A METASOMATIC NEURAL PHOTORECEPTOR IN THE SCORPION

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INTRODUCTION

There is increasing evidence to show that parts of the nervous systems of many animals are directly sensitive to light without involving any specialized photosensory structures. Instances of such neural photoreception have been reported in animals representing various invertebrate phyla: *Nephthys* amongst polychaets (Clark, 1956), giant ganglion cells of *Aplysia* (Arvanitaki & Chalazonitis, 1961), giant axons of *Sepia* (Chalazonitis & Chagneux, 1961), siphonal photoreceptors of the bivalves *Mya*, *Venus* and *Spisula* (Light, 1930; Kennedy, 1958*a*, *b*, 1960) amongst molluscs, and the radial nerve of sea urchin *Diadema* (Yoshida & Millot, 1959; Takahashi, 1964) amongst echinoderms. Amongst arthropods such receptors are known to exist in crayfish (Kennedy, 1963). Occurrence of a light sense organ in the 'tail' of the scorpion *Urodacus* has been reported recently (Zwicky, 1968).

Experimenting with the locally available species of *Heterometrus*, we discovered that such receptors are also present in these scorpions. An attempt was made to locate the receptor and to study the response at different intensities and the spectral sensitivity in different varieties of scorpions chosen.

MATERIALS AND METHODS

Two species of scorpions, *Heterometrus fulvipes* and *H. gravimanus*, were used for the study. Animals of the former species collected from different localities differed in average size and in the colour of the telson, variety I attaining larger size with reddish brown telson and variety II attaining relatively smaller size with yellowish telson; other characters of taxonomical interest were found to be the same.

The animals were dissected dorsally and the dorsal body wall and the visceral contents were removed. The subneural vessel was stripped off the ventral nerve cord. The experiments were conducted in darkness except for the test flashes.

A tungsten-filament microscope lamp giving a beam of light of variable intensity was used for the test flashes, and the illumination was monitored by a phototransistor and signalled on one of the channels of the oscilloscope. Absolute measurements of light used were made using a lux-meter. Light filters giving different wavelengths were used for spectral sensitivity analysis and the intensity at different wavelengths was adjusted to be the same and kept well above the threshold. The nerve impulses were displayed on a Tektronix type 502A Dual-Beam Oscilloscope after being amplified by Grass (model p 9) pre-amplifiers. Photographic recordings were made with a Grass C–4 kymograph camera.
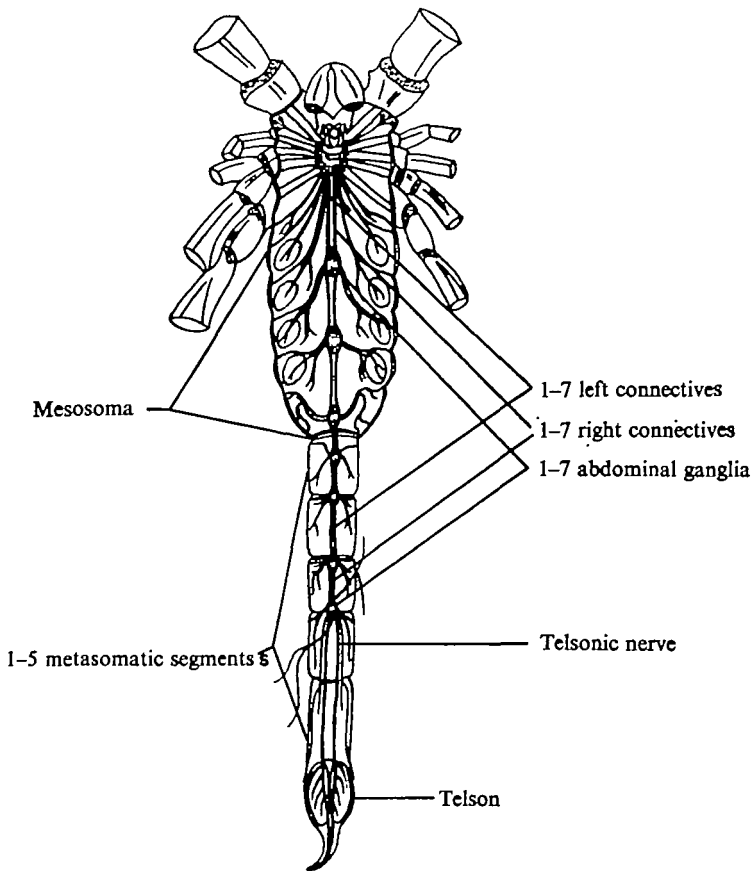
Fig. 1. Morphology of the central nervous system of *Heterometrus*, showing the location of the various connectives and the central ganglia with respect to the body segments (after Babu, 1965).

RESULTS

Location of the receptor

It was noticed that shining light on the intact metasoma evoked spikes, often in bursts, that could be picked up from the various connectives of the ventral nerve cord in the mesosomatic region. In the beginning of these studies *H. fulvipes* variety I was used, and it was observed that the response was best obtained when the light was incident on the region between the 2nd and 3rd metasomatic segments. Response was either absent or obtained only at abnormally high intensities when the segments 4, 5 and the telson (the ganglion-free region) were exposed (see Fig. 1 for the morphological relationship of the metasomatic segments and the metasomatic ganglia).

An attempt was therefore made to expose the metasoma and to locate the regions of sensitivity. It was noticed that the response persisted even after the removal of the cuticle. In *H. fulvipes* variety I the abdominal ganglia 5 and 6 were found to be sensitive to light. In many specimens cutting of all the nerves from the 7th ganglion did not interfere with the response to any noticeable extent. Moreover, specimens
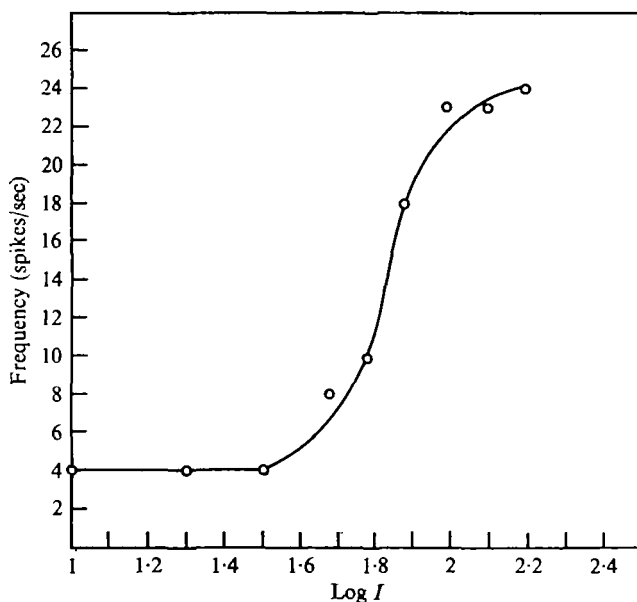
Fig. 2. Response from the telson of *H. fulvipes* var. II exposed to different intensities of white light, recorded from the III left connective. Peak response at each intensity is plotted against log *I*.

with the telson completely amputated could be successfully used to elicit the photo-response from the 5th and the 6th metasomatic ganglia. This does not agree with the earlier reports by Zwicky (1968) wherein the telsonic nerves were found to be the structures solely responsible for the light sensitivity of the *Urodacus* tail. Other locally available species of scorpion, namely *H. fulvipes* variety II and *H. gravimanus*, were therefore examined for this response. It was interesting to find that in *H. gravimanus* the region behind the 7th ganglion, including the telson, was found to be quite sensitive to light in terms of the threshold intensity required to elicit the response compared to the response from some of the metasomatic ganglia in the same animal (Fig. 4A, B). However, responses were also obtained at relatively higher intensities from the ganglia 5, 6 and 7 in these animals. Not much difference was noticed in the sensitivity of the telsonic and ganglionic regions of *H. fulvipes* variety II in a majority of the preparations (Fig. 4C, D).

Response to different intensities of light

The response was found to increase with intensity in that some fibres fired with greater frequency at higher intensities and more fibres were found to be excited with an increase in the intensity (Fig. 2). The latency of the response from the photo-receptor was found to decrease steadily with increase in the intensity in all the species studied (Fig. 3). This is true both for the ganglionic response and the telsonic response.
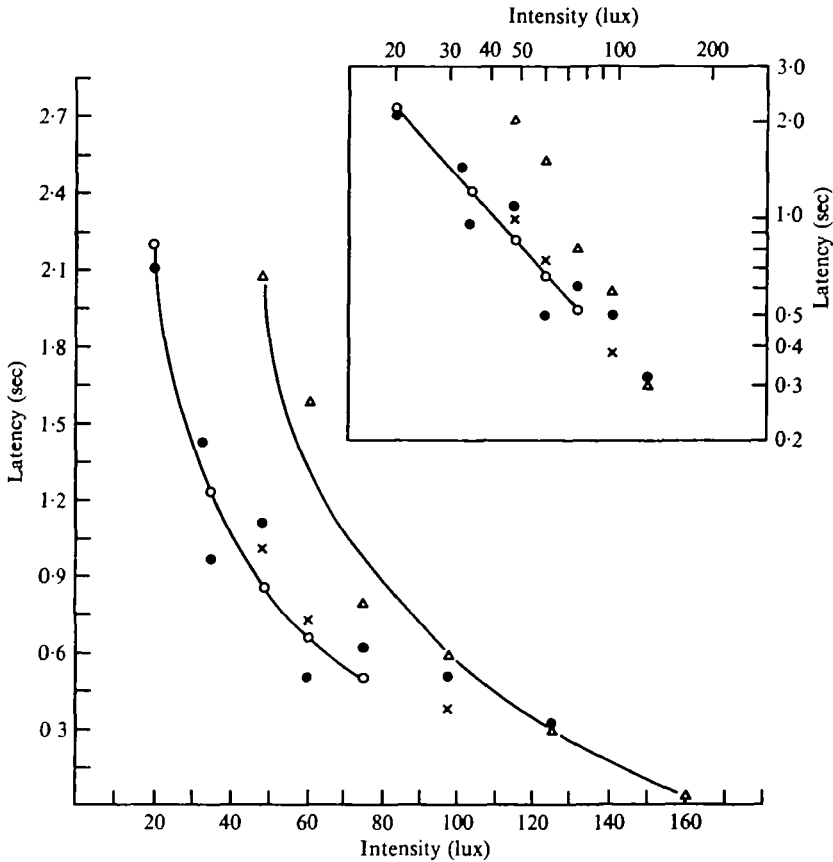
Fig. 3. Latency as a function of intensity of stimulus. O, Telson of *H. gravimanus*; ●, Telson of *H. fulvipes* var. II; ×, 6th ganglion of *H. fulvipes* var. I; △, 5th ganglion of *H. gravimanus*. Recordings in all cases were from the 2nd connective. Latency here is the duration between stimulus 'on' and the appearance of spikes at the recording site. The insert at top right shows the same data on a double logarithmic grid (one of the points for the 5th ganglion of *H. gravimanus* has not been shown on the insert since it is out of the scale).

Adaptation

Many of the units which were excited by light exhibited the phenomenon of adaptation on exposure to test flashes of long duration (Fig. 4). The frequency of spikes, after attaining the maximum for the given intensity of light, decreased and stabilized at this lower level with the receptor being constantly exposed to the light. The shape of these curves is similar in the telson and in the ganglia (*H. fulvipes*). It is seen in C and D of Fig. 4 that the activity, after reaching a peak on stimulation, comes down to a level nearly the same as that before stimulation, whereas in B (telson of *H. gravimanus*) the activity, although it falls after the peak, is maintained at a higher level compared to the activity before stimulation. However, the curve A for the response from the ganglion of *H. gravimanus* does not resemble the other curves. Fig. 6C clearly shows the fall in frequency of spikes after an initial peak on stimulation with light.
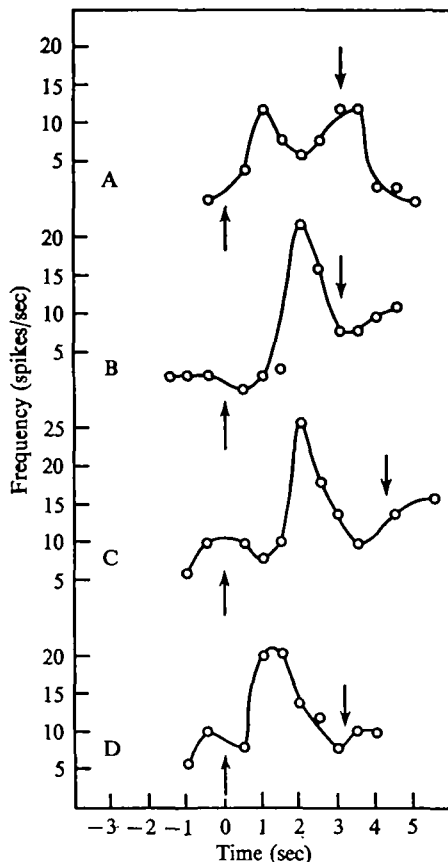
Fig. 4. Time course of response from (A) the 5th ganglion of *H. gravimanus*, (B) the telson of *H. gravimanus*, (C) the 7th ganglion of *H. fulvipes* var. I, and (D) the telson of *H. fulvipes* var. II. Records (A) and (B) were made from connective II and records (C) and (D) from connective III. The arrows indicate when the light stimulus is on and off.

Spectral sensitivity

The spectral sensitivity of these receptors was found to be the same in all the animals tested, irrespective of the location within the metasoma. Peak response was obtained at 568 nm, but there was a lesser second peak at 440 nm. Ultraviolet was found to be ineffective (Fig. 5A).

DISCUSSION

It is evident from our studies that cutting the telsonic nerves does not completely abolish the light sensitivity of the metasoma of the scorpions we have used, unlike the situation in *Urodacus* as reported by Zwicky (1968). It is also evident that there is considerable variation in the sensitivity of the different parts of the ventral nerve cord within the metasoma of different varieties of scorpions. Localization of these receptors to the telsonic nerves of *Urodacus* provides another example of such variation. However, the basis of such a variation is difficult to explain at the moment. This is unlike
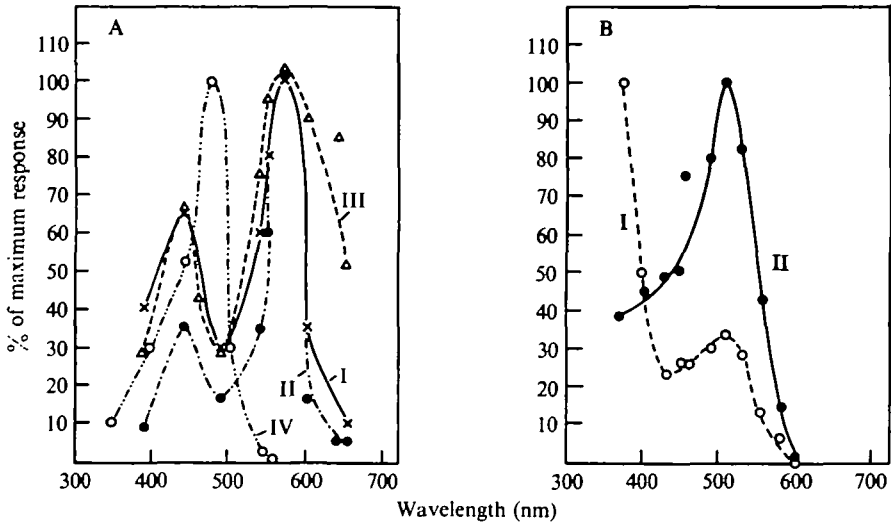
Fig. 5 (A). Normalized spectral sensitivity curves. I, 6th ganglion of *H. fulvipes* var. I; II, Telson of *H. fulvipes* var. II; III, 5th ganglion of *H. gravimanus*; IV, *Urodacus* tail (Zwicky, 1970) for comparison. The curves I to III were normalized by setting the point at wavelength 568 nm equal to 100.

(B) Normalized spectral sensitivity curves for the lateral (○) and median (●) eyes of scorpion, for comparison with the curves I to III of Fig. 5 A. Response is in terms of the reciprocal of the threshold intensity. Curve I normalized by setting point at 371 nm equal to 100 and curve II at 509 nm equal to 100.

the situation in crayfish where the photosensitivity is always located in the 6th abdominal ganglion (Prosser, 1934; Kennedy, 1958*b*, 1963).

Some units responding to light exhibited spontaneous activity in the dark, and the frequency of spikes in these units increased with light (Fig. 6A, B). Some units appeared only on excitation of the receptor and were not spontaneously active (Fig. 6C). The primary neurones responding to light in crayfish were shown to exhibit spontaneous activity by Kennedy (1963).

Unlike the response in crayfish (Kennedy, 1963), where only two units (one on each side) are shown to be photosensitive, it appears that in the scorpion several units are involved. However, it is not clear at present whether the responding units identified in the recordings from the whole connectives are all primary sensory elements or whether at least some of them are actually secondary neurones. But since the nerve cord is sensitive to light at different levels, more than one primary neurone may be expected to be operating.

It is clear from Fig. 3 that the latency of response decreases with increase in the intensity. It is also clear that this decrease in latency with increasing intensity is similar in degree in both the telson of *H. gravimanus* and the ganglia of *H. fulvipes*, suggesting that a similar phenomenon may be involved in all these cases. However, the curve for the ganglionic response of *H. gravimanus* is clearly to the right of the other curves, which may imply that the event occurring here may have different photochemical basis.
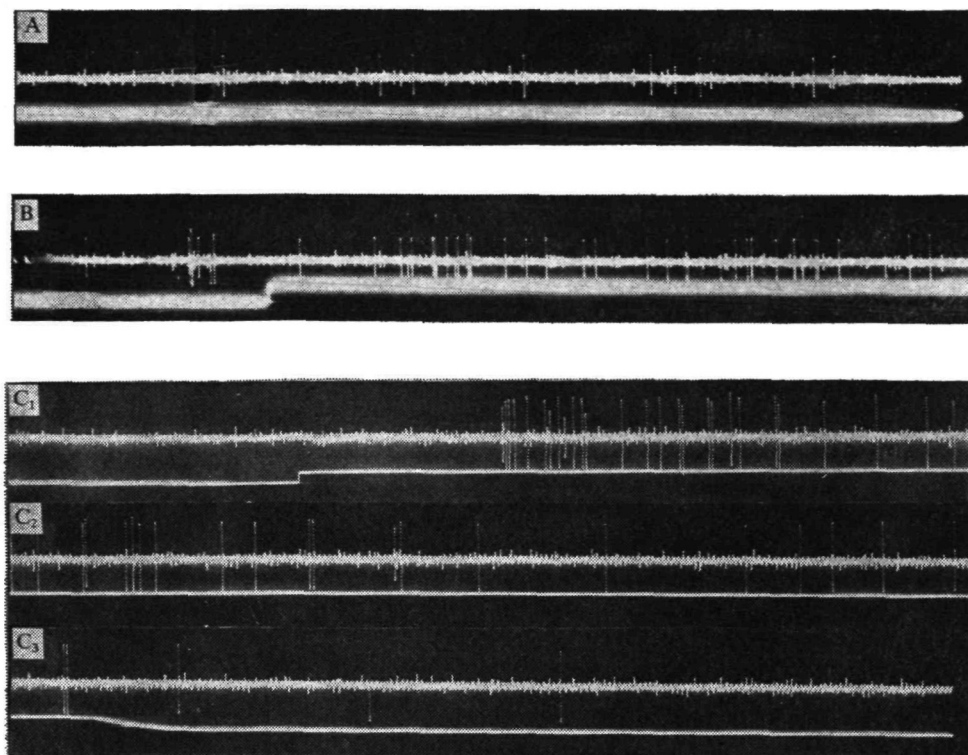
Fig. 6. (A) Spontaneous activity in darkness in the III left connective of ventral nerve cord of *H. fulvipes* var. I.

(B) Activity in the same connective of the same preparation on exposing the ganglion 6 to white light; it can be seen that the spike seen in the first record (A), increases in frequency with light.

(C₁–C₃) Activity recorded from the III right connective of the ventral nerve cord of *H. fulvipes* var. I; it is evident that a large unit appears with a certain latency after stimulus 'on' (lower beam). It can also be seen that the frequency of spikes gradually decreases showing adaptation. The time gap between the first impulse and the response of the photocell (lower beam) gives the latency. C₁, C₂ and C₃ form a continuous record. The lower beam in each case is the output of a photocell.

Studies on the spectral sensitivity show that it is the same in the various species of *Heterometrus* selected, indicating that probably similar pigments are involved. Our results agree with the results obtained from scorpion lateral eyes (Machan, 1968) in having two absorption maxima (Fig. 5). However, the wavelength at which the peak response is obtained is different. The spectral sensitivity curve for the tail of *Urodacus* also differs from the one we have obtained in its position and in that it has only one peak.

Further studies on the central course of the input from these receptors are in progress in our laboratory and will be published elsewhere.

SUMMARY

1. There are extraocular photoreceptors in the metasoma of different species of the scorpion *Heterometrus* (*H. fulvipes* var. I, *H. fulvipes* var. II and *H. gravimanus*).

2. The relative sensitivity of the different parts of the metasoma differs in the different species of *Heterometrus* studied.

3. The telsonic nerves, although sensitive to light, are not solely responsible for the extraocular perception of light, and cutting of the telsonic nerves does not abolish the response in any of the species of *Heterometrus* used.

4. With increase in the intensity of light stimulus the latency of response decreases and the impulse frequency increases in the responding units; and a greater number of units are excited.

5. With prolonged exposure of the receptors to light some units become adapted, and the rate of adaptation is different in the telsonic response as compared to the ganglionic response in *H. gravimanus*.

6. Spectral sensitivity is the same in the different species of *Heterometrus* tested, and the peak response is obtained at 568 nm with a smaller peak at 440 nm.

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