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RECEPTORS IN INSECT

III. Spectral sensitivities of ocelli in Oriental Fruit fly, *Dacus dorsalis* Hendel

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Chin-Yih Wu and Ming-Man Hsu (1989) Receptors in insect. III. Spectral sensitivities of ocelli in Oriental fruit fly, *Dacus dorsalis* Hendel. *Bull. Inst. Zool., Academia Sinica* **28**(4): 257-263. The electroretinograms (ERGs) of the ocelli in the Oriental fruit flies (*Dacus dorsalis* Hendel) were studied by means of different intensities and wavelengths of the electrophysiological method. When the ocelli are stimulated with the light, a sharp initial depolarized potential appeared firstly and followed by a plateau potential which is sustained until the light intensity decreases. The "ON" discharge is seen superimposed on the ERG at the relatively high light intensity offered upon the ocelli. In an estimated spectral sensitivity curves, there appears two peaks, at the UV (317-350 nm) and blue (408-471 nm) regions.

Key words: Spectral sensitivity, Ocelli, Oriental fruit fly, Electroretinogram, Compound eye.

Each Oriental fruit fly (*Dacus dorsalis* Hendel) has three ocelli; one median and two laterals. The three ones are situated on the top of the head and arranged in a triangular form.

The function of the ocelli, in spite of some differences existing among species of the insects, is generally considered as a moderator, which is used to modulate the visual sensitivity of the compound eyes or facilitate the brain activity, rather than as a colour discriminative organ (Eaton, 1975; Eaton and Pappas, 1977; Kerfoot, 1967; Mimura, 1969).

Because most ocelli are susceptible to ultraviolet (UV) light, Stange (1981) and Wilson (1978) had suggested that the insects could support their body balance by detection of the contrast between the UV radiance in the sky and the UV absorbent from the land.

At all events, the behavior of the fruit fly is somewhat related to the excitability of ocelli, brain activity, or environmental light.

About the electrophysiological studies on the identifying colour capability of the ocellus in insect, the most useful methods are by means of observing the electroretinograms (ERGs) (Chappell and Dowling, 1972; Broda and Willmund, 1981; Eaton, 1975; Labhart, 1986) and intracellular recordings (Chappell and Dowling, 1972; Chappell and Devoe, 1975; Hu *et al.*, 1978; Ichikawa and Tateda, 1980; Labhart,

1986; Martin, 1978; Milde and Homeberg, 1984; Patterson and Goodman, 1974; Simmons, 1982). In the following experiment, we will study the ERGs of the Oriental fruit fly by means of electrophysiological technique to determine the colour sensitivity of their ocellar activity.

MATERIALS AND METHODS

The design and preparations of the experiment were almost the same as described previously (Wu, 1989).

The ERGs tested from ocelli were carried out on intact animals that were mounted with soft bee wax and the surfaces of their compound eyes were covered with the black, soft bee wax (Eaton, 1976).

A fine tungsten recording electrode was diagonally inserted about 20–30 μm in depth through a small hole presented at the median ocellus, after by excising a small piece of the cuticle surrounded it.

Light emitted by a 300 W xenon arc lamp.

The different intensities of thirteen monochromatic lights were obtained by using five calibrated narrow band interference filters (Oriel Co.,) in the collimated beam between the lamp and the quartz light guide. The thirteen different narrow band wavelengths are as follows: 319, 350, 392, 408, 437, 471, 490, 520, 527, 556, 585, 686 and 698 nm.

The acquired action potentials (ERGs) were transferred to microelectrode amplifier to be shown on the oscilloscope screen, then the transformed results were photographed.

RESULTS

1. ERGs

When a relatively high intensity of the monochromatic light stimulation is offered on the ocelli, a sharp depolarizing potential appears firstly followed by a slow steady potential. This subsequent steady potential lasts so long as the duration of light stimulation, and it returns to the resting state as soon as the stimulation is vanished (Fig. 1).

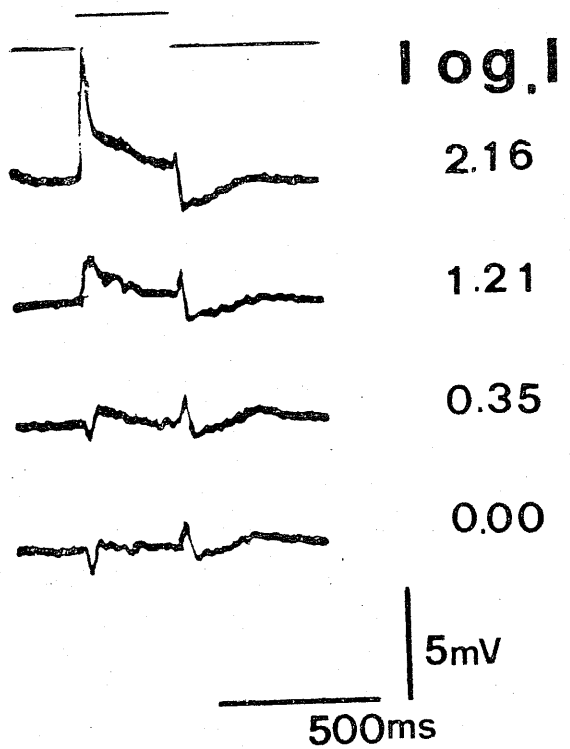

Fig. 1. ERGs of Oriental fruit fly.
wavelength: 437 nm
log I: log value of relative light intensity
stimulate dulation: 300 ms
calibration: 5 mV, 500 ms

Once the intensity of light stimulation is attenuated, the ERG is still existed, but the sharp potential becomes weakened and disappeared at a certain stimulation level except that the slow steady potential is remained.

2. Light intensities and ERGs (intensity-response curves)

When the ocelli were stimulated, the ERGs were generated. Their amplitudes of potentials were related to the stimulating monochromatic wavelengths and

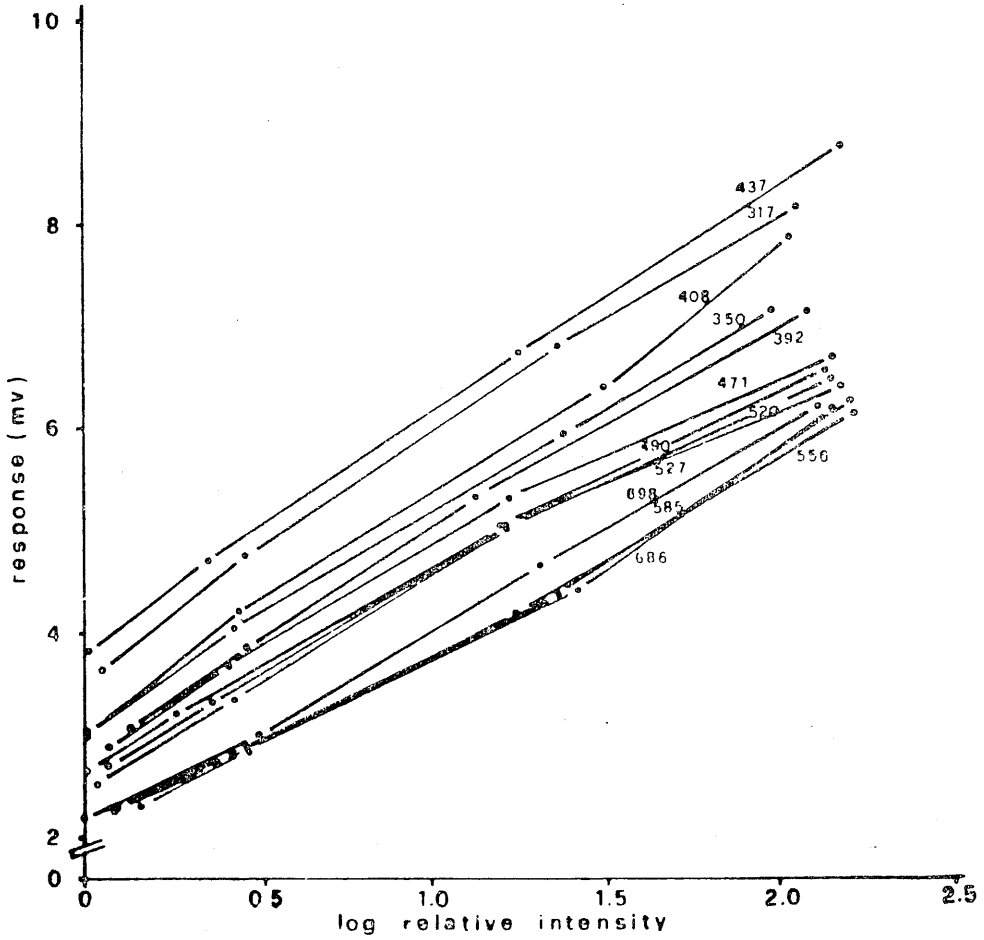

Fig. 2. Intensity-response curves. Number in fig.: 13 wavelengths

intensities. As far as the wavelengths were concerned, the higher intensities were given, and the large amplitudes of the ERGs were obtained. In this experiment, the maximal amplitude (voltage) was not excess 12 mV. Fig. 2 shows that the changes in ERG responding values acquired by stimulating the ocelli with different light wavelengths and intensities. There were thirteen different wavelengths adopted in Fig. 2, and the resulting intensity-response curves were almost parallel to one another.

We intended to record the activity of the nerves of the "OFF" discharge (Eaton, 1976) in the dark adaptation state, but had not successful. On the

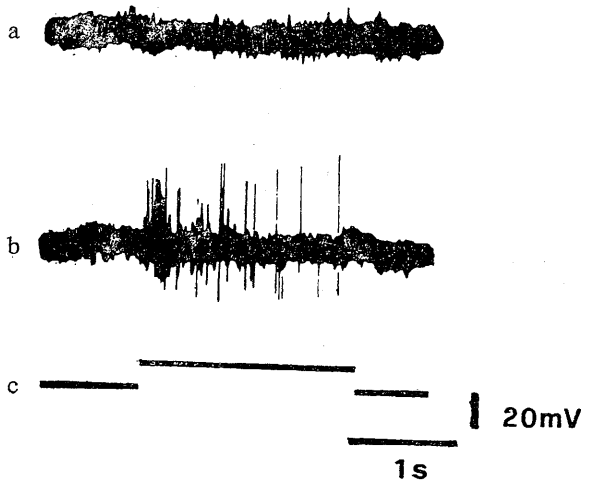

Fig. 3. "ON" discharge.
a : relative light intensity (log I=0.35)
b : relative light intensity (log I=1.21)
c : dulation of light stimulation

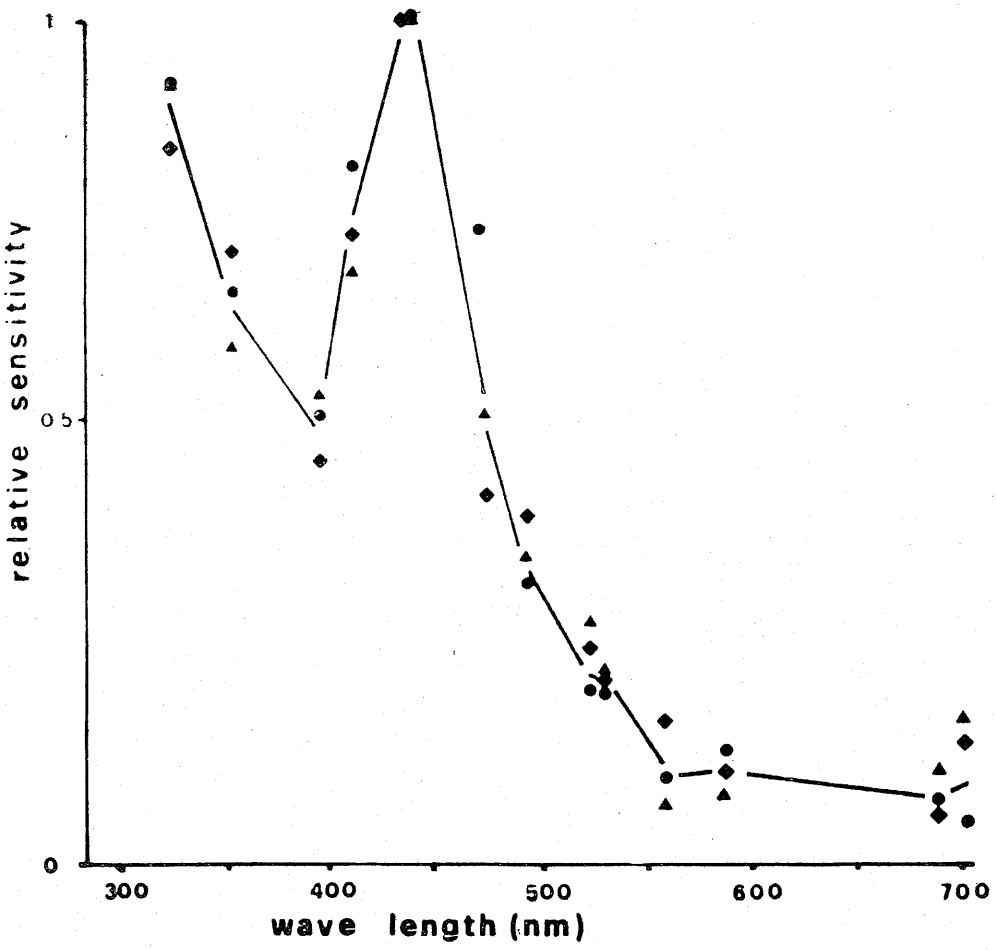

Fig. 4. Spectral sensitivity curves of the Orintal fruit fly. 3 examples (●, ◆, ▲)

contrary, when the ocellus was illuminated with the monochromatic light, "ON" discharge had been seen superimposed on the ERG upon the high stimulus intensity, but downgraded when the light intensities were decreased (Fig. 3).

3. Spectral sensitivity curve

The spectral sensitivity curve, the response value and the abcissa (the relative light intensities) representing some constant responses (the amplitude of ERG) through the intensity-response curve (Fig. 2 for example) were estimated (Wu, 1989).

Fig. 4 shows the sensitivities upon each wavelength in 3 insects. In our experiment, the spectral sensitivity of ocellus possessed at the UV (317-350 nm) and blue colour (408-471 nm) light.

DISCUSSION

The ERGs of the ocelli are mainly from the visual ocellus and ocellar nerve fibers (Eaton, 1975; Ruck, 1961a, 1961b, 1961c). According to Ruck's studies in dragonfly, the ERGs of the ocelli contain mainly three components. Component 1 is

a sensory generator potential; component 2, a depolarizing response of the receptor axon; and 3, a hyperpolarizing post-synaptic potential, which originates in the dendritic terminals of the ocellar nerve fiber.

In our experiment, when the light intensity increases, the photoreceptor depolarizes and, following an initial sharp wave, a plateau level of depolarization is continued until the light intensity decreases. This sharp initial potential of the ERG is such as a temporal "dynamic potential" (Tateda, 1975), which was observed by intracellular study in the flesh fly (Tateda, 1975) and dragonfly (Simmons, 1982).

The amplitude and the waveform of the ocellus in response to stimulating light are similar to that in other insects (Patterson and Goodman, 1975; Ruck, 1961a). In this experiment, we have not constructed the three components of the ocellar ERG as yet, however, this is a very interesting problem and will be resolved in future.

From Fig. 2, we may arrive at a conclusion that the curves are almost parallel to one another and bear no relation to the wavelengths. These phenomena are very similar to that in other insects (Chappell and DeVoe, 1975; Goldsmith, 1965; Hu *et al.*, 1978; Wasserman, 1973). On the studies of reported spectral sensitive curves, it shows that 1st, the most of dragonflies, possess the blue peak and green peak in addition to the UV peak (Stavenga *et al.*, 1979); 2nd, the bees (Goldsmith and Ruck, 1958) and moths (Eaton, 1976) have no blue peak; 3rd, the cockroaches possess green peak only (Goldsmith and Ruck, 1958). In this experiment, there are two peaks in the spectral sensitivity curves, one is located in the UV (319-350 nm) and the other in the blue-green region (408-471 nm). It may be concluded that the ocellus has two or more visual substances which may be distributed indefinitely in all visual cells or even possibly simultaneously contained in each cell (Chappell and DeVoe, 1975; Wu, 1989).

In current studies, using the high spectral resolution in ERGs of *Musca* and *Calliphora*, they were shown that the sensitivity of the ocelli had a vibrational fine structure in the UV light closed to 425 nm (Kirschfeld *et al.*, 1988). This result is very close to our experimental results.

Fig. 3 shows the ERG obtained from one fly responding to the white stimulation at some intensity levels. When the ocelli were stimulated with light, "ON" discharges were seen superimposed on the ERG. The discharge increases during the light stimulation continued, and it seems to adapt quickly. This "ON" discharge was believed to present an excitatory response from second order neurons of the fly's ocelli (Eaton, 1976; Mimura *et al.*, 1970).

The research about the spectral sensitivity of compound eyes of the Oriental fruit fly shows that the compound eyes also possess the maximal absorption of UV (λ max=348 nm), blue (λ max=431 nm) and green peaks (λ max=494 nm) (Wu, 1989).

The maximal absorption between the ocelli and the compound eyes is quite different. This will provide the ocelli and the compound eyes with different informations, and they both interact in the central nervous system to modulate the visual colours.

Therefore, the input of the ocelli and compound eyes should be taken into consideration simultaneously, which will cause insects to generate correct feeling of the colours (Kirschfeld and Lutz, 1977).

From our technique, it is much difficult to divide the ocelli into the median

ocellus and the two lateral ones, because the distance among them is quiet short (0.2 mm). However, the other researchers, focused on some insects, e. g. *Calliphora*, *Drosophila* and dragonfly, have already been carried out, and the results show that there is no difference of spectral sensitivity between the median ocelli and the laterals (Kirchfeld and Lutz, 1977; Hu *et al.*, 1978).

In conclusion, current studies show that the Oriental fruit flies possess photo-sensitive capability and they are liable to be excited by the UV and green-blue lights. However, in answer to how they can perceive visual colours, single recording from median or lateral ocelli must be accomplished in the future study.

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REFERENCES

Broda, H. and R. Willmund (1981) Fast phototaxis and electroretinograms in red-eyed and white-eyed retinal degeneration mutants of *Drosophila melanogasta*. *J. Insect Physiol.* **27**: 789-792.

Chappell, R. L. and J. E. Dowling (1972) Neural organization of the median ocellus of the dragonfly. I: Intracellular electrical activity. *J. Gen. Physiol.* **60**: 121-147.

Chappell, R. L. and R. D. DeVoe (1975) Action spectra and chromatic mechanisms of cells in the median ocelli of dragonflies. *J. Gen. Physiol.* **65**: 399-419.

Eaton, J. L. (1975) Electroretinogram components of the ocellus of the adult cabbage looper moth *Trichoplusia ni*. *J. Insect Physiol.* **21**: 1511-1515.

Eaton, J. L. (1976) Spectral sensitivity of the ocellus of the adult cabbage looper moth, *Trichoplusia ni*. *J. Comp. Physiol.* **109**: 17-24.

Eaton, J. L. and L. G. Pappas (1977) Synaptic organization of the cabbage looper moth ocellus. *Cell Tissue Res.* **183**: 291-297.

Goldsmith, T. H. and P. R. Ruck (1958) The spectral sensitivities of the dorsal ocelli of cockroach and honeybees (An elecrophysiological study). *J. Gen. Physiol.* **41**: 1171-1185.

Goldsmith, T. H. (1965) Do flies have a red receptor? *J. Gen. Physiol.* **49**: 265-287.

Hu, K. G., H. Reichert, and W. S. Stark (1978) Electrophysiological characterization of *Drosophila* ocelli. *J. Comp. Physiol.* **126**: 15-24.

Ichikawa, T. and H. Tateda (1980) Cellular patterns and spectral senitivity of larval ocelli in the Swallow butterfly (*Papilio*). *J. Comp. Physiol* **139**: 41-47.

Kerfoot, W. B. (1967) Dorsal light receptors. *Nature* **215**: 305-307.

Kirschfeld, K. and B. Lutz (1977) The spectral sensitivity in the ocelli of *Calliphora* (Diptera). *Z. Naturforsch.* **32c**: 439-441.

Kirschfeld, K., R. Feiler and K. Vogt (1988) Evidence for a sensitizing pigment in the ocellar photoreceptors of the fly (*Musca*, *Calliphora*). *J. Comp. Physiol.* **163**: 421-423.

Labhart, T. (1986) The electrophysiology of photoreceptors in different eye regions of the desert ant, (*Cataglyphis bicolor*). *J. Comp. Physiol.* (A) **158**: 1-7.

Martin, W. (1978) The functional organization of locust ocelli. *J. Comp. Physiol.* **124**: 297-316.

Milde, J. J. and U. Homeberg (1984) Ocellar interneurons in the honey bee (Characteristics of spiking L-neurons). *J. Comp. Physiol.* **155**: 151-160.

Mimura, K. (1969) Regulation of insect brain excitability of ocellus. *Z. Vergl. Physiol.* **62**: 382-394.

Mimura, K., H. Tateda, H. Morita, and M. Kuwabara (1970) Convergence of antennal and ocellar inputs in the insect brain. *Z. Vergl. Physiol.* **68**: 301-310.

Patterson, J. A. and L. J. Goodman (1974) Intracellular response of receptor cells and second-order cells in the ocelli of the desert locust, *Schistocerca gregaria*. *J. Comp. Physiol.* **95**: 237-250.

Patterson, J. A. and L. J. Goodman (1975) Componental analysis of the ocellar electroretinogram of the locust (*Scistocerca gregaria*). *J. Insect Physiol.* **21**: 287-298.

Ruck, P. (1961a) Electrophysiology of the insect dorsal ocellus. I: Origin of the components of the electroretinogram. *J. Gen. Physiol.* **44**: 605-627.

Ruck, P. (1961b) Electrophysiology of the insect dorsal ocellus. II. Mechanisms of generation and inhibition of impulse in the ocellus nerve of dragonflies. *J. Gen. Physiol.* **44**: 629-639.

Ruck, P. (1961c) Electrophysiology of the insect dorsal ocellus. III. Responses to flickering light of the dragonfly ocellus. *J. Gen. Physiol.* **44**: 641-657.

Simmons, P. J. (1982) The operation of connexions photoreceptors and large second-order neurones in dragonfly ocelli. *J. Comp. Physiol.* **149**: 389-398.

Stange, G. (1981) The ocellar component of flight equilibrium control in dragonflies. *J. Comp. Physiol.* **14**: 335-347.

Stavenga, D. G., G. D. Bernard, R. L. Chappell and M. Wilson (1979) Insect pupil mechanisms. III. On the pigment migration in dragonfly ocelli. *J. Comp. Physiol.* **129**: 199-205.

Tateda, H. (1975) Photoreception. Tokyo Univ. Press. Tokyo, Japan. pp. 175-201.

Wasserman, G. S. (1973) Invertebrate color vision and the turned receptor paradigm. *Science* **180**: 268.

Wilson, M. (1978) The functional organization of locust ocelli. *J. Comp. Physiol.* **124**: 297-316.

Wu C. Y. (1989) Receptors in insect. II. Electroretinogram of the compound eye in the Oriental fruit fly (*Dacus dorsalis* Hendel). *Bull. Inst. Zool., Academia Sinica* **28**(1): 7-13.

昆 蟲 之 受 器

Ⅲ、東方果實蠅單眼之光譜

吳京一 許明滿

使用電生理之方法，在東方果實蠅單眼上照射各種波長及强度之單色光，記錄其網膜電圖 (Electroretinogram, ERG)。

其 ERG，卽先有毀極性之銳波出現，隨後有平丘電位 (Plateau potential)，維持刺激時間 (duration)，然後俟至刺激光完了之後卽回復至原電位。

在本實驗中，如果刺激光强度稍强，常可記錄給刺激時的放電現象 (On discharge)。它可混在 ERG 上出現。

由刺激-反應曲線得知，東方果實蠅單眼光譜明顯的有兩峰。一爲紫外光部分 (317-350 nm) 及藍光 (408-417 nm)。其含有何種單色受器細胞 (colour receptor cell)？將俟將來之研究。