THE SPECTRAL SENSITIVITIES OF THE DORSAL OCELLI OF COCKROACHES AND HONEYBEES

AN ELECTROPHYSIOLOGICAL STUDY*

BY TIMOTHY H. GOLDSMITH AND PHILIP R. RUCK

(From the Biological Laboratories of Harvard University, Cambridge, and the Department of Biology, Tufts University, Medford, Massachusetts)

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ABSTRACT

The spectral sensitivities of the dorsal ocelli of cockroaches (*Periplaneta americana*, *Blaberus craniifer*) and worker honeybees (*Apis mellifera*) have been measured by electrophysiological methods. The relative numbers of quanta necessary to produce a constant size electrical response in the ocellus were measured at various wave lengths between 302 and 623 mμ.

The wave form of the electrical response (ERG) of the dark-adapted roach ocellus depends on the intensity but not the wave length of the stimulating light. The roach ocellus appears to possess a single photoreceptor type, maximally sensitive about 500 mμ.

The ERG's of bee ocelli are qualitatively different in the ultraviolet and visible regions of the spectrum. The bee ocellus has two types of photoreceptor, maximally sensitive at 490 mμ and at about 335 to 340 mμ.

The spectral absorption of the ocellar cornea of *Blaberus craniifer* was measured. There is no significant absorption between 350 and 700 mμ.

Many adult insects possess two or three dorsal ocelli in addition to the compound eyes. The ocelli are usually small and inconspicuous, and compared with the compound eyes have a fairly simple structure. A layer of photoreceptor cells lies beneath a cuticular cornea, which in some species is lens-shaped. The axons of the receptor cells make synaptic contact with second-order neurons deep in the ocellus. The second-order units, few in number relative to the receptor cells, comprise the ocellar nerve, which passes from the ocellus into the brain. (For further details of the anatomy see Redikorzew (1900) and Cajal (1918) for the bee ocellus, and Ruck (1957) for *Periplaneta*.)

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No information has been available on the spectral sensitivities of insect dorsal ocelli. This paper reports electrophysiological measurements of this function in two species of cockroaches (*Periplaneta americana* and *Blaberus craniifer*) and the honeybee (*Apis mellifera*). Because of the existing evidence, largely behavioral, that some insects respond to light in the near ultraviolet, our measurements extend from 302 mμ in the ultraviolet to 623 mμ in the red.

Methods

Fig. 1 shows a diagram of the apparatus.

Light Sources.—Two sources of stimuli were used. One was a 250 watt high pressure mercury arc (General Electric H5), with the outer glass jacket removed, operated with a voltage regulator and the appropriate transformer. The image of the arc was focussed

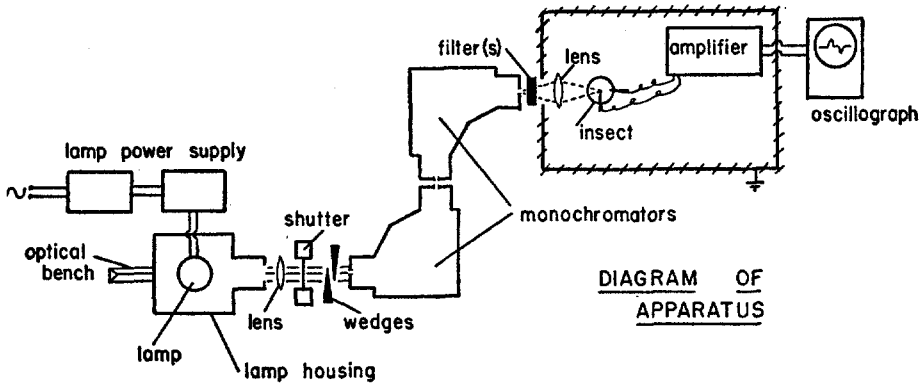

FIG. 1. Schematic diagram of the optical and recording apparatus. See text for description.

through a silica lens on the entrance slit of the first of two Gaertner quartz monochromators, used in train to form a double monochromator with double dispersion. Though such quartz instruments have a small dispersion in the visible region of the spectrum, they adequately isolate the series of mercury lines: 623, 578, 546, 491, 436, 405, 365, 334, 313, and 302 mμ. At all visible wave lengths the light emerging from the exit slit was examined for spectral purity with a spectroscope. With the slit widths used there was no significant contamination, either from lines in other parts of the spectrum or from the background continuum present in high pressure mercury lamps.

With this light source it was possible to explore sensitivities in both the visible and the ultraviolet regions of the spectrum, using essentially monochromatic light. However, a few of the mercury lines are quite feeble, and there are large gaps between some of the available lines. For certain purposes, therefore, a 100 watt zirconium arc lamp (Sylvania), which emits a continuous spectrum in the visible, was used in conjunction with a Bausch and Lomb grating monochromator. The monochromator slit

width was 1 mm. for all wave lengths, a setting which produced a half band width of 3.3 mμ at the exit slit. A 1 cm. layer of water served as heat filter between the lamp and the entrance slit. The glass walls of the heat filter removed all wave lengths shorter than about 340 mμ; thus the visible region of the spectrum to about 680 mμ was not overlapped by the second-order spectrum.

A manually operated shutter in the light path controlled the duration of stimuli. Intensities at 365 mμ and all longer wave lengths were controlled with a pair of annular photographic wedges, rotating in opposite directions so as to compensate each other. Their position was read from a dial in increments representing something less than 0.03 logarithmic unit of light intensity. The total range of the wedges corresponded to a millionfold change in intensity.

The glass and gelatin of which such wedges are made strongly absorb wave lengths shorter than 330 mμ. For this reason they were unsatisfactory at the shortest wave lengths and had to be removed from the light path. At 334, 313, and 302 mμ the intensity could be decreased 1 logarithmic unit by closing down one of the monochromator slits. When it was necessary to decrease the intensity in the ultraviolet further, filters were used, constructed of one to three large microscope cover glasses cemented together with Canada balsam. The filters, used in combination with the exit slit for fine control, provided a wide range of stimulus intensities.

Calibrations.—The relative energies of the monochromatic lights were determined by placing either a thermopile or Weston barrier layer photocell in the position of the insect. The spectral response of the photocell had been calibrated by the National Bureau of Standards. Only the photocell was sensitive enough to measure the weakest mercury lines; elsewhere in the spectrum, the two instruments provided a mutual check. The thermopile was a Kipp and Zonen "large surface" constantan-manganin pile, with 80 junctions covered by a quartz window. Both instruments were used in conjunction with a low resistance galvanometer. The transmissions of the wedges, filters, and monochromator slits were calibrated with a phototube (Welsh densichron).

Animal Preparation and Recording Methods.—Intact animals were fastened with "tacky wax" to a small platform. The head, except for the cornea of the experimental ocellus, was covered with aluminum foil. An image of the exit slit of the monochromator was focussed on the ocellus with a second silica lens. Each electrode was a stainless steel wire (0.012 inch diameter) electrolytically tapered to a fine point. With the aid of a micromanipulator, the active electrode was passed through the edge of the cornea until its tip lay at the distal surface of the receptor cell layer. The reference electrode was inserted into the flagellum of an antenna (roaches) or into a compound eye (honeybees). In both cases the reference electrodes were electrically indifferent to potential changes occurring in the illuminated ocellus, and the light shielding was adequate to prevent responses from the compound eyes at the stimulus intensities used. The amplifier was a Grass P6, which was operated push-pull, and either D.C. or at a frequency band pass of 1 cycle to 2 kc. per second. The responses appeared on an oscilloscope screen. In Figs. 2, 6, and 7, negativity of the ocellar electrode appears as an upward deflection.

After an animal had been fixed in the experimental position, it was allowed to dark-adapt for at least a half-hour. In this time the honeybee ocellus attains a stable, maximally sensitive state. The *Periplaneta* ocellus reaches a state which, if not maxi-

mally sensitive, is nearly so, and effectively stable for the durations of these experiments. The course of dark adaptation in *Periplaneta* and *Apis* has been studied by one of us (P. R.) and will be described elsewhere. Stimulus durations were one-tenth second in all experiments. The interval between test flashes was at least a minute, sufficiently long to permit recovery from the effects of the previous test flash.

RESULTS

Cockroach ocelli.—The electrical responses of roach ocelli have recently been described in some detail (Ruck, 1957). The ocellar electroretinogram (ERG) of *Periplaneta americana* contains three components: (1) a positive deflection

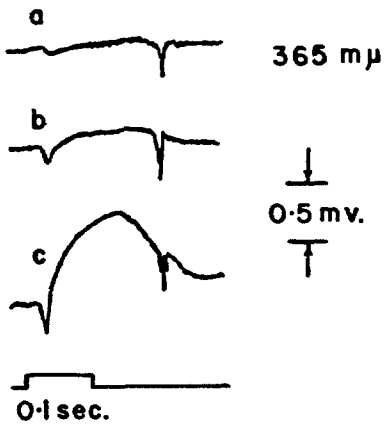

FIG. 2. Responses of a dark-adapted ocellus of *Periplaneta* to lights of increasing intensity. Stimulus strengths (log relative number of quanta): (*a*) 1.50, (*b*) 2.38, (*c*) 3.25. Wave length 365 mμ (the wave form of the ERG of this species does not depend on wave length). Stimulus durations (0.1 second) indicated below the responses. In Figs. 2, 6, and 7, negativity of the ocellar electrode appears as an upward deflection. These figures were traced from the photographic records, and the background noise, obvious at high gain settings, has been minimized. D.C. amplification.

at "on;" (2) a slow negative wave; and (3) a more rapid positive deflection at "off" ("off-spike"). The behavior of these three components with increasing intensity of stimulation is illustrated in Fig. 2 for a dark-adapted ocellus. According to Ruck's analysis, the positive and negative components which appear during illumination originate in the layer of photoreceptor cell bodies, presumably from the receptor cells themselves; the off-spikes originate in the largest ocellar nerve fibers. We find that the ERG's elicited by monochromatic light in the dark-adapted ocellus are the same in all respects as those elicited by white light.

In one experiment ERG's were obtained over the range of intensities available at each of the following wave lengths: 623, 578, 546, 491, 436, 405, and 365 mμ. The photographic records of these responses show that the wave

form of the ERG varies with stimulus strength in the same way at all wave lengths. One feature of the ERG, the amplitude of the negative wave, was measured. This amplitude in millivolts is plotted in Fig. 3 as a function of the

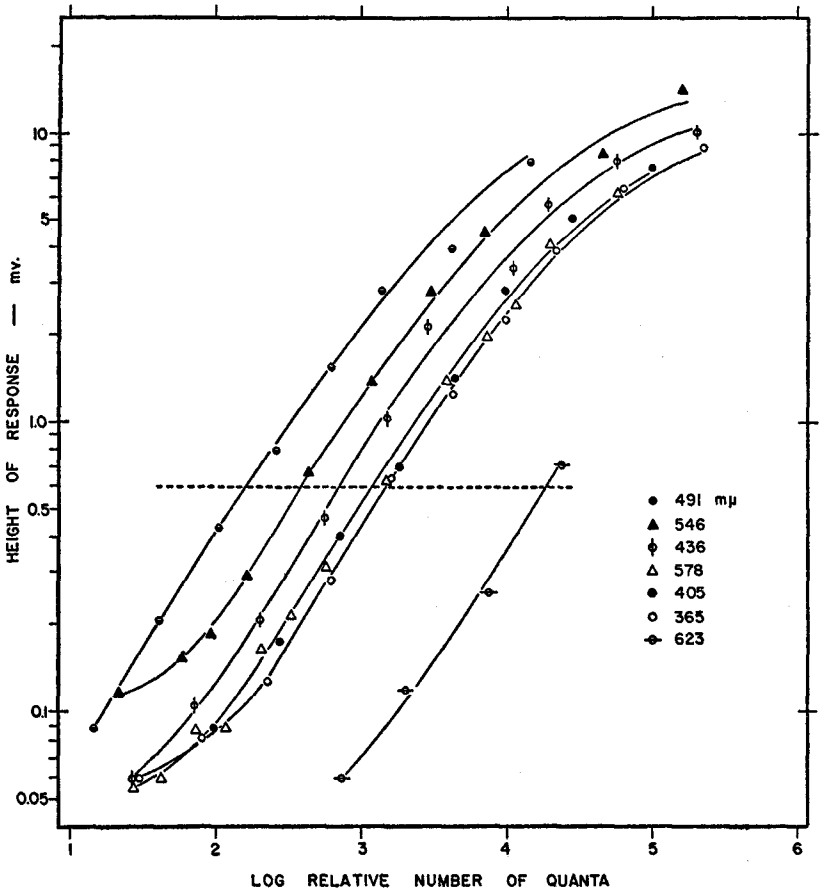

FIG. 3. Responses of the dark-adapted ocellus of *Periplaneta*. The height of the negative wave in millivolts is plotted logarithmically on the ordinate as a function of the log of the relative number of quanta. Data for seven wave lengths are plotted; the data at 405 mμ and 578 mμ are fitted by a single curve. The dashed horizontal line at 0.6 millivolt is the criterion response on which the spectral sensitivity curve plotted with crosses in Fig. 4 is based.

logarithm of the relative number of quanta delivered in the test flash at each wave length. The curves in Fig. 3 are parallel; any one of them can be superimposed on any other by a shift along the abscissa.[1]

[1] Two of the curves in Fig. 3 (365 and 546 mμ) show a second inflection at the lower end. We do not believe this is significant. The error in the measurement of

In our experience with *Periplaneta* ocelli, the ERG's at all wave lengths from 302 to 623 mμ can be matched with one another in all respects merely by varying the intensity. This observation, together with the similarity in form of the curves shown in Fig. 3, strongly suggests that the *Periplaneta* ocellus contains a single type of photoreceptor cell. In that case, both the positive and negative components of the ERG which Ruck has suggested originate in the layer of receptor cell bodies are the signs of excitation of a single type of photoreceptor cell.

By drawing an abscissa representing some constant amplitude of response—say 0.60 mv.—through the family of curves in Fig. 3, one can construct a spectral sensitivity curve. Fig. 3 yields directly the logarithm of the relative number of quanta necessary to produce a given level of response at each wave length; the reciprocal of this number of quanta is the relative sensitivity. Fig. 4 shows the sensitivity at each wave length, expressed as a fraction of the sensitivity at 491 mμ. The points marked with a cross are derived from the data of Fig. 3.

In order to localize more closely the wave lengths of maximum sensitivity and to expand the curve further into the ultraviolet, we have examined additional *Periplaneta* ocelli, two with the mercury arc and two with the zirconium arc. These results also are plotted in Fig. 4.

The following method was used to obtain these data. A negative wave of about 0.5 mv. was selected as the constant retinal response. One of us observed the oscilloscope screen and called for higher or lower stimulus strengths as they seemed to be required to yield this response. The operator adjusted the wedges, filters, and slits accordingly, and recorded instrument settings. Most of the time the observer was not aware of either the wave length being tested, or the stimulus strength recorded. Thus he could be asked to repeat previous determinations without prejudice. Such checks assured also that the sensitivity of the ocellus did not change during the course of an experiment.

The average sensitivities are plotted in Fig. 4. The *Periplaneta* ocelli we have examined appear to possess a single receptor type with a maximum sensitivity close to 500 mμ.

With this method we have also obtained spectral sensitivity data for two *Blaberus* ocelli. No differences appeared between *Blaberus* and *Periplaneta* in the region 440 to 623 mμ. Only the zirconium arc was used in the *Blaberus* experiments; therefore, this comparison does not involve the ultraviolet. In both species the sensitivity continued to decrease at wave lengths longer than 623 mμ.

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amplitudes is greatest for the smallest responses, for these deflections are only two or three times the noise level. Furthermore, these two wave lengths are widely separated in the spectrum; whereas if the inflections indicated a Purkinje shift, they should be close together.

Spectral Absorption by the Ocellar Cornea of Blaberus craniifer.—The ocellar corneas of *Blaberus* and *Periplaneta* appear transparent and colorless to the human eye. This fact implies that very little, if any, absorption occurs between 400 and 700 mμ. To learn something about corneal absorption in the near ultraviolet as well, we made a direct measurement, using the cuticular cornea of *Blaberus*. This cornea is relatively large—about 0.5 mm. in diameter in the individual examined—and has the approximate form of a disc rather than a lens.

A small circle of cuticle which included the cornea in its center was cut from the head and immersed in insect saline. The adhering soft tissues were

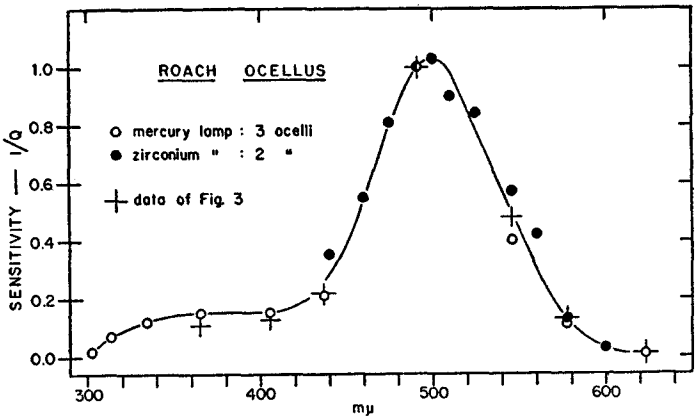

FIG. 4. Spectral sensitivity of the dark-adapted ocellus of *Periplaneta*. Sensitivity, the reciprocal of the relative number of quanta necessary to elicit a negative wave of a given height, is set equal to 1 at 491 mμ. The curve represents the average sensitivity of five ocelli, one of which is shown separately with crosses. The values for the points marked with crosses are calculated from the data of Fig. 3.

gently scraped from the back. While still moist, the disc was rapidly mounted and its absorption spectrum measured with a Cary recording spectrophotometer. The results are shown in Fig. 5. The extinction at 700 mμ has been arbitrarily set at 0. Because the back of the cornea is rough and no special pains were taken to mount it in a medium of the same refractive index, the gradual rise in extinction down to about 350 mμ may result primarily from light scattering. The main point is that the cornea of this ocellus is transparent to much of the near ultraviolet.

The absorption spectrum of the cornea of *Periplaneta* is probably very similar. Evidence presented in the following section indicates that the honeybee ocellus contains receptors which are maximally sensitive in the near ultraviolet; this, of course, implies that the cornea of the honeybee ocellus also is transparent to the near ultraviolet.

Honeybee Ocelli.—The ERG of the honeybee ocellus is similar to that of the roach. An initial positive wave is followed by a slower negative wave; off-spikes, however, have not been observed in the bee. Unlike the roach, the wave form of the ERG is qualitatively different in different parts of the spectrum.

In the ultraviolet (302 to 365 mμ), the *threshold* ERG of the dark-adapted ocellus is a *rapid positive deflection* at "on" (Fig. 6, 302 mμ, *a*). With increase of stimulus strength, the positive wave may grow somewhat, but its maximum size (in the dark-adapted ocellus) is attained at intensities not far above the threshold. The most conspicuous change in the ERG as the intensity rises is the appearance and growth of the negative wave, which eventually becomes much larger than the positive component (Fig. 6, 302 mμ, *b* and *c*).

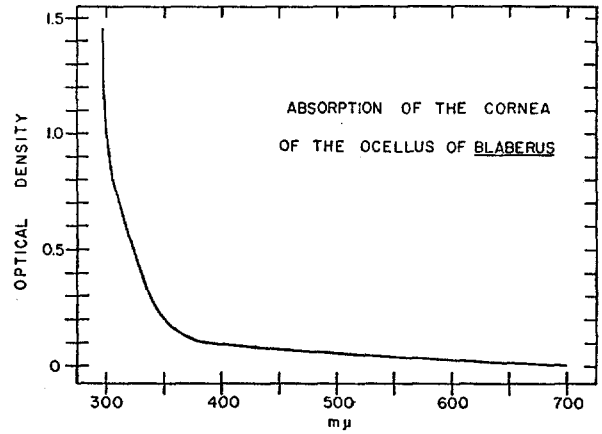

FIG. 5. Absorption spectrum of the cuticular cornea which covers the ocellar cup of the roach, *Blaberus craniifer*.

At all wave lengths longer than 405 mμ, the ERG at *threshold* is a *slow negative wave* (Fig. 6, 546 mμ, *a*) which persists as long as the light is on. With small increases of stimulus strength the negative wave remains the only component present; but suddenly the threshold for the positive wave is reached, and for all stronger stimuli the responses of the dark-adapted ocellus contain both positive and negative components (Fig. 6, 546 mμ, *b* and *c*).

The transition between the two types of threshold response occurs somewhere between 365 mμ and 405 mμ, a region in which no calibrated stimulus was readily available. At high intensities the two wave forms are indistinguishable.

Enhancement of the positive wave occurs, however, both in the ultraviolet and at long wave lengths. Whenever the positive wave appears in the dark-adapted ocellus, its amplitude may be increased by a second flash delivered a few seconds later (Fig. 7).

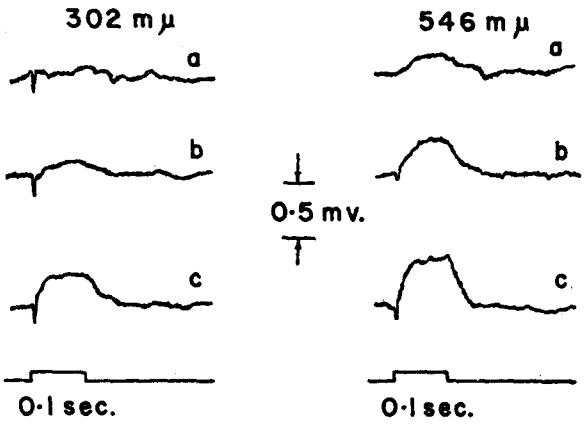

FIG. 6. Two series of responses of a median ocellus of *Apis*, illustrating the differences in wave form with wave length of stimulating light. Note the prominent positive "on" component present at threshold in the ultraviolet. Stimulus strengths (log relative number of quanta): 302 mμ: (*a*) 3.56, (*b*) 3.64, (*c*) 3.80; 546 mμ: (*a*) 2.93, (*b*) 3.10, (*c*) 3.30. Stimulus durations (0.1 second) are indicated below the responses. D.C. amplification.

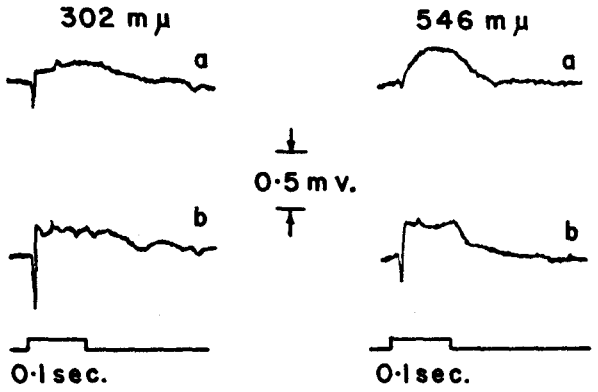

FIG. 7. The effect of repetitive stimulation of a median ocellus of the honeybee. Wave length 302 mμ: (*a*) response of a dark-adapted ocellus to a stimulus near threshold; (*b*) response to the same stimulus delivered 5 seconds later. Wave length 546 mμ: (*a*) response of a dark-adapted ocellus to a stimulus near threshold; (*b*) response to the same stimulus delivered 5 seconds later. Note the enhancement of the positive component and (particularly at 546 mμ) the increased rate of rise of the negative component, caused by repetitive stimulation.

Following flashes, even just above threshold, many seconds are required for recovery of the dark-adapted state. In general, however, 1 minute is adequate for full recovery. In our determinations of spectral sensitivity, a 1 minute interval separated the test flashes.

A further difference between the responses which appear at the two ends of the spectrum is the rate of rise of the negative component. In the ultraviolet, the negative component climbs more rapidly to its peak value than at longer

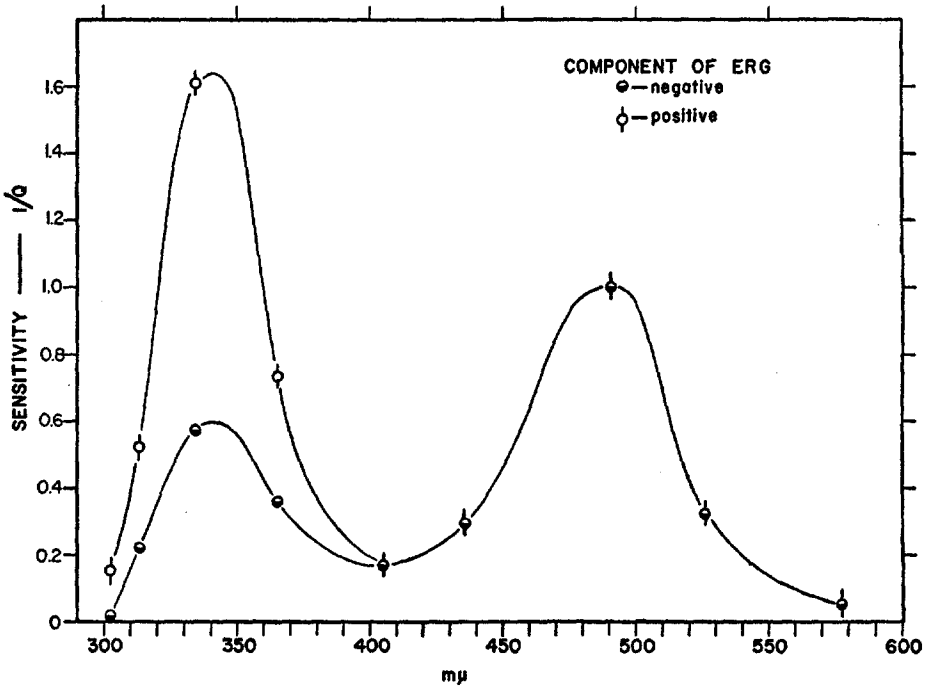

FIG. 8. Spectral sensitivity of a single median ocellus of *Apis*, showing the two maxima at about 490 mμ and 335 to 340 mμ. Sensitivity is defined as the reciprocal of the relative number of quanta required to produce a constant effect.

wave lengths. Similarly, the rate of rise of the negative wave is greater for the second of two test flashes delivered a few seconds apart (Fig. 7, particularly 546 mμ).

We believe that the differences in wave form with wave length indicate two types of photoreceptor cells in the honeybee ocellus, each type contributing positive and negative components to the electroretinogram. The spectral sensitivity curves support this explanation.

The method used to obtain the spectral sensitivity curve in Fig. 8 proved to be the most informative. As before, the relative numbers of quanta required to

elicit a constant response were determined at each wave length. However, in this case two sets of data based on two different criterion responses were obtained from the same ocellus. At 578 mμ a stimulus strength was found which elicited simultaneously: (1) a 0.3 mv. negative wave, and (2) a threshold positive wave (the smallest one which could be clearly discriminated). The relative numbers of quanta required to produce each of these responses were then determined at all wave lengths. Between 578 and 405 mμ the wave form of the response did not change; that is, at each wave length the same number of quanta which elicited the required negative response also produced the positive response. In this region the ocellus is maximally sensitive to light of about 490 mμ.

At 365 mμ and all shorter wave lengths, less energy was required to produce the threshold positive wave than the 0.3 mv. negative wave. Accordingly, there are two spectral sensitivity curves in the ultraviolet, one above the other. Both of them, however, agree in indicating that the ocellus is maximally sensitive in the ultraviolet at about 335 to 340 mμ.

TABLE I

Data Illustrating the Variation in Relative Heights of the Two Sensitivity Maxima (335 to 340 and 490 mμ) of the Honeybee Ocellus

There is a minimum in the sensitivity curve at about 405 mμ, and the ERG at 405 mμ is characteristic of the long wave length receptor. Note the relative constancy of the 405/491 ratio. Ocellus 3 is further described in Fig. 8.

No. of ocellus	Position of ocellus	Criterion component of ERG	Sensitivity ratio: 334 mμ/491 mμ	Sensitivity ratio: 405 mμ /491 mμ
1	Median	Negative	2.54	0.22
2	Median	Negative	0.63	0.28
3	Median	Negative	0.57	0.17
3	Median	Positive	1.61	0.17
4	Lateral	Negative	0.30	0.16

This result lends support to the conclusion that the honeybee ocellus possesses two different types of photoreceptor, one maximally sensitive at about 490 mμ, the other at about 335 to 340 mμ, and that excitation of either contributes to both the positive and negative components of the ERG.

We examined other bee ocelli with the mercury arc; in all cases the criterion response was a negative wave of about 0.3 mv. All the sensitivity curves that we have obtained from bee ocelli have two maxima, at about 490 and 335 to 340 mμ.

As Table I shows, however, there is much variation in the ratios of the heights of these peaks.[2] The meaning of this variation is not yet clear. In the

[2] A similar variation also was noted by Walther and Dodt (1957) in the compound eyes of *Periplaneta* and *Calliphora*.

case of the ocellus giving the lowest 334/491 ratio, the wave form of the response in the ultraviolet differed least from the wave form at long wave lengths. Conversely, the ocellus giving the highest 334/491 ratio showed the greatest difference in wave form. Thus the more pronounced the difference between ERG's at the two ends of the effective spectrum, the more prominent is the peak of sensitivity in the ultraviolet. In the two extreme cases (Table I, Nos. 1 and 4), however, the long wave length responses were nearly identical in wave form.

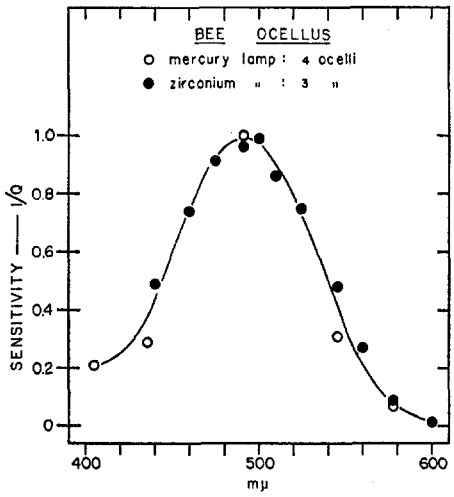

FIG. 9. Spectral sensitivity of the long wave length receptor of the bee ocellus. Average of seven ocelli. The sensitivity is defined as the reciprocal of the relative number of quanta necessary to produce a constant effect. The maximum sensitivity is at about 490 mμ.

To localize more accurately the position of peak sensitivity of the long wave length receptor, we measured spectral sensitivities at closely spaced wave lengths selected from the continuous spectrum of the zirconium arc. As before, we compared the numbers of quanta required to elicit negative waves of equal amplitude at the various wave lengths. The result is shown in Fig. 9. It establishes the maximum of the long wave length receptor close to 490 mμ.

DISCUSSION

The ocelli of *Periplaneta* and *Blaberus*, unlike the compound eyes and ocelli of most other insects, are completely free of accessory pigments. Furthermore, the bottom of the ocellar cup is lined with a white reflecting layer, and the cornea of the ocellus is nearly equally transparent to all wave lengths between 350 mμ and 700 mμ. For these reasons, a spectral sensitivity curve of this

photoreceptor should match closely the absorption spectrum of the visual pigment.

Because we have not determined the relative contributions of absorption and light-scattering in the absorption spectrum of the *Blaberus* cornea, it seems unwise to attempt to use this spectrum to correct the spectral sensitivity function of the roach ocellus shown in Fig. 4. On the basis of these data, nevertheless, it seems probable that between 300 mμ and 350 mμ the absorption spectrum of the visual pigment rises somewhat higher than the spectral sensitivity of the intact ocellus indicates, whereas at wave lengths longer than 350 mμ the spectral sensitivity curve of the intact organ probably closely approximates the absorption spectrum of the visual pigment.

We find a single type of receptor in the ocelli of *Periplaneta*; the spectral sensitivity curve has a single peak at 500 mμ and possesses a foot which extends into the near ultraviolet. The shape of this curve resembles the absorption spectrum of vertebrate rhodopsin, the visual pigment of vertebrate rods. There are other reasons for believing that the visual pigment of the ocellus is similar to vertebrate rhodopsin. Recently Goldsmith (1958) has reported the presence of retinene, a constituent of rhodopsin, in a photosensitive pigment in the honeybee. Visual pigments derived from retinene are known also in other invertebrates (squid (Hubbard and St. George, 1957–58); lobster (Wald and Hubbard, 1957)). The mechanisms of visual excitation employed in all groups of animals which possess well developed eyes—the insects included—appear to be biochemically similar.

Walther and Dodt (1957) have reported that the spectral sensitivity curve of the compound eye of *Periplaneta americana* has two peaks, at about 500 mμ and in the ultraviolet. Their curves end at 347 mμ in the ultraviolet, at which point the sensitivity still seems to be rising. The peak at 500 mμ in the compound eye and the peak we find in the ocellus may depend on the same visual pigment, present in both photoreceptors. The roach ocelli that we examined do not rise in sensitivity in the ultraviolet as these authors report for the compound eye.

In contrast to roach ocelli, the spectral sensitivity curves of honeybee ocelli have two regions of maximum sensitivity, one at 490 mμ and the other, less precisely localized, at about 335 to 340 mμ. Because stimulation in the ultraviolet produces a qualitatively different ERG from that produced by stimulation in the visible region of the spectrum, it is difficult to ascribe the two sensitivity maxima, which vary also in their relative heights, to a single visual pigment. We think it highly probable that the honeybee ocellus contains two visual pigments, localized in two separate types of photoreceptor cell. Histological studies (Redikorzew, 1900; Cajal, 1918), however, have failed to distinguish two anatomically different types of photoreceptor cell in honeybee ocelli.

Behavioral studies (Kühn, 1927; Bertholf, 1931; Daumer, 1956) indicate the existence of an ultraviolet receptor in honeybees. These experiments, however, do not establish whether the bees were responding to stimulation of the compound eyes, ocelli, or both. The function of the honeybee ocellus, and of dorsal ocelli in general, is obscure,[3] a situation which should change as appropriate behavioral experiments are performed.

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[3] When an image is formed by the ocellar cornea, it lies well behind the retina (Homann, 1924; Wolsky, 1931; Parry, 1947; Cornwell, 1955). Furthermore, there is much convergence in the afferent pathway (Cajal, 1918; Ruck, 1957). For these reasons it is generally believed that dorsal ocelli are not image-perceiving eyes.

Ocelli, by themselves, generally fail to direct phototaxes (Homann, 1924; Bolzer, 1926; Müller, 1931; Wellington, 1953; Cornwell, 1955—for possible exceptions see, however, Götze, 1927; Wellington, 1953). All these authors agree that the ocelli influence phototactic responses, apparently by increasing the responsiveness of the insect to light. For this reason dorsal ocelli are usually considered "stimulatory" organs (*cf.* Bozler, 1926; Wolsky, 1931). Harker (1956) has shown that the persistent diurnal activity rhythm of the roach, *Periplaneta americana*, is established through stimulation of these organs; to our knowledge this is the only response mediated exclusively by the dorsal ocelli.

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