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Basic Response Pattern and Classification of Oculomotor Nerve in the Crayfish, *Procambarus clarki*

By

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(With 8 Text-figures and 2 Tables)

Introduction

Crustacean eyestalk movement which is observable when the animal body is tilted and/or the spot light source is moved has been studied by many investigators. And it is well known that the control mechanism of the movement is dependent on mainly geotactic and visual informations except eye withdrawal reflex which can be induced by mechanical stimulus in head region. The contribution of the statocyst organ to this compensatory eyestalk reflex has been well known for a long time since the first appearance of the report by Clark (1896). The dependence of the eye position on gravity has rather extensively studied in recent works of Schöne (1951, 1954, 1956, 1959). Regarding to the contribution of the visual organ, several reports have mentioned the optokinetic response in horizontal plane and the influence of the light source to the eye position (Wiersma and Yamaguchi 1967, Wiersma and Oberjat 1968).

In the crayfish, anatomical arrangement of the eyestalk musculature has been reported by Robinson and Nunnemacher (1966) for *Orconectes* and by Sugawara et al. (1971) for *Procambarus*. According to them, any single muscle does not seem to function separately, and any eyestalk movement is produced by their consorting action. Hisada et al. (1969) observed the eyestalk movement in full 360° turn of the body and reported a new category of the compensatory eyestalk movement.

In their recent work, Wiersma and Oberjat (1968) reported response types of some oculomotor nerves with various stimuli in crayfish and Wiersma and Fiore (1971) also reported a similar work in crab. But, regarding to the optokinetic response, they were exclusively concerned in horizontal plane to which the statocyst organ did not contribute, so the optokinetic response in vertical plane and the eyestalk movement effected by integrated treatment of geotactic and visual

This report is dedicated to Dr. Haruo Kinosita for his 60th birthday.

informations are little known.

In this study, as a step to clarify the mechanism of integration from sensory to motor neurones, main attention is placed on the classification of oculomotor nerves found in the crayfish eyestalk and the contributions of both statocyst and visual senses on the response patterns of these neurones.

Material and Methods

Anatomy and Histology

Mature specimens of both male and female of the fresh water crayfish *Procambarus clarki* were used. In order to trace the nerve distribution, the eyestalk was isolated together with a dorsal anterior portion of the carapace, and excess parts were removed in van Harreveld's solution. The chitinous membrane of the eyestalk was carefully flayed at full length and the hard cuticle of the head part was removed to expose the brain (supraesophageal ganglion). The preparations were stained with methylene blue to observe the arising part of the oculomotor nerve bundle from the brain and the mode of innervation of the eyestalk muscles.

The transverse section of the oculomotor nerve bundle was made of isolated eyestalk. Customary method of softening dense chitin was so harmful for maintaining the inner structure intact that it was not applicable for the purpose. The preparation from which the whole chitinous parts were carefully removed by hand was fixed for 3 to 4 hours in 10% formalin, then dehydrated in ethanol and embedded in paraffin. Then sectioned and mounted according to the routine procedure and the sections (5–8μ) were stained by standard hematoxyline-eosin staining method.

Electrophysiology

The intact animal was suspended with a clamp placed over the carapace, while two chelipeds were fixed with the elastic threads and the walking legs were left free. Metalic extracellular electrode made of an insect pin sharpened and insulated with polystylene to the tip (tip diameter 3–5μ) was introduced through the soft membrane between the outer and inner eye segments to record the nerve activity. A preparation grounding was provided with a pin placed under the anterior carapace through a hole made at the cervical groove separating the anterior and posterior portion of carapace. After establishing the recording of single oculomotor fibre activity, the electrode was left untouched for about 15 minutes to have firmer lodging in place. This made the signal pick-up from one particular fibre possible for several hours even when the position of the eyestalk changed with rotation stimulus or with violent movement produced by an eye withdrawal reflex.

Then the animal with the clamp on was mounted on a specially constructed rotation device which allowed to rotate the animal around any desired body axis at various velocities. The rotation axis was installed with two ball bearings to reduce vibration and to ensure the smooth rotation. The rotation device also carried the striped drum which was used as a visual stimulus. Black and white stripes on the drum subtended an angle of 8.2° each at the crayfish eye. A moving point light was also used for visual stimulus.

Nerve impulses were led to the cathode-ray oscilloscope through a biological amplifier together with other stimulus parameters appearing on the separate channels. Oscillographic records were taken by a long recording camera. Impulse frequencies were calculated from the recorded film, and, if necessary, a computor was used for statistical treatment.

Results

Anatomy and Histology

Eyestalk muscles are innervated by two oculomotor bundles which originate separately from the brain (Fig. 1). Figure 2 illustrates schematically the innervation of oculomotor nerves to the eystalk muscles. Oculomotor I arises from the brain and follows a dorsolateral route over the optic nerve. Oculomotor II arises ventrolaterally and runs along the optic tract almost closely attached to it. The two bundles travel in parallel with each other within the eyestalk up to the level of the base of the optic cup. On the way, oculomotor II branches to the attractor muscle. At the base of the optic cup, oculomotor I divides into three branches (Ia, Ib, Ic), and oculomotor II divides into two branches (IIa, IIb). Nerve Ia fuses with IIa and then divides into three branches (Ia_1, Ia_2, Ia_3), and they supply two medial retractors and dorsal retractor in the dorso-medial region of the optic cup. Ib innervates the abductor muscle. Ic runs from latero-dorsal side to latero-ventral side and on the way, branches out to innervate ventral depressor, lateral rotator, and lateral retractors. IIb supplies ventral retractor.

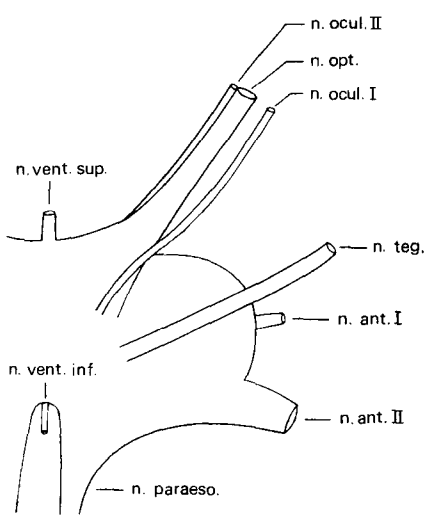

Fig. 1. Dorsal view of the right half of the brain (supraesophageal ganglion). Six pairs of cranial nerve, including oculomotor nerve I and II arise from the brain. n. ant. I: antennule nerve. n. ant. II: antennary nerve. n. ocul. I: first oculomotor nerve. n. ocul. II: second oculomotor nerve. n. opt.: optic nerve. n. teg.: tegmentary nerve. n. paraeso.: paraesophageal nerve. n. vent. inf.: inferior ventricular nerve. n. vent. sup.: superior ventricular nerve.

The transverse histological section shows two oculomotor nerve bundles contain relatively thick nerve fibres and both bundles are packed relatively loosely (Fig. 3). Oculomotor nerve I and II include 36 and 11 nerve fibres respectively. Figure 4 shows the histogram of thickness of nerve fibres. The diameter of the thinnest fibre is about 3μ and that of the thickest fibre is about 27μ. The fibres of about 4 and 11μ are most abundant, and the existence of three fibres of very large size (about 27μ) should be noted.

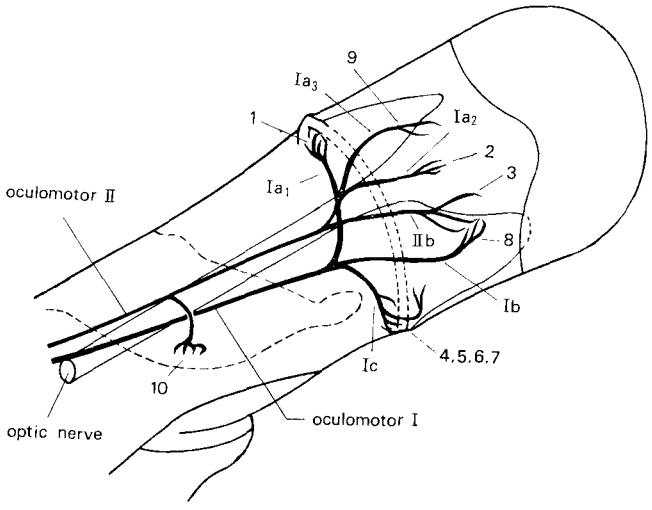

Fig. 2. Schematic representation of the innervation of oculomotor nerves to the eyestalk muscles. The nerve innervating each individual muscle is designated by the muscle number from 1 to 10. 1 and 2: medial retractors. 3: ventral retractor. 4: ventral depressor. 5: lateral rotator. 6 and 7: lateral retractors. 8: abductor. 9: dorsal retractor. 10: attractor.

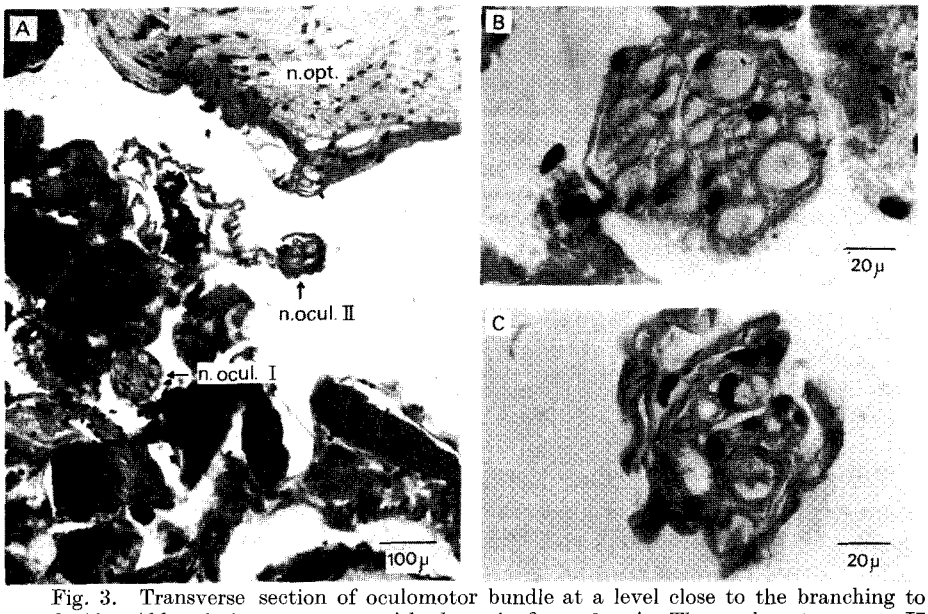

Fig. 3. Transverse section of oculomotor bundle at a level close to the branching to muscle 10. Abbreviations are same with those in figure 1. A: The oculomotor nerve II which originates from the brain in close attachment to the optic nerve runs separated at this level (×60). B: The oculomotor nerve I (× 300). C: The oculomotor nerve II (×300).

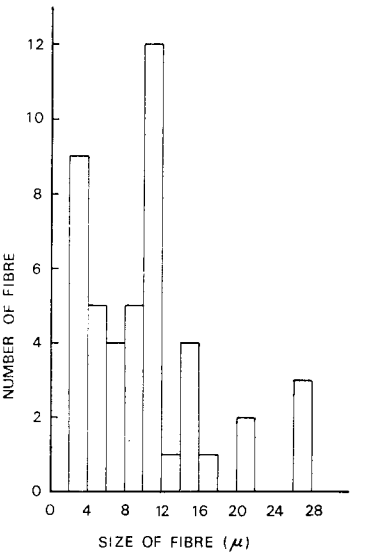

Fig. 4. The distribution of thickness of oculomotor nerve fibres. The total of both oculomotor I and II. Two groups of fibres of about 4μ and 11μ are most abundant.

Electrophysiological classification of the oculomotor nerve fibres.

Criteria of classification and basic pattern of response: The recorded nerve fibres were classified principally according to the rotational direction to which it showed initial phase of increase in discharge rate reaching to a maximum within 180° turn from the start. All of the fibres which received the sensory input from the statocyst organ showed almost essentially similar pattern of response for 360° full rotation of the body in regard of the instantaneous frequency change, although the rotational axis differs in each fibre. When the animal was rotated to the proper direction, the discharge rate of the fibre began to increase and approached a maximum at about 90° turn and then decreased to approach a minimum at about 270° turn, then another phase of increase followed till the discharge rate recovered to the level at the starting position. This change in impulse frequency was measured and plotted in 360° turn in each individual fibre. In general, entire response profile of impulse frequency is found to be able to be represented by the trigonometric function. There were usually considerable scatters of instantaneous frequency, though the general trend of trigonometric function was conspicuous. To obtain a quantitative information in regards of various experimental conditions, Fourier expansion into elementary harmonics was performed with an aid of general purpose computor, and this also served as a statistical treatment of raw data.

Figure 5 shows a typical frequency response profile of an oculomotor fibre when the animal was rotated in full 360° turn. The figure was obtained from a SD fibre, of which description will appear in a later section. Generally, the response profile of individual fibre can be resolved into the composing zero order to higher order harmonics by computor assisted Fourier expansion. The solid line

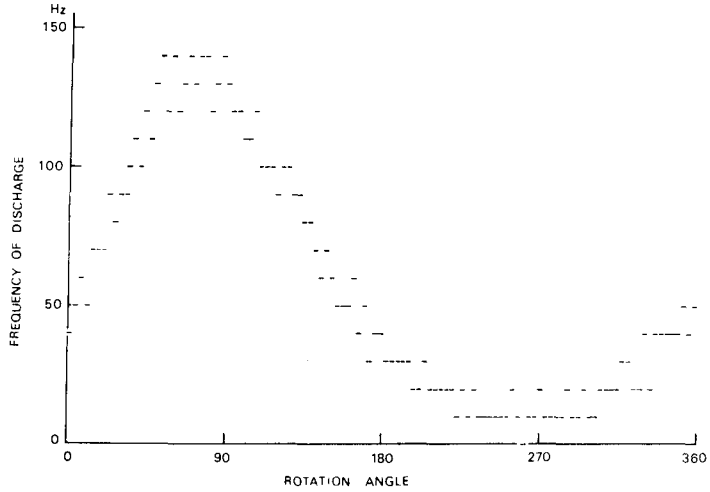

Fig. 5A. Frequency change of an oculomotor fibre (SD fibre) in response to a full 360° rotation of the animal. Frequency values were obtained by counting the number of discharge in each 2 degrees rotation of the animal body (Rotation speed: 20°/sec). Note the wide scatter of the frequency thus obtained, although a general sinusoidal profile is apparent.

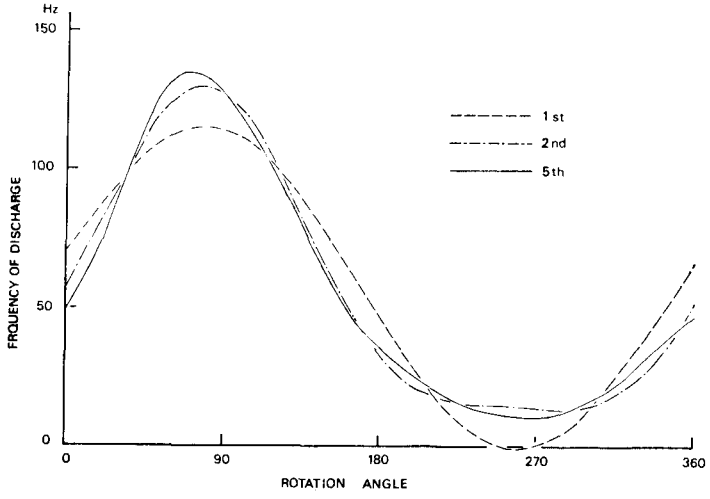

Fig. 5B. Harmonic components of the data appearing in A were calculated with the aid of computor. Then the curves were reconstructed and drawn by the addition of zero to 1st, 2nd or 5th order harmonics respectively.

in the figure was drawn by the addition of zero to fifth order harmonics thus derived. As is shown the characteristics of the curve can be well represented by the reconstruction of elemental harmonics up to fifth order, meaning the harmonics contained of higher than this order is usually negligibly small. In almost all the cases, the 0 to 5th order harmonics summed was found adequate to represent the characteristics of each curve.

1) Head down fibres (HD fibres)

The fibre of this type increase its discharge rate when the body was tilted in head down direction first around the transverse axis. In this type of rotation, both eyestalks always moved upward. These fibres could be found relatively easily, however, they could be found only when the recording electrode was placed into the proximal side of the eyestalk, where the oculomotor nerves did not branch out except the branching of oculomotor II to the attractor muscle. All of these fibres always showed relatively high frequency (from 30 to 50 Hz) background discharge. In the head down rotation, at a rotational velocity of 360° per 18 sec., the maximal discharge rate reached upto about 250 Hz, and minimum never fell to zero.

Illumination of front and back of the eye showed excitatory and inhibitory effect respectively. The light was equally effective in both ipsilateral (recording) and contralateral eye in both mode and magnitude. These excitatory and inhibitory fields coincided with visual field of sustaining fibres in the optic tract reported by Wiersma and Yamaguchi (1966): excitatory field with that of 038 or 014 and inhibitory with that of 020 or 030. In oculomotor nerves, however, the boundaries of the fields appeared to be more dubious than those of the visual fibres.

The vertical optokinesis was found in the HD fibres. The striped drum was rotated in the directions equivalent to head down and head up rotation of the body in which white and black stripes moved from lower to upper and *vice versa* in front of the eye respectively, while the animal was held in the normal level position. With this stimulation, a small optokinetic response was observed: The drum rotation equivalent to head down increased the discharge rate and the rotation equivalent to head up decreased the rate respectively. In regard to the optokinetic reaction in crayfish, the existence of fibres which show clear optokinetic response in horizontal plane has been known. Two types of the optokinetic fibre has been found, and both types respond to the movement of visual objects in the horizontal plane. Figure 6 shows the comparison of "vertical" and horizontal optokinesis.

Then a point light source was moved from lower to upper and *vice versa* at the various position in the visual field. The purpose of this experiment was to make certain of the existence of the vertical optokinesis. Because of the possibility that in the case of the striped drum, the movement of stripe both over and under the body, where the stripes moved rather in horizontal plane, could be

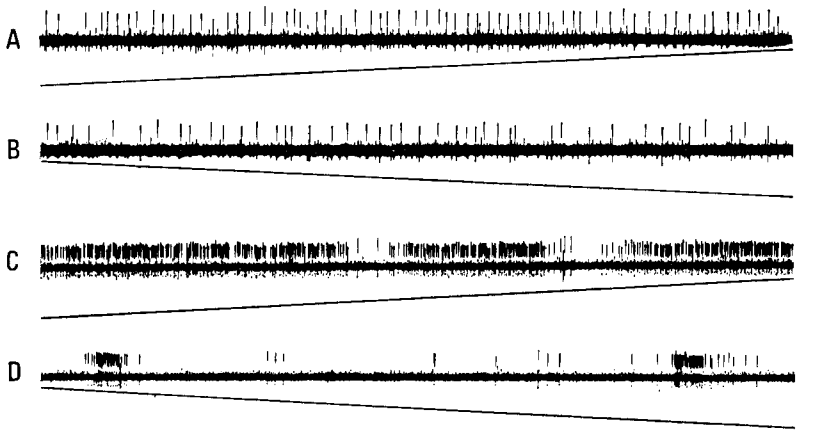

Fig. 6. The comparison of "vertical" and "horizontal" optokinesis. A and B: The response of HD fibre when the striped drum was rotated in the direction equivalent to head down rotation (A) and head up rotation (B). C and D: The response of horizontal optokinetic fibre when the striped drum was rotated in preferred direction (C) and null direction (D). Note the conspicuous "flip back" reaction, namely, a short pause in response in preferred direction and a short burst in response in null direction in horizontal optokinetic fibre.

effective to the oculomotor response via possible contribution of horizontal optokinetic fibres. Another purpose was to know the difference of magnitude of optokinetic response at the various parts of the eye. The vertical optokinetic response could be fully induced by the movement of the point light source. The up and down movement of light source subtending about 30 degree across the horizontal plane was most effective, and the efficacy decreased when the light source was held and moved either high above the horizontal level or low. As it is

Table 1. The counts of discharge in a HD fibre in 5 seconds while the light spot was moved from lower to upper or *vice versa* at various angles against the ipsilateral (recording) eye. The light angle designates the angular deviation of the plane in which the light source was moved from the sagittal plane (antero-posterior axis). Light angle 0° indicates the rostral side of the eye. Note the reversal of the preferred direction beyond 90°. B/A represent the magnitude of optokinetic response.

Light angle	A) lower to upper	B) upper to lower	B)/A)
0°	78	67	0.86
30°	81	66	0.82
60°	81	73	0.90
90°	86	80	0.93
120°	88	89	1.01
150°	87	90	1.02

expected, the preferred direction of the movement of the light spot was from lower to upper in the rostral side of the eye and in the caudal side was from upper to lower (Table 1).

2) Head up fibres (HU fibres)

The responses of the fibres of this type were the opposite of the HD fibres. They increased their discharge rate when the body was rotated in head up direction around the transverse axis. The fibre was rarely encounted in the experiment. Only four units were found and the three of them showed no background discharge in normal position. The other one showed relatively low background discharge rate. Figure 7 shows the response in 360° full rotation of the body. In one case, two fibres of this type were recorded simultaneously. One of the fibres which appeared to have a larger diameter than the other indicated by a large spike height was normally silent and fired only around the 90° head up position, and

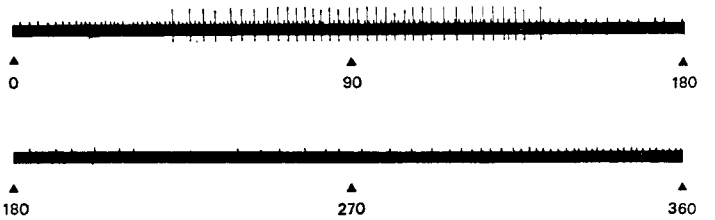

Fig. 7. The response of a HU fibre when the animal was rotated in full 360° turn. The responses of two fibres were recorded simultaneously. The numerals under solid triangle show the rotation angle of the animal body.

again remained silent at other positions. And the maximal rate of discharge was markedly smaller than other HU fibres. Thus the total response curve of this fibre in 360° turn is far from a continuous trigonometric function. On the other hand, the fibre which appeared to be smaller in size showed a background discharge at the normal body position, and general trend of waxing and waning was indicated.

To the visual stimuli of both rotating drum and spot light, the fibre with background discharge showed a vertical optokinesis in opposite direction of the HD fibre, though the response was smaller. These visual stimuli could not be determined to be effective to the fibres which were silent at normal position.

3) Side down fibres (SD fibres)

The fibre responded with increase in discharge rate when the side of recording eye was rotated and lowered around the longitudinal axis of the body. When the rotational stimulus of this type was given, the eyestalk of recording side moved upward and the other downward. The fibres of this type were found most abundantly at various points of the eyestalk. Their characteristics were of wide

variety, so the fibre characteristics were arbitrary subdivided into following three subgroups, however there appeared to be no clear demarcation between these three groups, suggesting they might belong to the same category.

Class 1: The fibres of this class showed no or very low (up to about 10 Hz) background discharge in normal position. In the 360° full rotation of the body, the maximal discharge at about 90° turn reached about 150 Hz and the minimum at about 270° turn usually fell to zero. In SD fibres, light illuminating effect, which has been already reported by Wiersma and Oberjat (1968), was inhibitory and excitatory on the whole of the ipsilateral (recording) eye and contralateral eye respectively. In this class, the inhibitory effect of illumination of the ipsilateral eye appeared to be weaker than the excitatory effect of the contralateral eye. Thus the total illumination of the visual background resulted in a tonic increase of discharge rate.

Class 2: The background discharge rate of this type was intermediate (10 to 20 Hz). The maximal discharge rate was close to 200 Hz and the minimum fell to near zero. The effect of illumination of ipsilateral and contralateral eye was almost counterbalanced, resulting in transient on and off response when the total background illumination of visual field was modulated.

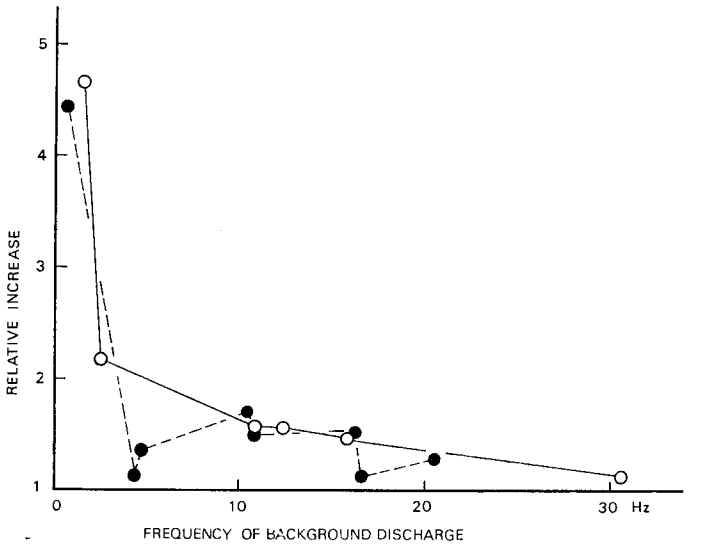

Fig. 8. The relationship between background discharge and increase in frequency produced by optokinetic stimulus in SD fibre. The relative increase in frequency is derived as a ratio of the discharge frequency of the fibre in response to the rotation of the striped drum in the direction equivalent to side down body tilt to the background discharge. The open circles represent the values of each individual fibre of various background discharge at normal position. The filled circles were those of a single fibre when the background discharge rate was modified by bringing the animal at various body positions.

Class 3: These fibres were of high background discharge (30–50 Hz). The maximum was over 250 Hz and the minimum never fell to zero. The illumination of the ipsilateral eye showed stronger inhibitory effect, therefore, the total illumination had inhibitory effect. Thus the fibres showed the excitatory tonic discharge during the background illumination was turned off.

As in the case of HD fibres the effects of the striped drum and the spot light moved in the directions equivalent to the side down and also the side up body tilts were tested in these three classes of the fibres. An interesting relation was found between background discharge rate and change in rate produced by optokinetic stimulus (Fig. 8). The response in term of ratio to the normal to the rotated striped drum equivalent to the side down body tilt was inversely proportional to the frequency of the background discharge of each individual fibre. However, a single SD fibre did not show this tendency when the background discharge rate was varied by bringing the animal at various body position and the stimulus was given in the same manner (Fig. 8).

The movement of point light source from lower to upper and from upper to lower were very effective to induce the optokinetic response (Table 2). The excitatory and inhibitory effects were most conspicuous when the light source was moved at direct front of the eye, namely at the extension of the longitudinal axis of the eyestalk. In the ipsilateral eye, the movement of light from lower to upper portion of the visual field was excitatory while from upper to lower was inhibitory. In the contralateral eye, the preferred direction became opposite. At the front of rostrum, where the light source was presented in the binocular field of both eyes, no effect was produced by the movement of the point light source in either directions.

Table 2. The counts of discharge in a SD fibre in 10 seconds while the light spot was moved from lower to upper or *vice versa* at the various position against the ipsilateral (recording) or the contralateral eye. The light angle 0° indicates the light source moved the sagittal plane, and both ipsilateral and contralateral eye saw the moving light spot. The magnitude of optokinetic response was, like HD fibre, shown by the ratio between two cases.

Light angle	A) lower to upper	B) upper to lower	B)/A)
Ipsi. 90°	99	50	0.55
Ipsi. 45°	62	54	0.87
0°	81	81	1.00
Contra. 45°	75	87	1.16
Contra. 90'	59	85	1.44

4) Side up fibres (SU fibres)

The nature of this type was the opposite of the SD fibres, increasing their discharge rate when the side of the recording eye was rotated in upward direction. These fibres could be rarely found, and only when the recording electrode penetrated into the distal side of dorsal side of eyestalk. Background discharge was

relatively low (5–10 Hz). To the visual stimulus, these fibres showed weaker response than SD fibres and in some cases showed no response.

Discussion

The complexity of eyestalk musculature which was reported by Robinson and Nunnemacher (1966) and Sugawara et al. (1971) suggests that any eyestalk movement is induced by coordinative actions of more than one and up to several muscles, and that in even very simple eyestalk movement, probably several muscles act simultaneously in different strength and timing. Moreover, it also suggests that there exist no definite synergistic or antagonistic relations between any pair of muscles, and that the complex and widely various responses of oculomotor nerve fibres are expected. But in opposite to this expectation the oculomotor nerve fibres showed almost similar response profile to the rotational stimulus of the animal body, though the axis around which the animal was rotated would be different. And also there exist clear synergistic and antagonistic relations among many pairs, thus making a definite contrast to the muscular arrangement. There are 10 muscles in the eyestalk and 47 oculomotor fibres. If we assume a simple relation, each one muscle is innervated by 4 to 5 nerve fibres in average. These facts show that the oculomotor nerves, of which single action are relatively simple, can produce complex eyestalk movements by way of various combinations. It is of interest to note here that the same group of muscles are probably working when the upward movement of the eyestalk is induced by either head down or side down rotation of the body, yet we could not establish the presence of the oculomotor fibre which is equally activated both in head down and side down rotations. This indicates that the oculomotor are range-fractionated in regard of the axis of rotation to generate the complicated movements of the eyestalk. And it is likely that one muscle may be innervated with two or more different types of the oculomotor fibres described in this paper. Further study of this functional arrangement may yield an interesting aspect of the motor control systems of crustacea.

A previous study (Hisada et al. 1969) showed an optokinetically induced eyestalk movement in response to the movement of the stripes in vertical plane, the presence of the vertical optokinesis is also indicated by the fact that the intact animal showed a higher gain in compensatory eyestalk movement especially around the normal level position than the blinded animal. Presumably the visual organ may be able to measure accurately a small relative angular movement of the visual objects while the statocyst organ may likely not to be sensitive enough to resolve a small movement. Therefore, when the animal is rotated in a large extent, the geotactic information mainly control the eyestalk movement, while the visual information may be more predominant when the animal is at the normal level position. In fact, in SD fibres, the fibres which have lower background discharge well respond to the visual stimulus, while the fibres with high back ground

discharge rate appear to be less sensitive to it. It may be said that the fibres having higher background discharge maintain the eyestalk position through their tonic activities and by changing the rate according to the statocyst input, these fibres produce more extensive movement of the eyestalk required to compensate the large bodily tilt, while the fibres of lower rate induce small positional changes required mainly for the adjustment of eyestalk position through the visual channel.

Many of intriguing aspects of the integrative mechanism of multimodal sensory inputs may well be revealed by a further study of the oculomotor nerves.

Acknowledgement

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Summary

The oculomotor innervation of crayfish eyestalk muscles was studied anatomically. The oculomotor nerve consists of two major branches, oculomotor I and II, and is composed of 47 nerve fibres in total. Fibre diameters range from 2 to 27 micrometer.

The response profiles of oculomotor nerve both to the rotation stimulus of the animal body and the visual stimulus were studied electrophysiologically. The fibres so far identified were classified into following four classes: Head down (HD), Head up (HU), Side down (SD) and Side up (SU) fibres depending on the direction of rotation in which each fibre responds with an increase of firing frequency. Additionally, the side down fibres could be subdivided into three groups according to the rate of their background discharge and the effect of illumination on ipsilateral and contralateral eye.

In each fibre, the existence of optokinetic response in the vertical plane was confirmed. Parallelism between the rate of background discharge and the magnitude of optokinetic response, was noted among the SD fibres.

References

Clark, G. P. 1896. On the relation of the otocysts to equilibrium phenomena in *Gelasimus pugilator* and *Platyonichus ocellatus*. J. Physiol. **19**: 327–343.

Cohen, M. J. 1955. The function of receptors in the statocyst of the lobster *Homarus americanus*. *Ibid.* **130**: 9–14.

Higuchi, T. 1973. The responses of oculomotor fibres in statocystectomized crayfish, *Procambarus clarki*. J. Fac. Sci. Hokkaido Univ. Ser. VI Zool. **18**: 507–515.

———— and M. Hisada 1973. Visual and geotactic contributions to oculomotor responses in the crayfish, *Procambarus clarki*. *Ibid.* **18**: 495–506.

Hisada, M., K. Sugawara and T. Higuchi 1969. Visual and geotactic control of compensatory eyecup movement in the crayfish, *Procambarus clarki*. *Ibid.* **17**: 224–239.

Horiuchi, E. 1967. Median giant fiber system in the crayfish cephalic ganglion. J. Nippon Med. Sc. **34**: 173–178. (In Japanese).

Paterson, N. F. 1968. The anatomy of the cape rock lobster, *Jasus lalandii* (H. Milne Edwards). Ann. S. Afr. Mus. **51**: 1–232.

Robinson, C. A. and R. F. Nunnemacher 1966. The musculature of the eyestalk of the crayfish, *Orconectes virilis*. Crustaceana **11**: 77–82.

Schöne, H. 1951. Die statische Gleichgewichts-orientierung bei dekapoden Crustaceen. Verhandl. deut. zool. Ges. **16**: 157—162.

———— 1954. Statozystenfunktion und statische Lageorientierung bei dekapoden Krebsen. Z. vergl. Physiol. **36**: 241–260.

———— 1956. Über den optischen Lageapparat der Krebse. Verhandl. deut. zool. Ges. **19**: 52–58.

———— 1959. Die Lageorientierung mit Statolithenorganen und Augen. Ergeb. Biol. **21**: 161–209.

Sugawara, K., M. Hisada and T. Higuchi 1971. Eyestalk musculature of the crayfish, *Procambarus clarki*. J. Fac. Sci. Hokkaido Univ. Ser. VI Zool. **18**: 45–50.

Wiersma, C. A. G. and L. Fiore 1971. Factors regulating the discharge frequency in optomotor fibres of *Carcinus maenas*. J. exp. Biol. **54**: 497–505.

———— and T. Oberjat 1968. The selective responsiveness of various crayfish oculomotor fibres to sensory stimuli. Comp. Biochem. Physiol. **26**: 1–16.

———— and T. Yamaguchi 1966. The neuronal components of the optic nerve of the crayfish as studied by single unit analysis. J. Comp. Neurol. **128**: 333–358.

———— and ———— 1967. Integration of visual stimuli by the crayfish central nervous system. J. exp. Biol. **47**: 409–431.