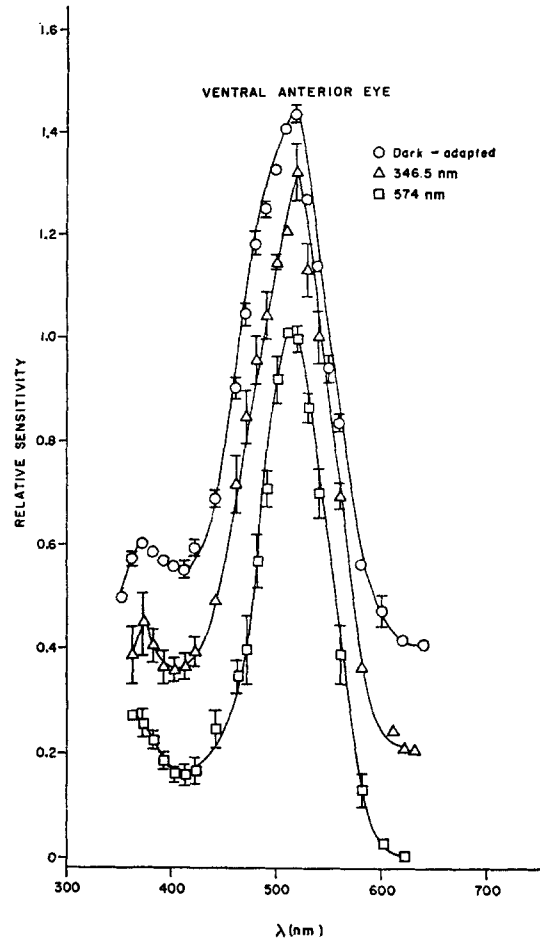
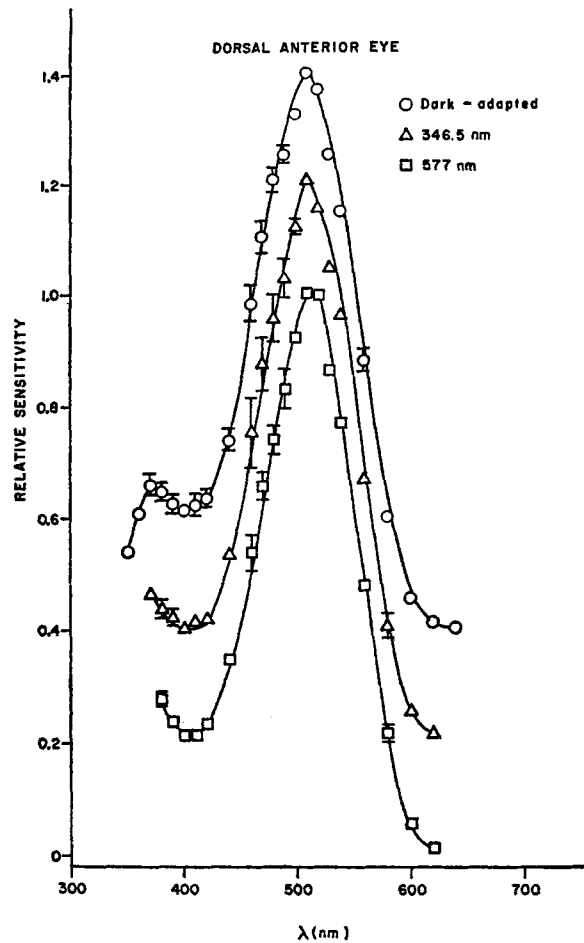


FIGURE 5. Spectral sensitivity curves for the dark-adapted and light-adapted compound eye. Comments for Fig. 2 also apply to this figure. The left set of curves shows the effect of yellow (574 nm, lower curve) and near-ultraviolet (346.5 nm, middle curve) adapting lights on the sensitivity of the ventral anterior mantis eye. For the dark-adapted eye, each point represents the mean of 19 determinations (upper curve). For the near-ultraviolet light adaptation (346.5 nm) each point represents the mean of three determinations, and for yellow adaptation (574 nm) each point represents the mean of five determinations. During yellow light adaptation (574 nm) the near-ultraviolet maximum (about 370 nm) was slightly enhanced (about 10%) as compared to the dark-adapted state. The right set of curves shows the effect of yellow (577 nm, lower curve) and near-ultraviolet (346.5 nm, middle curve) adapting lights on the sensitivity of the dorsal anterior eye (upper curve). For the dark-adapted eye, each point represents the mean of 12 different determinations. For the near-ultraviolet (346.5 nm) and yellow (577 nm) light-adapted eye each point represents the mean of three different determinations. During yellow light adaptation (577 nm) the near-ultraviolet maximum was also slightly enhanced (about 10%) as compared to the dark-adapted state. Further details are in the text.

FIGURE 5 *continued*

eye. The sensitivity was suppressed to approximately the same level throughout the spectral range 350 to 650 nm. It was noted with yellow (574 or 577 nm) adaptation that there was a slight but consistent rise in near-ultraviolet sensitivity in both the dorsal and ventral anterior eye. (In the dark-adapted ventral anterior eye the 370 nm maximum was 20% of 520 nm maximum. Following adaptation to yellow light, the 370 nm maximum was 28% of 520 nm maximum.)

It is conceivable that a near-ultraviolet receptor (wavelength maximum about 370 nm) does exist in the compound eye of the mantis but its frequency compared to the dominant green receptor is small and is not revealed by the long wavelength adapting procedures. In order to explore further the possibility that the slight change in sensitivity to near-ultraviolet light during yellow light adaptation is due to a near-ultraviolet receptor, the sensitivity of the

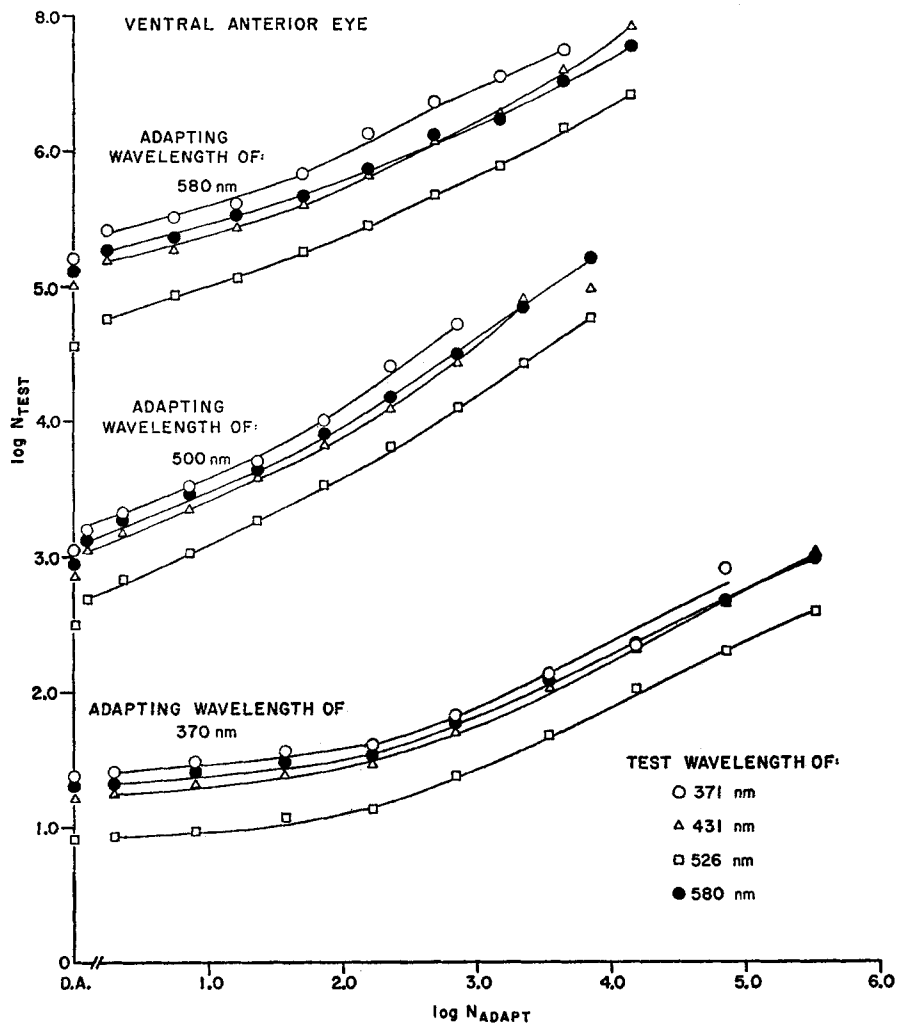
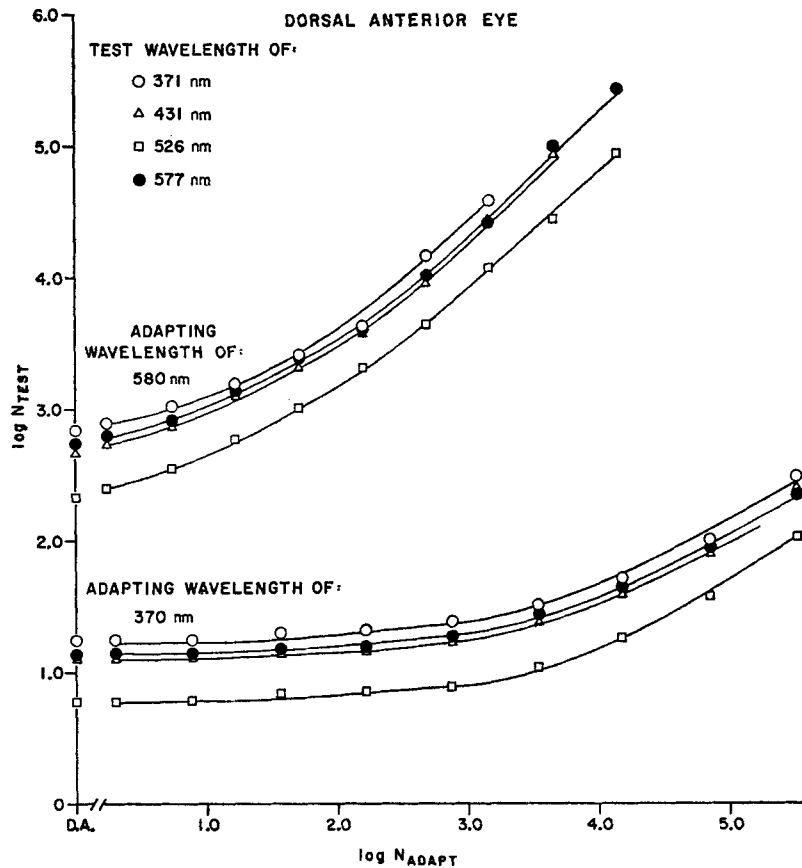


FIGURE 6. Threshold-intensity curves for the compound eye. Comments for Fig. 3 also apply to this figure. An adapting light of 500 nm (middle curve) was also used for the ventral anterior eye. Data are from single and separate preparations for the ventral anterior eye and the dorsal anterior eye.

compound eye was tested by varying the intensity of the adapting lights (increment threshold).

The logarithm of the relative number of quanta ($\log N_{\text{test}}$) needed to elicit a constant response of 200 μv varied with the energy of the adapting light ($\log N_{\text{adapt}}$) in the same way for each test wavelength used. It is clear that changes in intensity of either the ultraviolet (370 nm) or yellow (580 nm) adapting lights gave the similar results as shown in Fig. 6. Each family of curves obtained for both adapting lights is parallel, which suggests that the re-

FIGURE 6 *continued*

ceptors are all equally suppressed by the two adapting lights. Both parts (anterior ventral and anterior dorsal) of the compound eye which were tested gave similar results. These results strongly suggest that those receptors which contributed to the response have a similar spectral sensitivity.

It was determined that the shielding pigments surrounding the ommatidia of the compound eye did not influence the above results. This was tested by determining the spectral sensitivity of the compound eye under direct and indirect illumination. Indirect illumination was produced by placing an opaque "flag" in the light pathway which cast a shadow upon the eye over the recording electrode. The ERG response was thus recorded from the ommatidia stimulated by light only after it had passed laterally through the adjacent ommatidia (see Fig. 7). The spectral sensitivity functions obtained using indirect illumination were virtually identical with those obtained with direct illumination, suggesting that the shielding pigments were not "leaking" light in certain areas of the spectrum. Shaw (1969) also reported similar re-

sults for the apposition eye of the drone bee, where there was no appreciable escape of light from one facet into a neighboring ommatidia. This is a major consideration when reviewing spectral sensitivity studies for certain of the dipteran eyes (see Goldsmith, 1965; and Burkhardt, 1962, 1964, for an excellent discussion of this) whose shielding pigments "leaked" light at the red end of the spectrum.

The whole story of arthropod visual pigments may be considerably more complicated than is presently thought. Insect visual pigments may be different from vertebrate visual pigments, with stable products of photobleaching accumulating which act as effective screening pigments at certain wavelengths. Goldsmith, Dizon, and Fernandez (1968) report that the photoproducts of

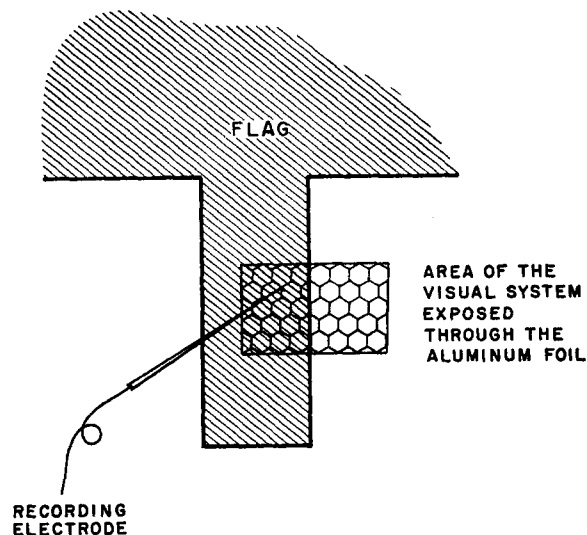


FIGURE 7. Diagram of the flag used to obtain indirect illumination. Aluminum foil covered all but a "window" ($3 \times 1\frac{1}{2}$ mm) of exposed ommatidia. The opaque flag was positioned in the light path so as to cast a shadow upon the eye immediately surrounding the recording electrode. This allowed only peripheral light to stimulate these ommatidia.

bleaching in the compound eye of the prawn, *Palaemonetes vulgaris*, may have maxima close to those of the parent pigments. Until the photochemistry of insect visual pigments has been determined and the effects of light adaptation upon the individual receptors in insect eyes are known, studies which utilize light adaptation will have to be considered with caution.

To summarize, it appears that the compound eye of the praying mantis, *Tenodera*, contains a homogeneous population of receptor types which have their maximum sensitivity in the green (510–520 nm) and a secondary area of sensitivity in the near-ultraviolet (370 nm). Neither selective light adaptation nor increment threshold studies were able to selectively divide the green

maximum into two or more receptor types. Although a second or third receptor type (blue or ultraviolet) was not established as present in the mantis compound eye in these studies, this lack of experimental evidence does not preclude the possibility that a second or third receptor type exists. If additional receptor types were relatively few compared to the receptors contributing to the green maximum, these spectral sensitivity studies would fail to reveal the activity of the second or third receptors. Single cell studies and/or microspectrophotometric studies on mantis eyes are necessary before final conclusions can be drawn. The various parts of the compound eye, both dorsal anterior and ventral anterior, behave physiologically in a similar manner.

The author is greatly indebted to the late Dr. Phillip Ruck, under whose supervision the work was accomplished.

The work was supported by grants from Wisconsin Alumni Research Foundation and the Air Force (Grant AF-AFOSR-909-65) to Dr. Phillip Ruck, Department of Zoology, University of Wisconsin, Madison, and a Ph.D. Development Grant from the University of Wisconsin Center System to the author.

I would also like to acknowledge with gratitude my wife, Dr. Ruth Bennett, Dr. L. M. Passano, and Mrs. Phillip Ruck for their assistance in completing this work.

Received for publication 12 February 1970.

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