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Citation	北海道大學理學部紀要, 18(4), 495-506
Issue Date	1973-04
Doc URL	http://hdl.handle.net/2115/27545
Type	bulletin (article)
File Information	18(4)_P495-506.pdf

Visual and Geotactic Contributions to Oculomotor Responses in the Crayfish, *Procambarus clarki*

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(*With 6 Text-figures*)

Introduction

Crustacean eyestalk with its compensatory movement appears to offer a useful system to analyse the integrative mechanism in dealing with information derived from more than one sensory organs.

Studies concerning with this theme have been done by some investigators using various approaches. The contribution of statocyst organ alone to the compensatory eyestalk reflex has been known for long time, since the first appearance of the report by Clark (1896). This has been followed by many detailed but sometimes conflicting descriptions, until a rather unified view has been given by Schöne in his several papers (1951, 1952, 1954, 1956, 1959). His studies covered the dependence of the eyestalk position on gravity and also the effect of light direction in the crayfish, *Astacus* as well as in some shrimps. A rotational compensatory movement of the eyestalk is newly found and described recently as to be controlled by both geotactic and visual information (Hisada *et al.* 1969). In some crayfish, structural arrangements of eyestalk musculature were investigated (Robinson et al. 1966, Sugawara et al. 1971), and the arrangements appear to be rather complex. Neuronal response of the oculomotor fibres which activate these muscles have also been studied and various types of the oculomotor have been described (Wiersma et al. 1967, 1968, Hisada et al. 1973). In all experiments, however, the results appeared to be insufficient to delineate the mechanism of integration of sensory information brought by the statocyst organ and the visual organ.

As a step toward the understanding of the integrating mechanism in the oculomotor systems, details in responses of two typical oculomotor fibres, head down (HD) and side down (SD) fibres to the static change in position and to the dynamic rotation were compared and the modulating action of the visual input to the statocyst controlled oculomotor activity was investigated.

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

Jour. Fac. Sci. Hokkaido Univ. Ser. VI, Zool. 18 (4), 1973.

Material and Methods

The crayfish, *Procambarus clarki,* was suspended with a clamp which held the carapace while two chelipeds were solidly tied with an elastic strand, and walking legs were left free. A steel recording electrode sharpened then insulated to the tip was introduced in the soft membrane between the outer and inner eye segment, and a ground electrode was introduced in the anterior carapace at one side just in front of the cervical groove between the anterior and posterior portion. After the oculomotor fibre was found, the type of the fibre is determined according to the classification described in the preceding paper (Hisada et al. 1973). The process is repeated till a desired fibre was located. Methods employed in giving the rotational and other stimuli were identical with the preceding paper. Rotation apparatus was also equipped with a point light source which could be placed in any desired position or could be rotated in various speed. Nerve impulses were led to the cathode-ray oscilloscope through a biological amplifier with other stimulus parameters, and the recorded with a long recording camera. Impulse frequency were manually counted and, if necessary, processed through a computor for statistical analysis.

Results

The response profile of the oculomotor nerve to 360° full rotation of the animal has been already described (Hisada et al. 1973). The fibre increases its discharge rate when the animal is rotated in the direction by which the fibre type is defined, for example, head down direction around the transverse axis in case of the head down (HD) fibre. In almost all the types of fibres, the maximal and the minimal points of discharge rate is response to the rotation are at about 90° and 270° respectively and the appearances of the curves of the instantaneous frequency are striking similar and can be represented by trigonometric function.

Figure 1 shows the change of discharge rate of one side down (SD) fibre, which responds when the animal is rotated around its longitudinal axis to the side down direction, thus carrying the side of recording eye first downward. The curves represent the instantaneous frequency changes in five separate trials in 360° full side down rotation of the same fibre. Since this series of experiment was performed in the total darkness, sensory change in visual system was not present and thus not contributing to the nerve responses except the effect of darkness itself. When there is no active movements of appendages and/or telson which were often triggered by rotation, the fibre shows very stable response profiles to the 360° rotations (solid lines in the figure). The disturbance of response induced by the movements of appendages and/or telson were readily detected in listening to an audio-monitor as a sudden increase or decrease of the discharge rate. In most of the case, these movements induced the temporary excitatory effect and occasionally inhibitory effect (dotted lines in the figure). The analysis of the triggering mechanism of this response was not intended in the present paper. However, it seems to be of interest since this active movement of appendages which sometimes develop into full flexions of abdomen and tail flips invariably start when the animal is brought close to the upside down position.

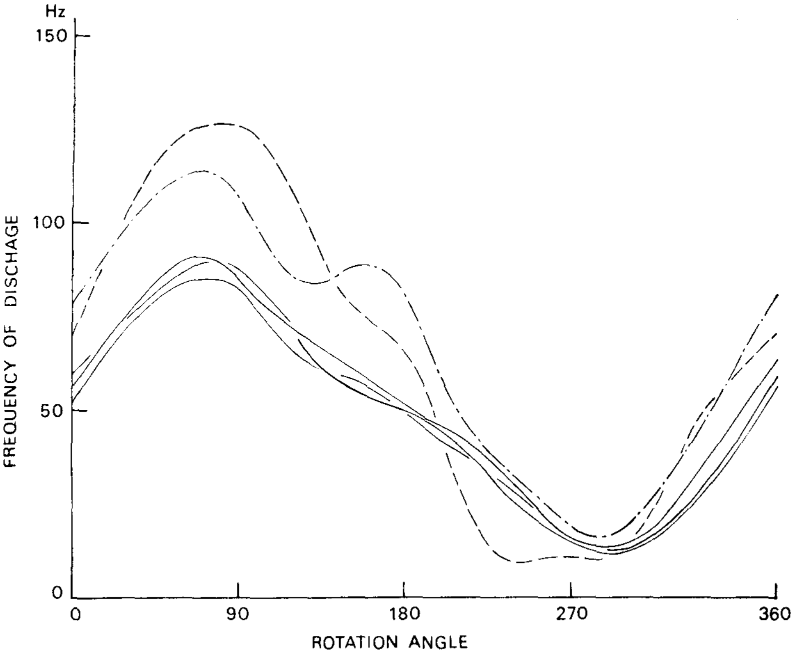

Fig. 1. The change of discharge rate of one SD fibre in five separate trials in 360° full side down rotation. Solid lines show very stable response profiles without disturbance induced by avtive movements of appendages and/or telson. Dotted lines show the response with disturbance introduced by the movements of appendages and/or telson.

Contribution of statocyst organ

Although the general trend of waxing and waning of the discharge depending on the body position remains, the rate of discharge at any given point of rotation is dependent on the rotation velocity. Therefore, the response of oculomotor nerves in dynamic rotating and static conditions were compared. While the oculomotor nerve showed almost constant background discharge in normal position, the discharge rate abruptly increased when the rotation of the body was initiated, and then proceeded to show the frequency change profile corresponding the position of the body as mentioned in the previous paper (Hisada et al. 1973). The stimulus in such a dynamic condition included two elements, namely, the change of body position and the rotation of the body. When the animal was held at a certain body position for more than 10 seconds, i.e. when transient increase induced by actual dynamic rotation, the rate of discharge of oculomotor nerve became much lower and less than half of what obtained at the same position during dynamic rotation (Fig. 2). There appears to be no detectable change in the position of the maximal and the minimal response. The frequency of discharge in this static condition at various rotational position was measured after about 10 seconds from the stop of the rotation of the body. Figure 3 shows the frequency change of oculomotor nerve in shifting from static state to dynamic state and *vice versa*. In the static state, oculomotor fibre showed the almost constant discharge rate which corresponded to the body position and abruptly increased in the discharge rate at the time when the rotation was initiated, if the direction of rotation was the one by which the fibre could be classified. Then the rotation

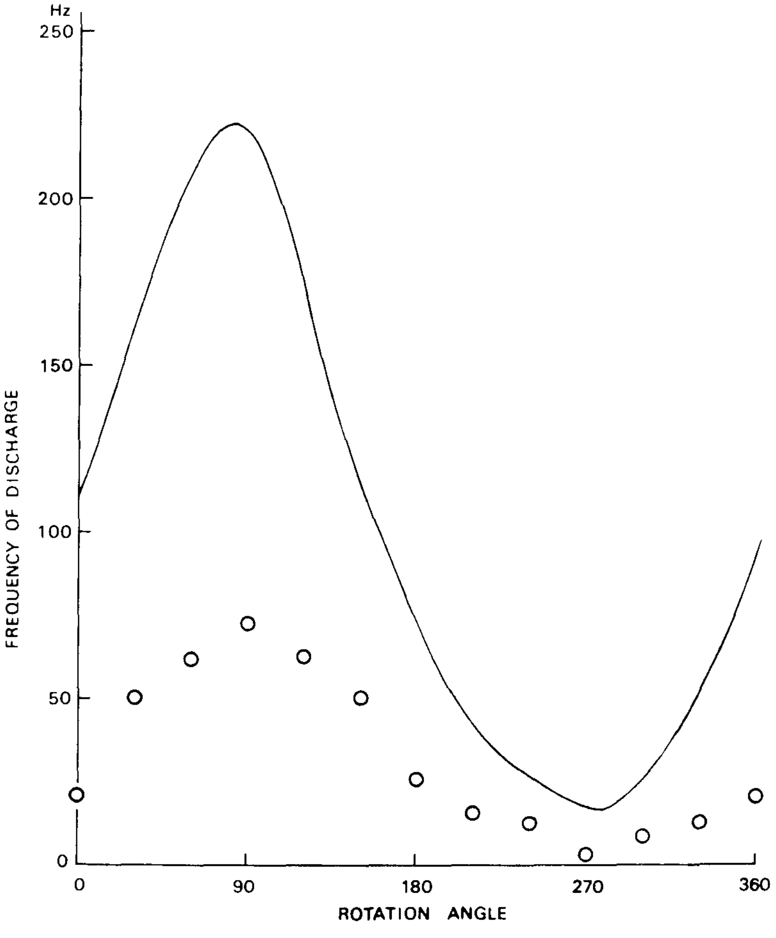

Fig. 2. Dynamic and static change of discharge rate of a HD fibre. Solid line; in 360° full head down dynamic rotation. Open circle; in static condition at various body position.

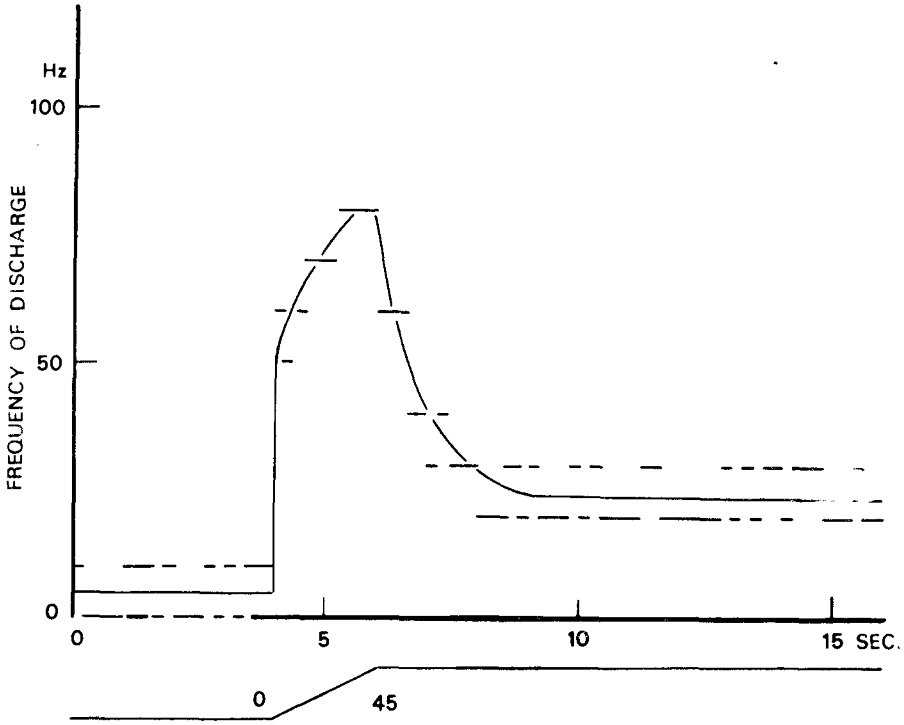

Fig. 3. The frequency change in shifting from static state to dynamic state and *vice versa* in one SD fibre. The animal was held first in normal body position. The the side down rotation was initiated. The rotation was terminated at 45° turn and then the animal was held stationary in the position.

interrupted, the responses rapidly decreased to the level of static state within about three second and thereafter the fibres showed the constant discharge rate which corresponds to the position.

Then the change of response of the oculomotor nerves by the change of rotation velocity was studied. Especially, chief attention was paid on the shifting of rotational body position showing the maximal discharge, but such a tendency was not observed in any fibres. At various rotation velocities studied, the points of the maximal discharge of all fibres were found between 85° to 90°, and none of the fibres showed significant displacement of the maximal point.

Figure 4 shows the frequency change of one HD fibre when the animal was rotated to both head down and head up direction. When the rotation of animal was initiated in head up direction, HD fibres decreased their firing rate and gradually increased when it past about 160° turn and then reached the maximal frequency at about 270°. The modes of increase and decrease of response in these two cases

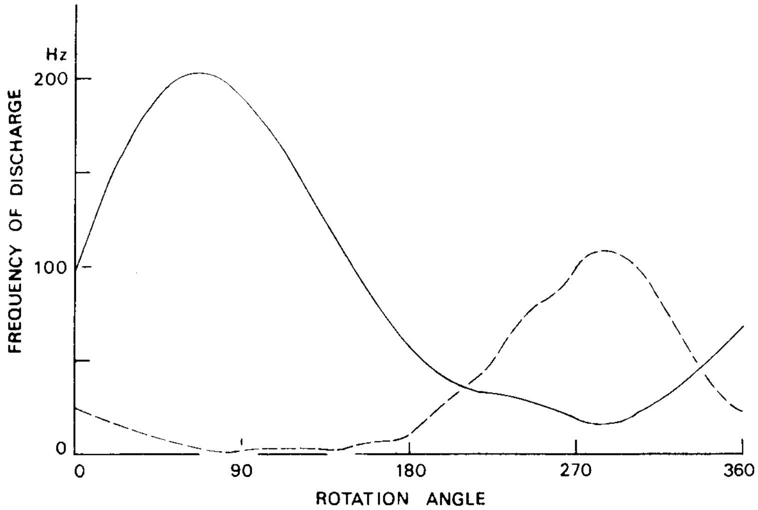

Fig. 4. The frequency change of a HD fibre when the animal was rotated to both head down and head up direction. Solid line; head down rotation. Dotted line; head up rotation.

were of opposite sign in each other, but at the same relative position of animal to gravitational direction the fibre showed the maximal and minimal discharge rate. However, the magnitude of total response in term of amplitude in frequency change in the rotation to head up direction was about half of it to head down direction. Similar characteristics were also obtained in other fibres. Namely, in the rotation of animal to opposite direction, oculomotor nerves showed the maximal discharge rate at different position from in the rotation to ordinary direction and the magnitude of response became far smaller. These facts are very important to know the relationship between the oculomotor nerves and statocyst organ. The reason why this discrepancy occurs between the rotation in preferred rotation and its counter-rotation could not be explained at present, but may indicate an interesting relationship to the sensory input from the statocyst organ.

Modulation by the visual input

The change in response type in 360° full turn under the following four different visual conditions was compared, namely, A) under the overhead light, B) in the darkness, C) with a local illumination of the excitatory area, and D) with a local illumination of the inhibitory area.

1) In HD fibre

The figure 5 illustrates the results obtained under the above mentioned conditions.

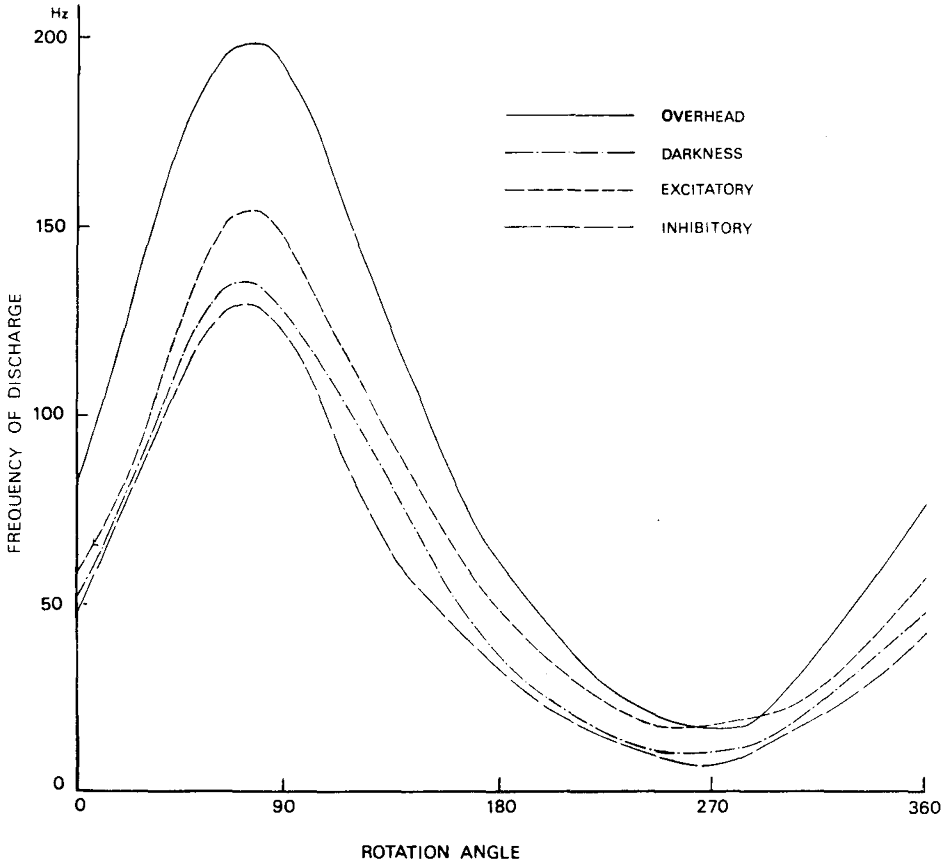

Fig. 5. The changes in response in four different visual conditions in HD fibre. Overhead; under the overhead light. Darkness; in the darkness. Excitatory; with a local illumination of the excitatory area. Inhibitory; with a local illumination of the inhibitory area.

The HD fibre could be excited by illuminating the visual field which roughly corresponded with that of the optic fibre 038 and be inhibited by illuminating that of the optic fibre 020 respectively.

When a stronger illumination than other visual field is given on one of these field, the discharge frequency of HD fibre either increases or decreased depending on which field is illuminated, regardless to the position of animal. Namely, the illumination of the field closely related to that of 038 always increase the discharge frequency of the HD fibre either when the animal is at normal, at upside down or at any other position. The same is true to the inhibitory field.

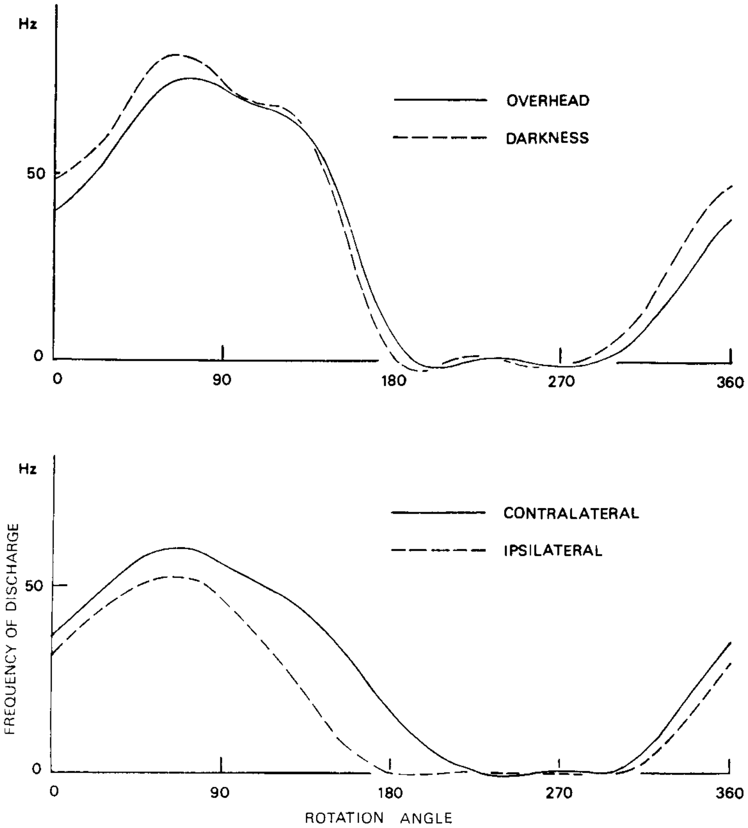

Fig. 6. The changes in response in four different visual conditions in SD fibre. Overhead; under the overhead light. Darkness; in the darkness. Contralateral; with a local illumination of the whole contralateral eye. Ipsilateral; with a local illumination of the whole ipsilateral eye. In SD fibre, the excitatory and inhibitory area correspond to the whole contralateral and ipsilateral eye respectively.

2) In SD fibre

In SD fibre, the excitatory and inhibitory area correspond to the whole visual fields of the contralateral and the ipsilateral eye respectively. Efficacy of illuminating either the contralateral or the ipsilateral eye is different depending on the subclass of the SD fibres as described in the previous paper (Hisada et al. 1973). In the case of the fibre shown in the figure 6, the magnitude of response in the darkness was larger than that obtained under the overhead light, and this fact showed that the effect of illumination on the ipsilateral eye was larger than that on the contralateral eye.

Discussion

It is obvious that the eyestalk movement in crayfish is controlled by two main sensory inputs, namely, geotactic and visual inputs. However it is not necessary for these two inputs to act equally with each other. In a series of our previous studies, it became obvious that the geotactic input occupies the main part of sensory input and the visual one acts rather auxiliary in case of the rotation of the animal body. The contributions of the sensory information derived from the joint receptors or proprioceptors to the oculomotor system are still not clear, but the fact that the movement of appendages and/or telson induce the temporary disturbance of oculomotor response suggests that those receptors probably deal with the information in regards of the movement of animal body but not of the true detection of the body position in space and of the rotating direction. This supposition becomes clear by the experiment in statocystectomized animal in which both HD and SD fibres shows only minor fluctuation around the spontaneous level in the rotation of the body in the darkness (Higuchi 1973). Thus, when the animal is rotated in the darkness, the response profile of oculomotor nerve is produced by the input only from the statocyst organ.

Under the overhead light, the visual input to these neurones consists two elements. One is the vertical optokinetic reaction, which increases the magnitude of total response during the rotation of the body to preferred direction, head down and side down direction in HD and SD fibre respectively. The other is the effect of light illumination on the particular part of the eye. In both HD and SD fibre, when the animal is rotated up to 90° in preferred direction, the excitatory visual area which exerts an excitatory effects is most illuminated and when turned 270°, the inhibitory area is most illuminated. Thus, the maximal frequency increased and the minimal one decreases. When the animal was rotated with constant local illumination of the excitatory area, there the excitatory effect is maintained constantly during a full 360° rotation. In this case, moreover, there is no optokinetic reaction because the constant visual input is maintained during the rotation and thus no sensory cue of rotation through the visual sensory channel is furnished. So the maximal discharge becomes lower than the case of under overhead light. However, in the case of under overhead light, the minimal frequency is lower because the increase introduced by optokinetic reaction should be offset by the decrease introduced by the illumination of inhibitory area in near 270° turn. On the other hand, when the animal is rotated with local illumination of the inhibitory area, the oculomotor response is inhibited during a full 360° rotation, so the magnitude of response decreases and becomes lower than other three cases. Therefore, in HD fibre in which placing in the darkness produces a total level down of the magnitude of response below the level under overhead light, the order of response magnitude becomes as follows; 1) under overhead light, 2) with local illumination of excitatory area, 3) in the darkness, 4) with local illumination of inhibitory area. In SD fibre, placing in the darkness results in excitation or inhibition depending on the subclasses as mentioned in previous paper (Hisada et al. 1973). In a SD fibre of which response is shown in figure 6, placing in the darkness results in excitation. When the animal is held stationary in any given position, the fibre shows higher discharge rate in the darkness than under overhead light. However, there exists no appreciable difference in the magnitude between the responses in the darkness and under overhead light in the rotation of the body. This can be explained by that the response magnitude in the rotation under overhead light is enhanced by the increase of discharge frequency resulting from the optokinetic contribution.

The condition under overhead light is likely close to the natural condition that the animal encounters in their habitat. Therefore, the fact that the response magnitude under overhead light is largest seems to be quite reasonable.

When the sensory input in oculomotor system is limited to the only one from statocyst organ by rotating the animal in the darkness, the oculomotor shows very stable response profiles to the 360° rotation. During the rotation of the animal body, two stimulus elements, namely, the change of body position and the rotational movement act simultaneously. On the other hand, only the former acts when the animal is held in fixed position. Therefore the response which the oculomotor nerve shows in same spacial position becomes smaller in fixed position than during the rotation of the body in any position. The fact that the response rapidly decreases within about three seconds and shows constant discharge rate when the rotation of the body is terminated indicates that each stimulus element above mentioned can act independently with each other although the two act simultaneously during the rotation of the body. Moreover, the fact that the maximal point of response does not shift depending on the change of rotation velocity suggests that the system is such that the body position can be detected independently in spite of the change in rotation velocity, as far as the body is rotated in same direction.

The most perplexing problem is that the response magnitude decreases when the animal is rotated in non-preferred direction. It is difficult to suppose that the phenomenon is derived from the characteristics of the sensory organ, because that the statocyst nerve is likely to have the almost same magnitude of response in spite of the reversal of rotational direction has been observed (unpublished data). Therefore, the cause of change of response magnitude introduced by the reversal of rotational direction may lie in the central mechanism rather in the peripheral system.

Acknowledgement

The authors wish to express their sincere thanks to Prof. Mituo Tamasige for his kind encouragement and reading of the manuscript.

Summary

1. Details of the contribution of statocyst organ and the modulation by the visual input in two typical oculomotor fibres, head down (HD) and side down (SD) fibres were investigated.

2. When there is no active movements of appendages and/or telson, the oculomotor nerve shows very stable response profiles.

3. When the animal was held at a certain body position, the rate of discharge of oculomotor nerve became much lower and less than half of what obtained at the same position during dynamic rotation but there was no detectable change in the position of the maximal and minimal response.

4. Oculomotor response abruptly increased when the rotation was initiated and rapidly decreased when it was terminated, and became almost constant corresponding to the body position.

5. When the animal was rotated to opposite direction, the fibre showed the maximal and minumal discharge rate at the same relative position of animal to gravitational direction in the rotation to ordinary direction, while the magnitude of response became far smaller.

6. The change in response type in 360° full turn under four different visual conditions was compared, and the effects of both light illumination of the eye and the vertical optokinetic reaction became clear.

References

Clark, G. P. 1896. On the relation of the otocysts to equilibrium phenomena in *Gelasimus pugilator* and *Platyonichus ocellatus*. J. Physiol. **19**: 323–343.

Cohen, M. J. 1955. The function of receptors in the statocyst of the lobster *Homarus americanus*. *Ibid.*, **130**: 9–34.

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

Hisada, M. and T. Higuchi 1973. Basic response pattern and classification of oculomotor nerve in the crayfish, *Procambarus clarki*. *Ibid.* **18**: 481–494.

——— and K. Sugawara 1969. Sensory output from crayfish statocyst. Zool. Mag. **78**: 11 (Japanese abstract in Proc. 39th Ann. Meet. Zool. Soc. Japan).

———, ——— and T. Higuchi 1969. Visual and geotactic control of compensatory eyecup movement in the crayfish, *Procambarus clarki*. J. Fac. Sci. Hokkaido Univ. Ser. VI Zool. **17**: 224–239.

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.

——— 1952. Zur optischen Lageorientierung ("Lichtrücken-orientierung") von Dekapoden. Naturwissenschaften **39**: 552–553.

——— 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 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.