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Photosensitivity of the Central Nervous System of *Limulus polyphemus*

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ABSTRACT—The photosensitivity of the central nervous system (CNS) of the horseshoe crab, *Limulus polyphemus*, was investigated by analyzing changes in motor nerve activity in the segmental nerves of prosomal and opisthosomal ganglia. Spontaneous efferent impulses were recorded in the dark from all the investigated segmental nerves. Impulse trains from the 7th dorsal nerve in the prosomal CNS were inhibited in response to illumination of the whole CNS. Impulse trains from each of the 9–13th dorsal nerves in the isolated opisthosomal CNS were inhibited, and the impulse train from each the 14–16th dorsal nerve was elicited or inhibited upon illuminating the whole CNS. Spontaneous rhythmic bursts at 20–80 s intervals were recorded in the dark from the ventral nerves of the isolated opisthosomal CNS. In the presence of light, the rhythmicity of spontaneous bursts disappeared and other species of impulse trains were elicited. In single ganglion preparations, isolated from the rest of the CNS by surgically severing the connectives, similar photoresponses were recorded before and after isolation. These results demonstrate that the CNS of *Limulus* is a photosensitive organ.

Key words: *Limulus*, CNS, photosensitivity

INTRODUCTION

Certain neurons in the central nervous system (CNS) of arthropods exhibit photosensitivity that is not associated with visual function. Photoreceptors in the brain have been reported in spiders (Yamashita and Tateda, 1983), crayfish (Sandeman *et al.*, 1990), and insects (Ichikawa, 1991; Hariyama, 2000); in the terminal abdominal ganglion in crustaceans (Prosser, 1934; Kennedy, 1963; Wilkens and Larimer, 1972; Wilkens and Larimer, 1976) and in the butterfly (Arikawa *et al.*, 1991); and in the metasomatic ganglia (Geethabali and Rao, 1973) of scorpions.

The horseshoe crab, *Limulus polyphemus*, is often referred to as a “living fossil” because it has a primitive morphology that has apparently changed little during the last 200 million years or so (Sekiguchi, 1988). *Limulus* has four kinds of photoreceptors: lateral eyes, median ocelli, ventral photoreceptors and mini-ommatidia. The latter two kinds of photoreceptors are located internally: the ventral photoreceptors are distributed along the ventral optic nerves and are most sensitive to light of 535 nm (Millecchia *et al.*, 1966); and the mini-ommatidia are distributed in the median

optic nerves and are sensitive to light of 380 nm (Samie *et al.*, 1995). In addition, it has been suggested that there are photosensitive cells in the telson (Hanna *et al.*, 1985; 1988). Although *Limulus* has a number of photosensitive organs in its body, photosensitivity of the *Limulus* CNS has not been reported. Comparison with other arthropods suggests the possibility that the CNS of this “living fossil”, too, is photosensitive. The presence of photosensitivity in the CNS of *Limulus* is interesting from a phylogenetic viewpoint, to investigate the extent to which central nervous photosensitivity is a primitive or more recently acquired property.

In the present paper, the photosensitivity of the *Limulus* CNS was examined by extracellular recording to reveal the distribution and extent of photosensitivity.

MATERIALS AND METHODS

Horseshoe crabs (*Limulus polyphemus* Linnaeus) were purchased from the Woods Hole Marine Biological Laboratory (Massachusetts, USA). The imported animals were reared throughout the year in aquaria at the Shimoda Marine Research Center. Adult animals of both sexes (body size 17–21 cm in carapace width) were used.

The CNS, including the prosomal or opisthosomal ventral nerve cord, was surgically isolated with associated segmental nerves (Fig. 1) and was placed on the bottom of a perfusion chamber (7×2×0.5 cm). Preparations of a single ganglion obtained by severing the connectives were each placed in a smaller perfusion

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chamber (3×2×0.7 cm). The perfusion saline consisted of 530 mM NaCl, 10.7 mM KCl, 18.0 mM CaCl₂, 24.6 mM MgCl₂, 2.3 mM NaHCO₃ and 3 mM glucose (Kuramoto and Ebara, 1984), and was saturated with air by bubbling at a flow rate of 0.13 ml/s. The distance between the preparation and the water surface was approximately 1 mm. A heat exchanger was placed in the perfusion line to stabilize perfusate temperature, which was monitored with an electric thermometer and maintained at 17–19°C.

The total electrical activity of each segmental nerve was recorded using a suction electrode and amplified by an AC amplifier

(AB621G, Nihon Kohden). To elucidate the photosensitivity of an isolated single ganglion, all connections with the ventral nerve cord were severed.

For white light stimulation, a 100 W halogen lamp was used, illuminating the whole area of each preparation using a fiber optic guide. A stimulator (SEN 3301, Nihon Kohden) controlled the power supply (LG-PS2, Olympus) to switch the light on and off. A heat-absorbing filter (AQ4698000, Olympus) was placed just before the fiber optic guide. The end of the light guide was placed at 5 cm apart from the preparation. The light intensity was measured by a

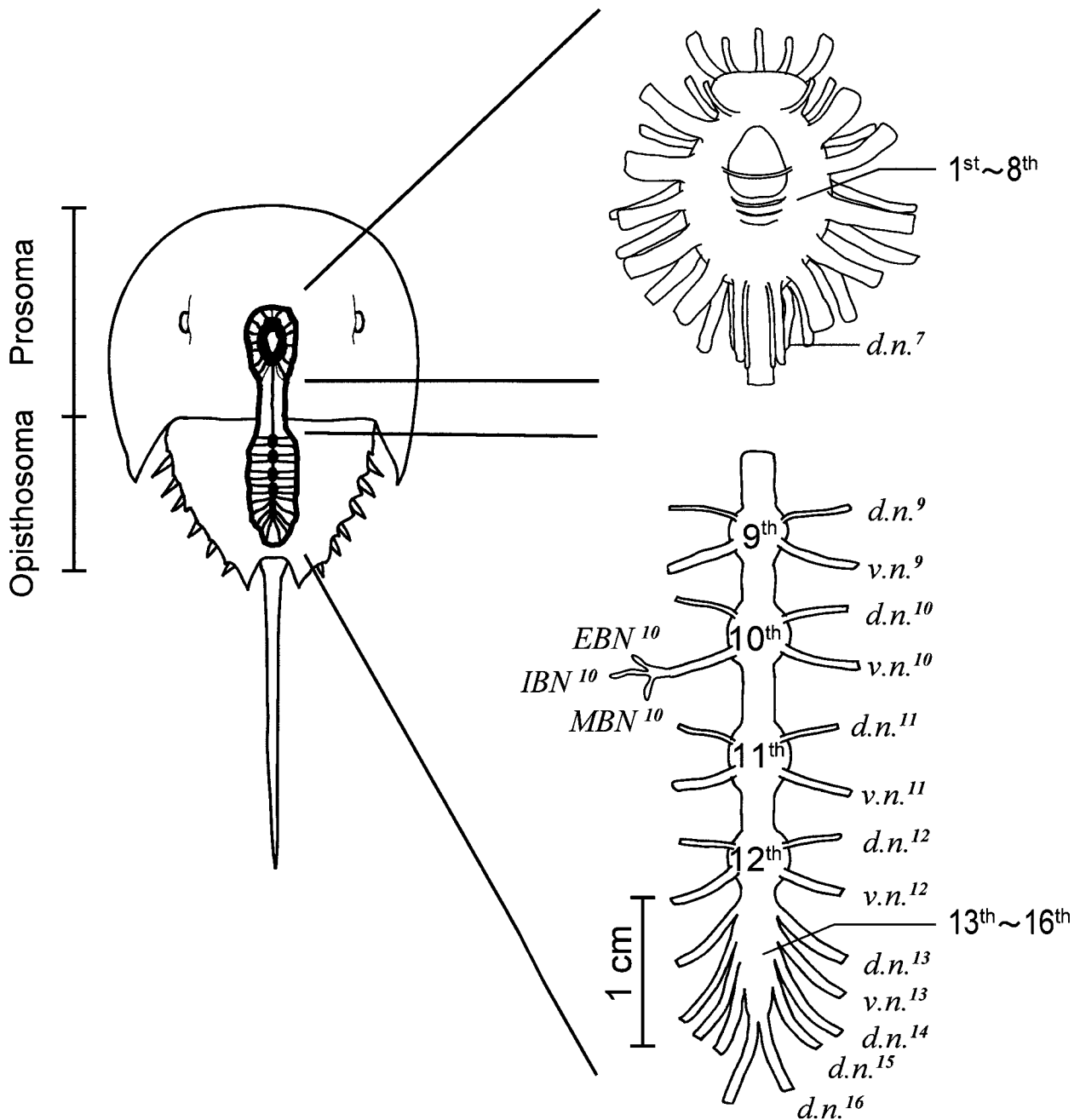


Fig. 1. Schematic drawings of the prosomal and opisthosomal CNS of *Limulus*, superimposed on a dorsal view of the whole animal, and the isolated ganglia in a ventral view. The CNS lies ventrally and consists of 16 ganglia. Ganglia 1–8 form the prosomal CNS, and separated ganglia 9–12 and fused ganglia 13–16 form opisthosomal ganglia. Ganglia 1–13 each has two pairs of segmental nerves, dorsal (*d.n.*^{7, 9–13}) and ventral (*v.n.*^{9–13}), while ganglia 14–16 has a pair of dorsal nerves (*d.n.*^{14–16}) only. The ventral nerves are divided into three branches (external, median and internal branchial nerves) as illustrated for the 10th ventral nerve (*EBN*¹⁰, *MBN*¹⁰ and *IBN*¹⁰).

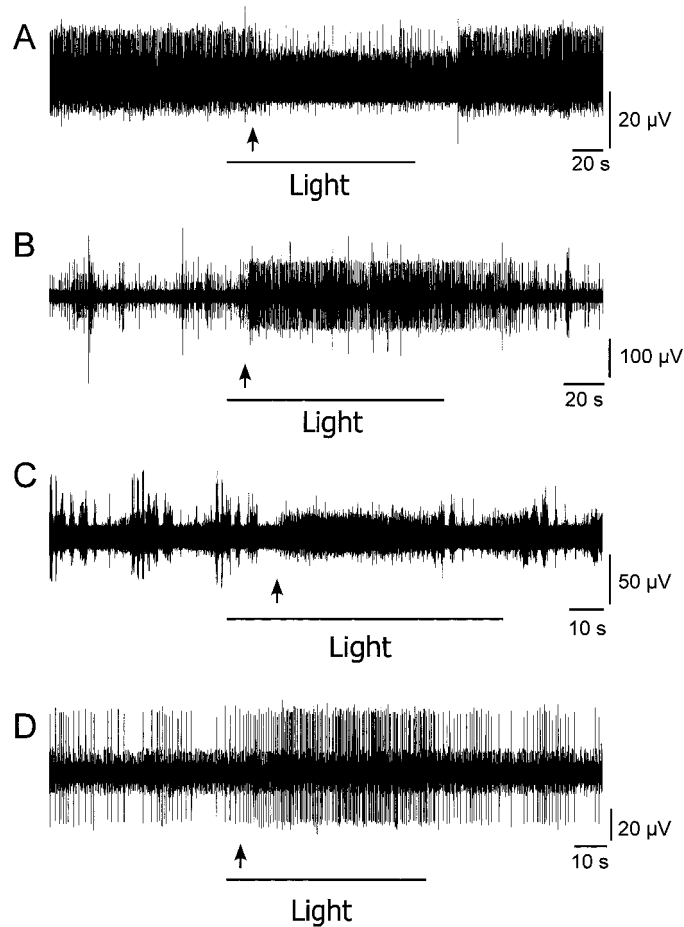


Fig. 2. Photoresponses manifested as changes in the spontaneous motor nerve activities from segmental nerves (dorsal and ventral). **A:** Impulse train recorded from the dorsal nerve of the 10th ganglion. Note the population of spontaneous impulses of approximately 30 μV , which decrease in frequency after a delay of approximately 17 s (arrow). **B:** Example of the photoresponse of the dorsal nerve 15, which shows an excitation with a delay of 7 s (arrow). **C:** Rhythmic bursts recorded from the ventral nerve of the 10th ganglion were inhibited about 15 s after the onset of illumination and replaced by frequent discharge of other population of impulses approximately 40 μV amplitude (arrow). **D:** Photoresponse recorded from the dorsal nerve 7 in the prosomal CNS. An illumination increased the frequency of impulses after a delay of about 4 s (arrow).

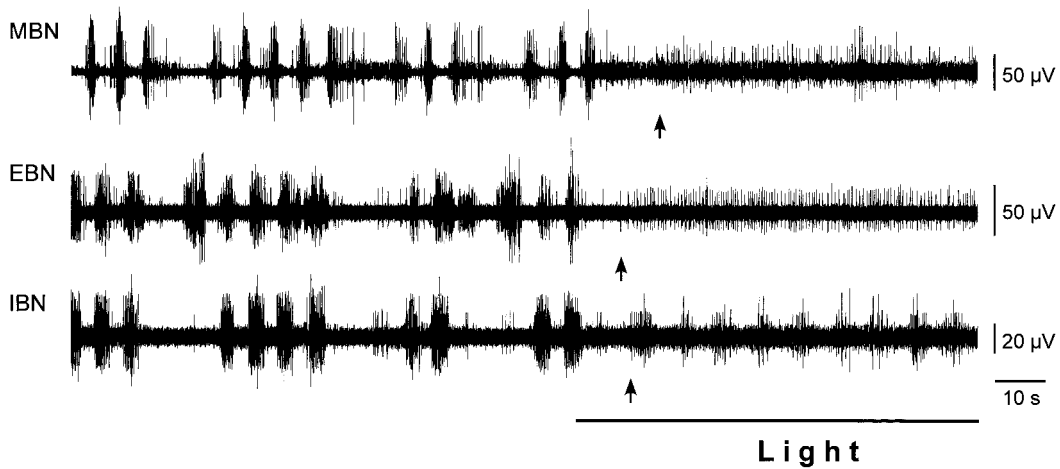


Fig. 3. Light-induced changes in motor nerve activities recorded simultaneously from the three branches (MBN, EBN and IBN) of a ventral nerve from the isolated 9th ganglion. All show spontaneous rhythmic bursts in the dark, and ceased completely in the MBN and EBN during illumination. Bursting of the IBN was incompletely inhibited and other species of impulses of approximately 40 μV and 60 μV appeared in the EBN and MBN. (Approximate points of onset of changes indicated by arrows).

digital illuminance meter (T1, Minolta) and was 10,000 lx at the surface of the preparation.

Light from a 100 W halogen lamp was passed as a parallel beam (using appropriate lenses) through a shutter, a heat absorption filter and one of several narrow-band interference filters (450, 500, 550, 600 and 650 nm; Optical Coatings Japan), and focused on the preparation using a set of lenses. With the aid of neutral density filters, the intensities of monochromatic lights were adjusted to an equal number of photons (1.6×10^{14} quanta/cm² · s) at the surface of the preparations. Light stimuli were delivered through a shutter controlled by a stimulator (SEN 3301, Nihon Kohden).

Electrical signals were stored on a tape of a data recorder (PC208Ax, SONY), and recorded on a thermal array recorder (WR7700, Graphtec). The signals were digitized using an analogue-to-digital converter (Digidata 1200B, Axon), and saved on the hard disk of a personal computer for analyzing frequencies, durations and latencies of motor nerve activities (AxoScope software, Version 9, Axon).

RESULTS

The central nervous system (CNS) of *Limulus* consists of 16 ganglia and their connectives, which show a bilateral symmetry. In the prosomal area, the 1st to 8th ganglia are fused to form the brain. In the opisthosomal area, the 9th–12th ganglia are separated, and the 13th–16th ganglia are fused (Fig. 1). Each of the 1st–13th ganglia has two pairs of segmental nerves, dorsal and ventral, whereas each of 14th–16th ganglia has only one pair of dorsal nerves. Photoresponses were manifested as a change in the motor nerve activity in the 7th dorsal nerve of the prosomal area and all dorsal and ventral nerves in the opisthosomal area. Spontaneous efferent impulses were obtained in the dark from all the investigated segmental nerves (Figs. 2, 3, 4).

In the opisthosomal CNS, the dorsal nerves of the 9th–13th ganglia (which innervate the visceral organs) discharged impulses of two or three different amplitudes under dark conditions. The frequency of the impulses was usually constant but sometimes changed periodically in some preparations. Fig. 2A shows an example of the motor output pattern of the 10th dorsal nerve. It consisted of two species of impulses of different amplitudes. When the preparation was illuminated, the frequency of the large impulses (30 μ V in amplitude) decreased from approximately 2 impulses per second (ips) to 0.2 ips after about 17 seconds. The impulse trains observed in the dark for all dorsal nerves 9–13 were inhibited by illumination.

The motor nerve activities of dorsal nerves 14–16 consisted of more than five populations of impulses. Fig. 2B shows an example of the impulse train of motor nerve activities consisting of six kinds of irregularly spaced impulses. When the preparation was illuminated, three populations of impulses increased in frequency: impulses of 40 μ V increased from 0.16 ips to 1.5 ips; 30 μ V impulses increased from 0.58 ips to 2.7 ips; and 20 μ V ones increased from 2.4 ips to 9.2 ips. After the cessation of light stimulation, the augmented impulse frequency was maintained for 40 seconds. Irregular impulses originating from dorsal nerves 14–16 were observed in darkness and increased in frequency

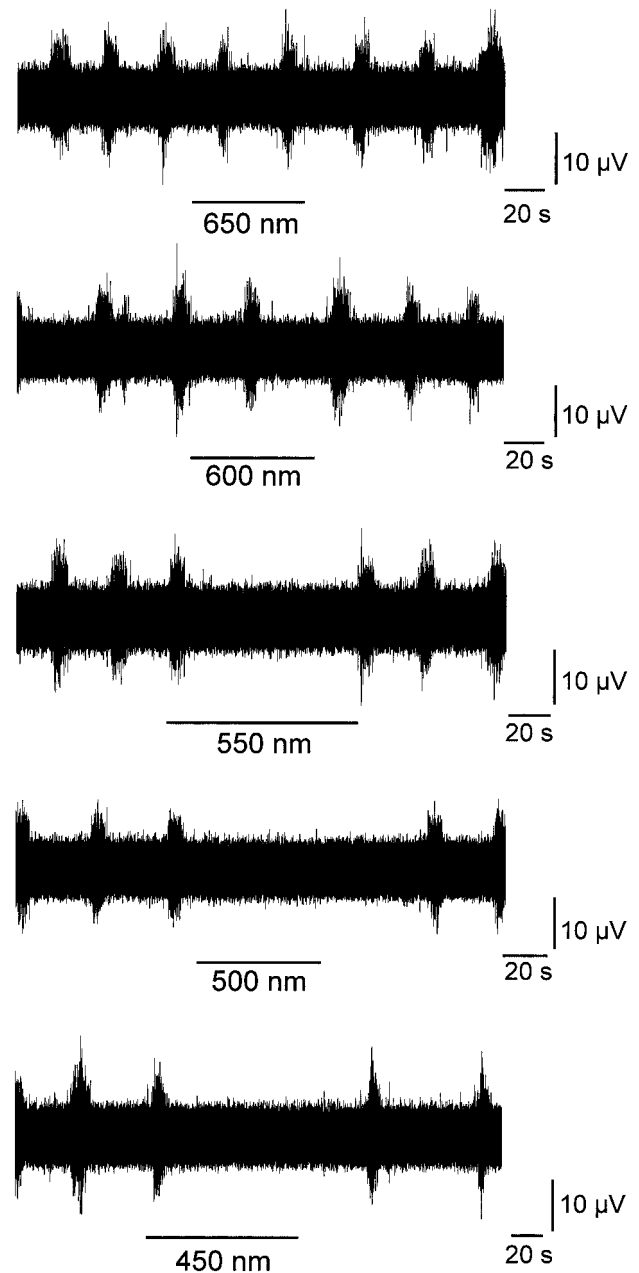


Fig. 4. Photoresponses of the 10th ventral nerve to monochromatic lights of the same intensity (1.6×10^{14} quanta/cm² · s). Light of 450–550 nm inhibited a bursting activity, while light of 600 and 650 nm failed to elicit any response.

upon illumination. Inhibition of impulses in the dorsal nerve 16 was also observed.

The ventral nerves discharged bursts of impulses in the dark. Fig. 2C shows an example of the motor nerve activity of ventral nerve 10. Rhythmic bursts at intervals of approximately 20 s were found in the absence of illumination. When illuminated, the bursts were inhibited and other species of impulses of 40 μ V at about 11 ips appeared 15 seconds after the light-on. The duration and frequency of bursts from the ventral nerves differed from one preparation to another (5–60 s in duration and with periods of 20–80 s).

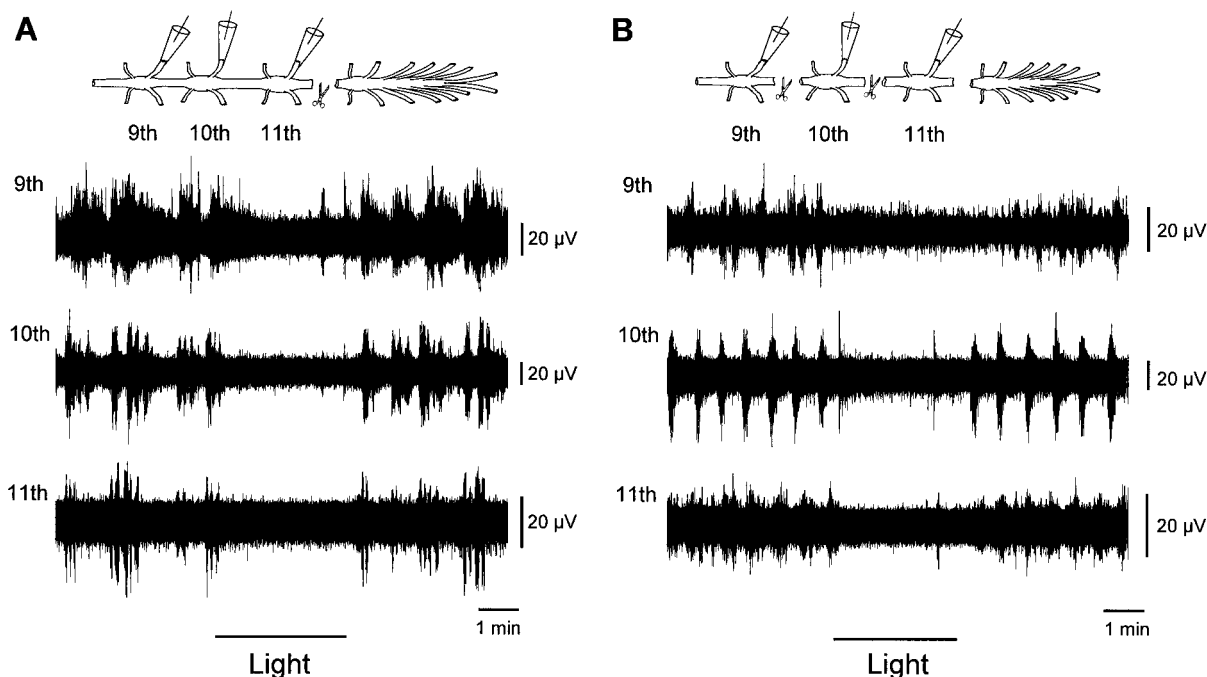


Fig. 5. **A:** Motor activities recorded simultaneously from ventral nerves of 9th–11th ganglia. Synchronous rhythmic bursting in the ventral nerves was inhibited upon illumination. **B:** Motor activities simultaneously recorded from the same ventral nerves shown in A, after severing all the connectives between these ganglia. Bursting was no longer synchronous and clearly inhibited during illumination.

In the prosomal CNS, motor activities of the dorsal nerve 7 were changed upon illumination (Fig. 2D). Spontaneous activity consisting of three classes of impulses was recorded in the dark (ca. 70 μ V, 30 μ V and 10 μ V). Illumination increased the frequencies of the impulses of 70 μ V and 30 μ V from 0.5 to 2.5 ips and 3.3 to 5.2 ips, respectively, with a 4 s latency.

The ventral nerves of opisthosomal CNS innervate the skeletal muscles of the gill plates, controlling the movements of abduction and adduction of the gill plates (Patten and Redenbaugh, 1900). To elucidate whether inhibition of the bursts from the ventral nerves was related to inhibition of gill plate abductor and/or the adductor activity, the illumination-driven changes in the motor nerve activity of the branchial nerves were investigated (see Fig. 1). Spontaneous activity, rhythmic bursts and impulse trains could be recorded from all three branchial nerves in the dark. They were more often recorded from a single ganglion preparation rather than a preparation of the (9th–16th) opisthosomal ganglia. Fig. 3 shows a typical example of spontaneous efferent activities of the branchial nerves and its change by illumination. The EBN, IBN and MBN generated synchronous bursts: the phase relationship between the first and second nerves was in-phase and the third one was anti-phase to the two. The burst durations of the EBN and IBN were 5 s and that of the MBN was 1–2 s. These bursts repeated three to six times and then became silent for 5–30 s or more. When the ganglion was illuminated, the rhythmic bursts of the EBN and MBN ceased completely and that of the IBN was inhibited partially, while the frequency of the

tonic impulse trains (60 and 40 μ V in MBN and EBN) increased (Fig. 3).

We tried to record photoresponses to monochromatic lights of different wavelengths in seven preparations, but the responses were successfully obtained only in two preparations: they were sensitive to monochromatic lights of 450–550 nm, but insensitive to the light of long wavelengths within a range of 600–650 nm (Fig. 4).

The photoresponses could be detected from each single opisthosomal ganglion. After severing the connective between the 11th and 12th ganglia, the spontaneous rhythmic bursts were recorded from each ventral nerve of all ganglia and they changed upon illumination in a similar fashion to those before severing (Fig. 5A). Moreover, the bursts could be recorded from each ventral nerve of each single ganglion preparation of which the connectives between the ninth and 10th and 10th and 11th ganglia had been severed. The rhythmic bursts were inhibited by illumination in a similar fashion to those before severing (Fig. 5B). Similar photosensitivities were detected in the isolated 12th and fused ganglia 13–16 (data not shown).

DISCUSSION

Four different classes of photoreceptor are well known in *Limulus* and have been used extensively in neurophysiological research. However, there have been no reports concerning the photosensitivity of the CNS in *Limulus*. The CNS displays a large degree of fusion, the first eight segments being fused together to form the brain. A ventral nerve cord

with four segmental ganglia and a fused terminal ganglia consisting of four ganglia extend through the abdomen. The present study has demonstrated that spontaneous motor activity in the segmental nerves of the CNS were enhanced or inhibited by direct illumination of the CNS, including the dorsal nerve 7 in the prosomal area, the 9th–16th dorsal and the 9th–13th ventral nerves in the opisthosomal area. The modifications of the impulse activities in response to light were characteristic for each segmental nerve (Figs. 2, 3 and Table 1): some impulses showed excitatory and others inhibitory responses. Photoresponses in the segmental nerves have been reported in the crayfish and the swallowtail butterfly. In the crayfish, illumination of the terminal abdominal ganglion evokes a cyclic firing pattern from the abdominal tonic flexor motor neurons, as recorded from the nerve roots (Edwards, 1984; Simon and Edwards, 1990). Spontaneous discharges were recorded in the dark from the sixth peripheral nerve of the terminal abdominal ganglion of the butterfly, and the frequency of some impulses was enhanced or inhibited upon direct illumination of the ganglion (Arikawa *et al.*, 1991). It therefore seems that arthropod segmental nerves responsive to light have similar properties of impulse modification in response to light.

Table 1. Light-induced changes in motor nerve activities of individual segmental nerves.

Ganglion	Segmental nerves	Spontaneity	Response
7th	dorsal	Impulse	2/3
9th	dorsal	Impulse	11/14
	ventral	Burst	11/18
10th	dorsal	Impulse	10/11
	ventral	Burst	21/28
11th	dorsal	Impulse	5/6
	ventral	Burst	19/20
12th	dorsal	Impulse	2/4
	ventral	Burst	11/19
13th	dorsal	Impulse	3/5
	ventral	Burst	9/14
14th	dorsal	Impulse	5/7
15th	dorsal	Impulse	9/18
16th	dorsal	Impulse	3/6

Impulse trains or bursts were recorded from all segmental nerves. The column "Response" shows the number of responded preparations among the total number of preparations examined.

The apparent response to a light stimulus could be due to an effect of heat irradiation from the halogen lamp, because a halogen lamp emits infrared radiation and the responses had a long latency. The experiments using monochromatic lights (450, 500, 550, 600 and 650 nm) excluded this possibility, that is, the motor nerve activity was significantly changed by an illumination of 450–550 nm but not by an illumination of 600 and 650 nm (Fig. 4). The

responses were successfully observed only in two of seven preparations. This could be due to a relatively lower intensity of the monochromatic light. However, the intensity of the monochromatic light was 1.6×10^{14} quanta/cm²·s, the value which roughly corresponds to the brightness of a fine day. A further study will be required to understand why strong light is needed to elicit a photoresponse from the *Limulus* CNS.

Intensity-response functions and spectral characteristics of the responses are essential for the identification of the origin of photosensitivity in the CNS. However, the preparation used in the present study did not have a long stability to perform such a work.

The latency of the responses was significantly long, compared with that of other *Limulus* photoreceptors with a latency of less than 1 s. This might be explained by the motor neurons not being directly responsive to illumination. That is, putative photoreceptors in the CNS might be interneurons, and their signals modulate firing rhythms of motor neurons controlled by a specific central mechanism (Fournier *et al.*, 1971; Wyse, 1972). The caudal photoreceptors in the terminal abdominal ganglion of the crayfish are multimodal interneurons (Kennedy, 1963; Wilkens and Larimer, 1972; Flood and Wilkens, 1978), and that of the butterfly is assumed to be an interneuron (Arikawa *et al.*, 1991).

In the crayfish, photosensitive sites were located in the terminal ganglion (Prosser, 1934; Kennedy, 1963; Wilkens and Larimer, 1972) and the brain (Sandeman *et al.*, 1990). Photoreceptors in the brain have been reported in spiders (Yamashita and Tateda, 1983) and insects (Ichikawa, 1991; Hariyama, 2000). Scorpions have the photosensitive sites in the 5th–7th abdominal ganglia (Geethabali and Rao, 1973), and the butterfly has a photosensitive terminal abdominal ganglion (Arikawa *et al.*, 1991). The photosensitive sites in the *Limulus* CNS are different from these other arthropods: the results reported here clearly show that the surgically isolated prosomal ganglia and single opisthosomal ganglia are sensitive to light and send a photic signal as a change in the motor nerve activity to peripheral targets. That is, *Limulus*, the "living fossil", has the most extensive distribution of photosensitive areas among all the species for which CNS photoreception is known. This might therefore reflect the primitive condition among the arthropods.

Horseshoe crabs live in shallow water on soft bottoms, plowing through the upper surface of the sand. They are able both to walk along the bottom and to swim by flapping their appendages. The role of photosensitivity of the *Limulus* CNS in their life remains to be examined. However, because photoresponses were manifested as a change in the motor activity of the segmental nerves innervating the heart and the gill plates, it is assumed that photosensitivity plays a significant role in the animal. Electrical stimulation of dorsal nerves results in a decrease of heart rate (Pax, 1969; Von Burg and Corning, 1970), so it is likely that an inhibition of the dorsal nerve activity by light (Fig. 2A) may accelerate the heart rate. The activities of the ventral nerves are accompa-

nied by ventilatory and swimming movements of the gill plates (Fourtner, *et al.*, 1971; Knudsen, 1973; 1975). The ventral nerve divides into three branches: the EBN innervates the abductor muscle, the MBN innervates the adductor muscle and the IBN does the inner and outer lobe muscle (Patten and Redenbaugh, 1900). Inhibition of rhythmic bursts of the EBN and MBN in response to light suggests that the movements of the gill plates would be changed in intact animals responding to environmental light (Fig. 3). In a preliminary experiment, blue illumination shed on restrained animals with an embedded LED between the gill plates sometimes accelerated the heart beat and the movement of the gill plates after moving the opisthosoma (unpublished observation). This finding suggests that the photoreponse of the opisthosomal ganglia is indeed functional in the intact animal. It is interesting to note that juvenile horseshoe crabs are much more transparent than adults and sometimes swim on their back. The photoreponse might have a significant role in a juvenile horseshoe crab, rather than in a mature one.

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REFERENCES

- Arikawa K, Uchiumi K, Eguchi E (1991) Extraocular photoreceptors in the last abdominal ganglion of a swallowtail butterfly, *Papilio xuthus*. *Naturwiss* 78: 82–84
- Edwards DH Jr (1984) Crayfish extraretinal photoreception. I. Behavioural and motoneuronal responses to abdominal illumination. *J Exp Biol* 109: 291–306
- Flood PM, Wilkens LA (1978) Directional sensitivity in a crayfish mechanoreceptive interneuron: analysis by root ablation. *J Exp Biol* 77: 89–106
- Fourtner CR, Drewes CD, Pax RA (1971) Rhythmic motor outputs co-ordinating the respiratory movement of the gill plates of *Limulus polyphemus*. *Comp Biochem Physiol* 38A: 751–762
- Geethabali, Rao KP (1973) A metasomatic neural photoreceptor in the scorpion. *J Exp Biol* 58: 189–196
- Hanna WJB, Pinkhasov E, Renninger GH, Kaplan E, Barlow RB Jr (1985) The tail of *Limulus* contains photoreceptors that modulate a circadian clock. *Biol Bull* 169: 552–553
- Hanna WJB, Horne JA, Renninger GH (1988) Circadian photoreceptor organs in *Limulus*. II. The telson. *J Comp Physiol A* 162: 133–140
- Hariyama T (2000) The brain as a photoreceptor: intracerebral ocelli in the firefly. *Naturwiss* 87: 327–330
- Ichikawa T (1991) Brain photoreceptors in the pupal and adult butterfly: fate of the larval ocelli. *Zool Sci* 8: 471–476
- Kennedy D (1963) Physiology of photoreceptor neurons in the abdominal nerve cord of the crayfish. *J Gen Physiol* 46: 551–572
- Knudsen EI (1973) Muscular activity underlying ventilation and swimming in the horseshoe crab, *Limulus polyphemus* (Linnaeus). *Biol Bull* 144: 355–367
- Knudsen EI (1975) Centralgenic motoneuron bursts accompanying various gill plate movements in *Limulus polyphemus* (Linnaeus). *Comp Biochem Physiol* 51 A: 465–469
- Kuramoto T, Ebara A (1984) Effects of perfusion pressure on the isolated heart of the lobster *Panulirus japonicus*. *J Exp Biol* 109: 121–140
- Millecchia R, Bradbury J, Mauro A (1966) Simple Photoreceptors in *Limulus polyphemus*. *Science* 154: 1199–1201
- Patten W, Redenbaugh WA (1900) Studies on *Limulus*. II. The nervous system of *Limulus polyphemus*, with observations upon the general anatomy. *J Morph* 16: 91–200
- Pax RA (1969) The abdominal cardiac nerves and cardioregulation in *Limulus polyphemus*. *Comp Biochem Physiol* 28: 293–305
- Prosser CL (1934) Action potentials in the nervous system of the crayfish. II. Responses to illumination of the eye and caudal ganglion. *J Cell Comp Physiol* 4: 363–377
- Sandeman DC, Sandeman RE, de Couet HG (1990) Extraretinal photoreceptors in the brain of the crayfish *Cherax destructor*. *J Neurobiol* 21: 619–629
- Samie FH, Jinks RN, Weiner WW, Chamberlain SC (1995) The morphology and physiology of a “mini-ommatidium” in the median optic nerve of *Limulus polyphemus*. *Vis Neurosci* 12: 69–76
- Sekiguchi K (1988) Biogeography. In “Biology of horseshoe crabs”. Ed by Sekiguchi K, Science House, Tokyo, pp 22–49
- Simon TW, Edwards DH (1990) Light-evoked walking in crayfish: Behavioral and neuronal responses triggered by the caudal photoreceptor. *J Comp Physiol A* 166: 745–755
- Von Burg R, Corning WC (1970) Cardioregulatory properties of the abdominal ganglia in *Limulus*. *Can J Physiol Pharmacol* 48: 333–341
- Wilkens LA, Larimer JL (1972) The CNS photoreceptor of crayfish: morphology and synaptic activity. *J Comp Physiol* 80: 389–407
- Wilkens LA, Larimer JL (1976) Photosensitivity in the sixth abdominal ganglion of Decapod Crustaceans: A comparative study. *J Comp Physiol A* 106: 69–75
- Wyse GA (1972) Intracellular and extraocular motor neuron activity underlying rhythmic respiration in *Limulus*. *J Comp Physiol* 81: 259–276
- Yamashita S, Tateda H (1983) Cerebral photosensitive neurons in the orb weaving spiders, *Argiope bruennichii* and *A. amoena*. *J Comp Physiol A* 150: 467–472

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