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Author(s)	HISADA, Mituhiko; SUGAWARA, Kiyoshi; HIGUCHI, Takashiro
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Visual and Geotactic Control of Compensatory Eyecup Movement in the Crayfish, *Procambarus clarki*

By

Mituhiko Hisada, Kiyoshi Sugawara*, and Takashiro Higuchi

Zoological Institute, Hokkaido University

(*With 6 Text-figures*)

Abstract: A new category of the compensatory eyecup movement is found in crayfish. The compensatory rotation of the eyecup around its longitudinal axis is induced by geotactic and/or optokinetic stimuli. Geotactically controlled compensation is mediated through the statocyst, and the compensatory process in full 360° turn of the body is characterized by four distinct consecutive phases: 1) positive compensation of high gain, 2) null compensation, 3) negative compensation for recovery, and 4) positive compensation of low gain. A large hysteresis is also observed. The eyecup will take quite different positions at the same body position depending on the direction of approach.

In ordinary condition, the geotactic and optokinetic factors are found to operate synergetically to maintain the dorsoventral axis of the receptive visual surface parallel to the gravitational vertical. The gains of the two systems are separately measured experimentally as well as the gains in synergetic and antagonistic cases. A model of control system is proposed to describe the contribution of the two systems. The model well predicts the responses measured in the present experiment.

Introduction

Image stabilization on the photoreceptive surface is apparently a basic prerequisit for the wide varieties of animals to draw the most from the information obtained through the visual channel. The visual system should preferably be kept steady in reference to the gravitational field rather than to the animal's own body which will inevitably be unsteady and moving. The stabilization is accomplished by locomotory activity of the whole animal and/or by the compensatory reflex movement of certain part or parts of the body. Two sensory modalities are mainly responsible for this type of the mechanism, namely, visual and geotactic

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1) Contribution No. 851 from the Zoological Institute, Faculty of Science, Hokkaido Univiersity, Sapporo, Japan 060

* Present address: Department of Physiology, School of Medicine, Gumma University, Maebashi, Gumma, Japan

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information. In ordinary cases, the visual information cooperates with the equilibrium sense conveyed through the vestibular organs in vertebrates and statocyst organs in invertebrates.

Crustacean eyestalk movement which is observable on tilting the animal has perhaps been the most widely known and thoroughly studied of the synergetic case of these two modalities. Contribution of the statocyst organ to the compensatory eyestalk reflex has been known for long time since the first appearance of the report of Clark (1896) followed by many detailed but sometime conflicting descriptions (Bethe, 1897, Fröhlich, 1904, Kühn, 1914, Lyon, 1900, Prentiss, 1901, von Buddenbrock and Friedrich, 1933). Apparent conflict between some of these results is now known to be derived from the insufficient experimental control of the visual input, and the recent studies of Schöne now well explain the apparent contradiction of the results of the earlier works and gave us rather unified view of the mechanism of the compensatory eyestalk movement (Schöne, 1951, 1954, 1957, 1959). His studies indicate the gravitational cue will cause the angular deviation of the eyestalk relative to the body axis and, up to some extent, counteract either pitching or rolling of the body by maintaining relatively steady position in space, as far as the amount of compensation does not exceed the architectural limitation. However, this type of deviation in virtue of the angular deflection of the eyestalk is insufficient for the stabilization of the image. This is clear if one realize that the pitching movement, the headup or headdown movement of the animal, will actually include the rotational component of the eyestalk displacement around its own longitudinal axis and this rotation is by no means compensated by the mere elevation or depression of the eyestalk relative to the body. Present study will describe a new category of the compensatory eyestalk movement which results in the rotational compensation of the eyecup effected by the eyestalk muscles around logitudinal axis of eyestalk, and which also stabilized the dorsoventral orientation of the arranged array of the ommatidia constituting the compound eye. Present analysis of the reflex brought out the sensory cues utilized and the nature of the contributing control system.

Material and Methods: Intact or unilaterally or bilaterally blinded crayfish, *Procambarus clarki* was used. Well grown adults of relatively large size were chosen.

Rotation device: The animal is suspended with a clamp which holds the carapace while all appendages are fixed solid with the elastic threads. If the appendages are left loose and free to move, their own weight will cause the changes in position of the articulations and the afferent signal thus generated by proprioceptors will supply the information about the angular change of the body position.

The clamp holding the animal is then mounted on a specially constructed rotation device which allow the mounted crayfish to be rotated around any desired body axis. The rotation axis has two ball-bearings installed to reduce vibration and to ensure the smooth rotation.

Rotation apparatus also carries the striped drum which was used as the visual stimulus. Black and white stripes of the drum subtend angle of 8.2° each at the crayfish's eye. The drum is mounted so that it can be either rotated accompanying with the animal or kept stationary. Relative position of the animal to the drum is also changeable. The drum can be rotated around either one of three axes of the crayfish body, longitudinal, transverse, and vertical.

Measurement of angular deviation of the eyecup: Present study mainly concerns with the rotational angular change of eyecup around its own longitudinal axis. A small indicator flag of light weight paper is attached to the eyecup, so that the point of indicator moves in the plane of angular deviation concerned. And the deviation is read either by direct observation with the aid of a protractor or by photographic recording. To blind the eye, a small cap made of soft but completely opaque black paper is placed on the eyecup without causing any appreciable disturbance of the eye movement. For the purpose of blinding the eye, painting is found unreliable, because pinholes are frequently formed.

Outline of the system and teriminology: In the eyecup movement associated with bodily tilt, two sensory modalities furnish input information about the extent of tilt angle, visual information through the eye about the relative movement of the surrounding objects, and geotacitic information through the statocyst about change in body angle relative to the gravitational field. These sensory attributes are separately carried to the central nervous system and after integration converge on the same effector set, eyecup muscles, to proudce the relative eyecup movement to the body. The geotacitic system is not closed with feedback loop, because the sensor, statocyst, is born on the body and not on the actuated eyecup and has no means to monitor the output. Thus the geotactic system makes a straight feed-forward control system. On the contrary, the visual optokinetic system is definitely more elaborate, because, in normal condition, the output eyecup movement will by itself produce the relative displacement of the image, furnishing the information of how much angle it moves through. Since the sign of the information thus brought into the central nervous system is negative in regard of the input stripe displacement, the entire system makes up a negative feedback control system. A model is proposed to describe these characteristics and diagrammed in Figure 1. Further details of the argument will be given in later section. Accordingly, in the optokinetic system the true signal to activate the system is the slip (S) which is given by the subtraction of the eye angle (E) from the drum angle (D), thus

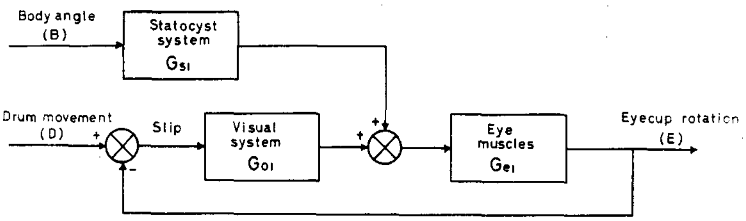

Fig 1. Diagramatized model of the control systems of the eyecup movement. Statocyst system detects the body angle change of (B), and through the central integrative step with gain G_{s1}, furnishes the information to the eye muscles of gain G_{e1} and results in angular eyecup rotation (E). Optokinetic visual sytem of gain G_{o1} is driven by the slip (S=D-E), and through the same eye muscle system of Gain G_{e1} produces the eye angle change of (E).

$$S = D - E \tag{1}$$

In the case of stationary visual objects and bodily tilt of angle (B),

$$D = B \tag{2}$$

Therefore, both systems operate in a synergetic way. In experimental set-up, however, it is possible to procure the situation in which $D \neq B$.

An estimate of the ability of the eyecup to compensate the bodily tilt in geotactic response and to follow the moving image in optokinetic response will, in the first place, be expressed in term of *apparent gain*,

$$G_{sa} = \frac{\varDelta E}{\varDelta B} \qquad \text{in geotactic control} \tag{3}$$

$$G_{oa} = \frac{\varDelta E}{\varDelta D} \qquad \text{in optokinetic control} \tag{4}$$

Since the optokinetic system is thought to be of a closed loop negative feedback, the true forward gain should then be

$$G_o = \frac{\varDelta E}{\varDelta S} = \frac{\varDelta E}{\varDelta D - \varDelta E} = \frac{G_{oa}}{1 - G_{oa}} \tag{5}$$

and for open loop condition of this system

$$G_o = \frac{\varDelta E}{\varDelta D} \tag{6}$$

because D=S.
In geotactic system, true gain is

$$G_s = \frac{\varDelta E}{\varDelta B} = G_{sa} \tag{7}$$

If we postulate the gain of the statocyst system inclusive of the central process as G_{s1}, of visual system also inclusive of the central process as G_{o1} and of eyestalk muscle system as G_{e1}, then

$$G_o = G_{o1} \cdot G_{e1} \tag{8}$$

$$G_s = G_{s1} \cdot G_{e1} \tag{9}$$

Results

1) Eyecup response to bodily tilt

A) *Blinded animal.* A totally blinded specimen with measuring flag attached on the eyecup is rotated around the transverse axis of the body. The blinding eliminates the visual cues and also opens up the feedback loop, thus, in this experiment the eyecup can be considered as solely controlled by the geotactic information supplied through statocysts. A full 360° turn of the body is performed either in headup or in headdown direction. A typical example is shown in Figure 2, where the change of eye angle relative to the gravitational vertical is indicated in abscissae while the body angle also relative to the gravitational vertical is shown in ordinates. It is obvious that if the same angular position is approached from opposite direction, eyecup takes quite different position.

In the first quadrant of the rotation, the eyecup angle increases at a smaller rate than the body angle, indicating presence of a compensatory system (Compensatory phase), then the eyecup gradually increases the rate of angular change

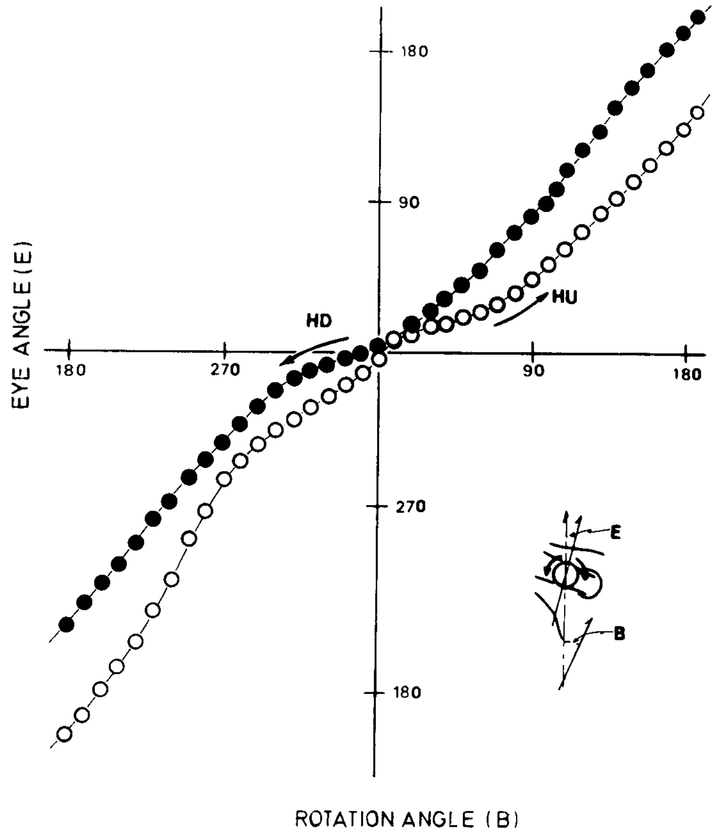

Fig. 2. Compensatory rotation of the eyecup around its longitudinal axis in response to the bodily tilt around the transverse axis. Eyecup position expressed as an angle between the dorsoventral axis of eyecup and the gravitational vertical is shown in ordinates while the angle of bodily tilt also relative to the gravitational vertical is expressed in abscissae. Animal is blinded. Rotation speed, 1 revolution in 30 minutes. The animal is rotated in either headup (HU, open circle) or headdown (HD, filled circle) direction through complete 360° turn.

until the eyecup starts to follow completely and passively the rotation of the body (Follow-up phase). And at the third quadrant, the eyecup starts to move in the direction to reduce the angular deviation so that the resultant angular change brings back the eyecup quite close to the original angle in the eyesocket, though occasionally small angular deviation remains. At the end of the second quadrant the deviation of the eyecup angle is maximal and the discrepancy of the eyecup angles by opposite rotations is largest at the upside down position. The position held by the eyecup will persist for quite a long time, if the rotation is stopped at this or any other point. When this position is approached from headup direction, the eyecup is strongly twisted and its original dorsal top is now pointing dorsorostrally, while when approached from headdown direction, the eyecup will be twisted dorsocaudally. The angular discrepancy amounts about 60° resulting from the

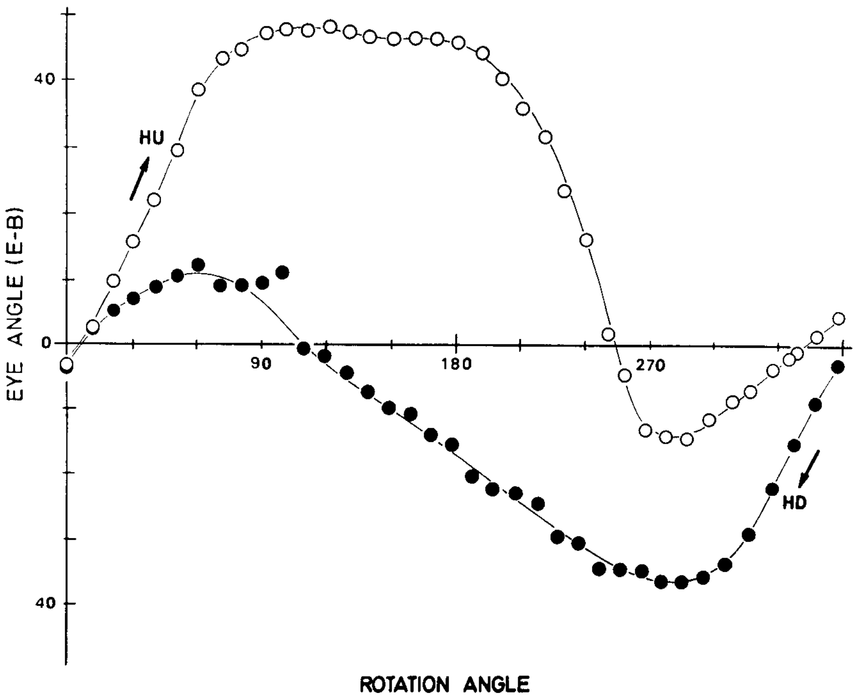

Fig. 3. Relative displacement of the eyecup to the body. Ordinates indicate the angular deviation of the drosoventral axis of the eyecup to that of the body, abscissae angle of bodily tilt relative to gravitational vertical. Accumulated angular deviation amounts up to 45° in headup direction. The distance between curves of headup (HU, open circle) and headdown (HD, filled circle) at a certain body angle indicates the discrepancy of the eyecup positions when the bodily angle is approached from different directions. Animal is blinded.

cumulative compensatory eyecup twisting. The whole process constitutes a kind of hysteresis loop and quite suggestive of the ambiguity in the controlling system. The processes of compensation may be more readily conceivable in Figure 3, where the change in eyecup angle is taken as relative angle to the body instead of the gravitational vertical. In headup rotation, upward increase means positive compensatory movement, and the horizontal excursion means no compensation, while the downward movement indicated recompensation or recovery process. In headdown case, they should be read in reverse.

As a control system we can calculate the apparent gain of this system by equation 3, and the gain is plotted in Figure 4. The existence of three phases of eyecup movement is also conspicuous in this figure, with mirror image relation between headup and headdown tilts. Starting from a intermediate value of around 0.5, the gain goes up gradually close to unity. After a gradual decline, null gain position follows and the consecuitive recompensation phase turns into the positive gain phase before the original zero position is reached.

B) *Normal seeing animal.* When the animal sees surrounding object, such as fixed striped drum, while rotated, the gain is improved closer to unity even at a small tilt of the body from the normal zero position,without causing conspicuous

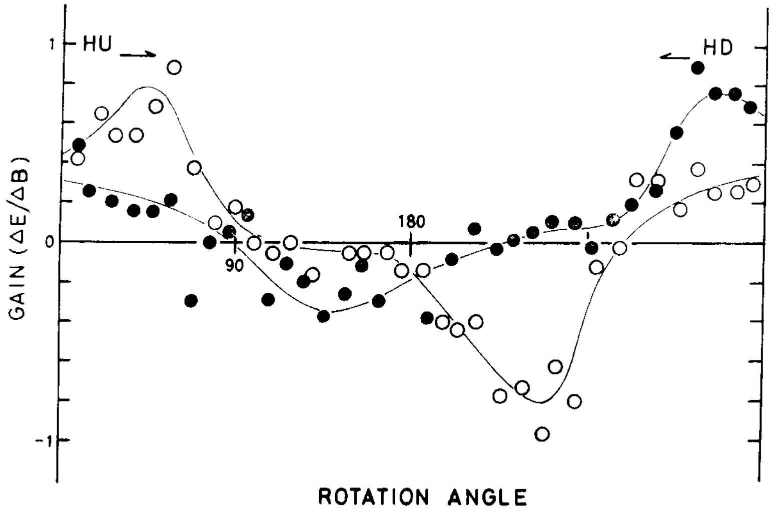

Fig. 4 Apparent gain (G_a) of the eyecup compensation calculated by dividing incremental eyecup angle ΔE by incremental bodily tilt ΔB. Headup direction in open circle (HU), headdown direction in filled circle (HD). Positive value in gain means that the eyecup rotates in opposite direction to the direction of bodily tilt, thus performing a positive compensation. Zero gain means the eyecup keeps in pace with bodily rotation, thus no compensation at all, while the negative value means the eyecup is recovering from the accumulated angular deviation relative to the body which resulted from the previous positive compensation. Animal is blinded.

difference in other features of the eye movement. Large hysteresis and succession of positive, null, negative and then positive compensation phases on one whole turn remain unchanged in comparison with the results from the blinded one. Inference is that the optokinetic response is working synergetically to the geotactic system particularly close to the zero position, and resulting in improved compensatory ability even in small variation of the body position in gravitational field. This is tested in the following experiments.

2) Analysis of the contributing factors.

Since a difference is found between the blinded and the seeing individuals in the accuracy of the eyecup compensation in response to the bodily tilts of small angular deviation from the normal position, further studies are concentrated on the behavior of the eyecup in response to the bodily tilt of up to atmost 90° in both headup and headdown directions.

A) Blinded individual exhibits an inferior compensatory gain of about 0.4 to 0.5 in a small range near the normal position, B) while the same individual shown with stationary striped drum gives an improved gain of 0.85 (Figs. 4, 5). In seeing individual the relatively high gain region is also extended in both headup and headdown directions resulting in a wider positive compensation range and followed by fall-off of the gain at around 90° tilt. While the gain in the blinded animal reached 0.6 only in narrow range around ±20° apart from the normal position, and characterized by relatively gradual fall-off of the gain. (C) If the striped drum is rotated simultaneously accompanying with the rotated animal, the eyecup shows no mesurable gain in any body position. The optokinetic response seems to counteract to geotactic system and two systems are apparently cancelling

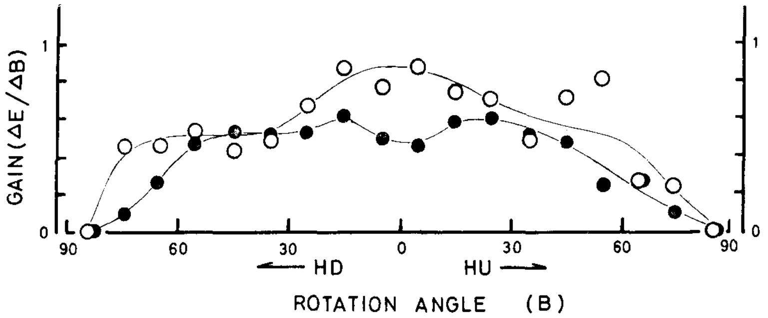

Fig. 5. Apparent gain (G_a) of rotatory compensation of eyecup in seeing and blinded animal. Seeing animal is rotated in a fixed drum with black and white stripes of equal spacing which subtend 8.2° on the crayfish eye (open circle). Blinded animal (filled circle) shows inferior compensation around 0° and also quick fall-off of the gain which starts around 45° of the bolily tilt. While the seeing one shows higher and wider range of the gain. Averages of three measurements of the same individual.

each other. The result is quite revealing in view of the function of a control system and will be discussed in later section. D) Purely optokinetic contribution is measured by rotating the striped drum around the stationary animal. The drum is turned in a very small speed (30 minutes per one complete turn) around the animal which is held horizontally. The optokinetic change of the eyecup rotation shows gain value of about 0.7 to 0.8 in a small range around the 0° drum rotation, but this high gain falls low at about 30° in both directions (Fig. 6).

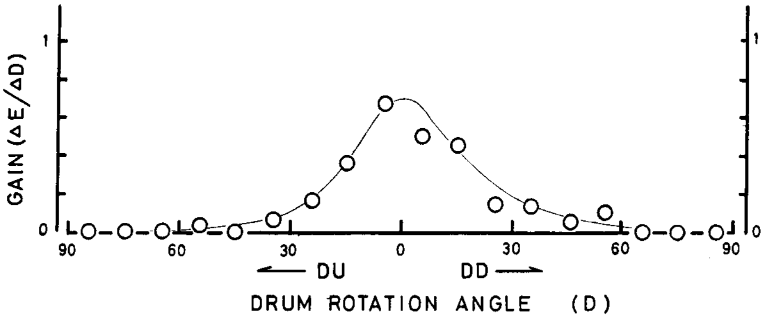

Fig. 6. Optokinetically controlled eyecup rotation of the fixed animal. The eyecup rotation is induced by rotating the striped drum around the transverse axis of the animal. Drum rotation in abscissae and apparent gain ($GA=\Delta E/\Delta D$ where ΔD is incremental drum rotation) in ordinates. DD (Drum down) means drum is rotated in a direction in which the stripe in front of the animal moves down and the eyecup moves in the same direction as in headup rotation of the body. DU (Drum up) indicates reversed relation. Average of three measurement of the same individual.

3) Heterolateral eye control

Regarding as a control system, it is of interest to know the forward gain of the optokinetic system. The forward gain Go can be only indirectly derived from the apparent gain Goa which is measurable by the equation 5, unless the direct measurement in homolateral eye is performed by opening up the feedback loop. This procedure requires a rather sophisticated system because of the contradictory requirement of the measuring system, in which the rotating drum should be given to the eye as the stimulus, while the image of moving drum being given exactly to the same ommatidium of the eye. On the other hand, we can readily determine the forward gain of the crosswise control of the heterolateral eye, by blinding the heterolateral eye and measuring the angular change while showing moving drum to the seeing homolateral eye which is glued to the socket. In *Carcinus*, Horridge (1966) has obtained a larage crosswise forward gain which well explains the coordinately movement of the both eyes in this animal.

The measurement performed in the present experiment of the crayfish resulted in a quite low and almost negligible cross forward gain. This makes a striking contrast with that of *Carcinus*, and follwing two possibilities are proposed. 1). Cross coupling between the bilateral eyecup movement in optokinesis may intrinsically be quite poor in the crayfish, which appears to be highly likely because of the architectural limitation of the binocular overlap in crayfish. 2). The discrepancy may arise from the difference in measured responses. In crab, the drum is rotated in horizontal plane with horizontal eye movement measured, while in the crayfish the drum is rotated in vertical plane and the rotatory eyecup movement is measured.

Second possibility is tested in the crayfish. The drum is rotated horizontally while the horizontal movement of the blinded heterolateral eye is measured., The homolateral eye which will drive the blinded eye is either left free (stimulus: $S=D-E$ as closed loop condition) or glued to the socket (stimulus: D as open loop condition). In either case, we found an almost null forward gain in crayfish. Homolateral eye has shown characteristic eye flip-back which brings back the position of eyecup in horizontal plane after following up the stripe for about 10° to 20°. The flip-back has been also noticed by Wiersma and Oberjat (1968), and also by Horridge and his co-workers in *Carcinus* (1964, 1968). This result indicates again the rather negligible crosswise linkage in optokinetic response of the crayfish, supporting the first possibility.

Discussion

Open loop characteristics of geotactic eyecup control system: Statocyst mediated geotactic control system differs from the optokinetic system in one very important feature. The statocyst which serves as a detector of the bodily tilt is born on the basal segment of the antennule, and the actuator system, eyecup, moves independently, reflecting no information back to the detector, thus having no closed feedback loop, while the optokinetic system is closed wth negative feedback loop through the visual channel.

However, the open loop characteristic of the geotactic system may be said to be in some sense imposed artificially, because, in natural habitat, the loop is usually remotely closed by the compensatory movement of the trunk and appendages which serve to lessen the imposed tilt by reducing the total angular displacement. In the experimental condition, this feedback is removed by clamping fast the whole crayfish body and preventing any compensating movement of the body. Even in natural condition, the feedback loop is quite indirect and the system can be practically considered as of open loop forward feed type. The gain which is measured as an apparent one in the blinded animal with bodily tilt thus directly represent the true gain of the system (equation 3 and 7 in outline section) and was found to be less than unity. It is apparent from this argument that as far as this system works as of a compensatory nature, the gain is expected to be at most equal or less than unity.

Negative feedback characteristics of the optokinetic system: Optokinetic system is intrinsically closed with visual feedback passway. The forward gain, therefore, could be expected to be higher than unity, unless we postulate a particular backward gain other than unity.

The calculated forward gain according to the equation 4 and 5 from the measurement performed on homolateral gain is in good agreement with this expectation. This optokinetic gain is, of course, dependent on the frequency of the stimulus or velocity of the rotation of the striped drum. Slower drum speed gives higher forward gain, and consequently higher apparent gain of the system. Direct measurement of the forward gain is left to be desired, because of the complication of required condition.

Parallel control of the eyecup by optokinesis and geotactic compensation: Roll and pitch of the crayfish body which trigger the activity of the statocysts sensory hairs in natural habitat are likely to be accompanied with the shift of visual image. The statocyst activity is reflected to the eyecup as the well known compensatory eyecup movement to the bodily tilt and minimize the relative eyecup displacement to the gravitational field. The shift of the image which occurs simultaneously also triggers optokinetic response which also works to lessen the relative movement of the eyecup to the surrounding visual objects.

Since, in ordinary condition, the contrasting object such as the surrounding landscape, are fixed in the gravitational field, these two activities are expected to work somehow synergetically to the eyecup movement through the motoneuron activities to the eyecup muscles after the integrative process in the central nervous system. Exception is in the movement around the vertical axis, yaw, which basically triggers only the optokinetic response, unless the acceleration exceeds certain limit, because the crayfish statocyst is built so that only the rotations around transverse and longitudinal axes but not vertical are effective (Hisada and Sugawara, 1969, and a paper in preparation) as in *Palinurus*, making contrast with crabs (Dijkgraaf, 1955a, b, 1956).

The incapability of perception of horizontal movement and the weak optokinetic linkage between two eyes in crayfish may be suggestive of the fundamental difference in biological significance of the horizontal displacement between crab and crayfish.

The synergetic effect of optokinesis and geotactic response is proved in the present experiment as high gain compensation of close to the unity in wide range of angle. Optokinesis alone is effective in small angle around the normal position but the effective range is limited. The geotactic control is wide in range and high in gain aronnd ±30° but has considerably lower gain around 0° position, namely, there is a dip in gain around the normal position. This dip in gain might be directly related to the characteristics of the primary afferent signals form the statocyst. Our experiment shows the incremental frequency change of primary output of the statocyst to the unit angular change is high around 30° but remains low in small angle range of tilt to both sides of the normal position either in pitch and roll (Hisada and Sugawara, 1969, and a paper in preparation).

Experimental results described here indicate the different shortcomes of the two system are complemented in the synergetic relation. The remaining question is whether the postulated system can explain this.

The postulated system in figure 2 will give the eyecup response with bodily tilt in fixed striped drum as

$$\{(D-E)\,G_{o1}+B\,G_{s1}\}\,G_{e1}=E \qquad 10)$$

from equation 8 and 9,

$$(D-E)\,G_o+B\,G_s=E \qquad 11)$$

and since in this case D=B (sign of the relative drum movement is defined according to the resultant eyecup movement and actually in opposite direction with the bodily tilt),

$$B\,(G_o+G_s)=E\,(1+G_o)$$

$$E=\frac{G_o+G_s}{1+G_o}\,B$$

Hence the apparent gain in synergetic case ($G_{(s+o)a}$) is

$$G_{(s+o)a}=\frac{E}{B}=\frac{G_o+G_s}{1+G_o}$$

$$=\frac{\dfrac{G_{oa}}{1-G_{oa}}+G_s}{1+\dfrac{G_{oa}}{1-G_{oa}}}$$

$$=G_{oa}+G_s-G_{oa}\,G_s \qquad 12)$$

where

$$0\leqq G_s\leqq 1, \qquad 0\leqq G_{oa}\leqq 1$$

hence

$$0\leqq G_{(s+o)a}\leqq 1$$

Thus the proposed system is well fit to the synergetic relation proved experimentally. For example, at 0°, the measured G_{oa} is 0.7 and G_S 0.5 thus the synergetic gain of about 0.85 will be derived. Extension of relatively high gain region in the seeing animal is also readily explicable. Even at 60°, the relative displacement of the eyecup to the body is less than 16° as the cumulative result of good compensation up to this point. This means the optokinetic gain is still high enough to extend compensation further, until the architectural limitation enables no further turning of the eyecup. Cumulative angular deviation at 90° bodily tilt amounts up to 50° in the seeing animal making contrast with 30° of the blinded animal.

However, it should be reminded that the components of the system are not likely to behave in linear function and actual system is certainly much more complicated.

Very low and negligible apparent gain observed in the experiment in which the striped drum is rotated around accompanying with the animal reveals more about the adequacy of the postulated system.

Since the drum is rotating simultaneously with the animal we have D=0 in equation 10, thus

$$(-E\,G_{o1} + B\,G_{s1})\,G_{e1} = E \qquad 13)$$

$$-E\,G_o + B\,G_s = E \qquad 14)$$

hence, the gain in this antagonistic case

$$G_{(s-o)a} = \frac{G_s}{1+G_o} = \frac{G_s}{1+\dfrac{G_{oa}}{1-G_{oa}}} \qquad 15)$$

$$= G_s - G_s\,G_{oa}$$

since $0 \leqq G_s \leqq 1$, and $0 \leqq G_{oa} \leqq 1$

$$G_{(s-o)a} \leqq G_s \qquad 16)$$

Equation 16 indicates if the optokinetic gain G_{oa} is high and close to unity, the eyecup will show almost no compensation to the bodily tilt. And the experimental set up is so that the optokinetic system works at the maximum gain at any angle of the bodily tilt, because the visual feedback prevents significant eyecup deviation. This prediction was verified in experiment.

Enhancement of oculomotor efferent impulses during the bodily tilt in consequence with the increase in visual cues has also been reported by Wiersma (1966) and Wiersma and Yamaguchi (1967). Further study of the oculomotor system as well as the related central integrative function, therefore, seems to be necessary for detailed understanding of the mechanism of the synergetic function. This is also concomitant with Schöne's observation of dependence of the angular deviation of eyestalk produced by the unilaterally directed illumination on the animals of vaious orientation in the gravitational field. He found that the strongest influence of light appears when the statocyst lies horizontal and, therefore, not affectd by any shearing force (Schöne, 1961). His conclusion is even more interesting and favorable to the present formulation, because the system postulated here can predict this relation. Equation 12 means if either one of optokinetic or geotactic system becomes low in gain the remaining one becomes predominant and contributed mainly to the final response.

Though the response described in these two papers are in more relation with the dorsal light response rather than with the optokinetic reactions, contribution of visual cues on principally a geotactic eyecup movement is apparent and relevant to the present observation.

Ambiguity in detection of absolute position in crayfish geotactic system: Present observation clearly demonstrates the eyecup will take two completely different postitions relative to the body depending on which direction, headup first or headdown, a particular angle of bodily tilt has been approached from. In upside down postition where this discrepancy is maximal, the difference in eyecup angle amount as much as 60° in the blinded animal, suggesting a large ambiguity in the system of angular perception.

Cohen (1955) has shown that in *Homarus*, the statocyst hair output of his Type-I position receptor shows a characteristic bell-shape curve of reponse, which shifts the angle of maximum response depending on which derection the maximum is approached from. Our study of the primary afferent output of the crayfish statocyst (Hisada and Sugawara, 1969, and also a paper in preparation) also clearly proved the phase shift of maximum by the rotation in opposite directions. Therefore, the ambiguity arises very likely, at least in part, from the characteristics of statocyst organ itself.

Cross linkage of heterolateral eye in optokinesis: In the crab *Carcinus*, tight cross linkage of heterolateral eye has been proved and the high open loop gain is observed by Horridge (1966). Close linkage of both eyes may have significance in the sun dial movement of the eye in this brachyura. Measurement with crayfish indicated no such highly close linkage between two eyes, apparently suggesting the two eyes are not strongly linked in binocular function in optokinetic responses. Wiersma and Oberjat (1968) were able to demonstrate a slight cross linkage in optokinesis of the eye-up and -down fibers. But the response is limited to these two classes of oculomotor fibres and moreover, the evidenece is that the response by light is quite limited in magmitude and does not compete with that by statocyst. Smaller binocular field is significant in crayfish in comparison with the crab. In crayfish the eyestalks are usually held almost 150° apart and only a very narrow binocuoar overlap is expectable in the visual field, while in *Carcinus* the overlap seems to be more extensive.

Stabilizing eye assembly in space: It should be emphasized that the present observation described the first time the rotational compensation of the eyecup around its longitudinal axis, while all the previous observations dealt with the angular deflection of the eyecup in up and down movement of its longitudinal axis relative to the body. The rotatory compensation of the eyecup described here appeared even more important if one consider the ability of various crustaceans to perceive the plane polalized light as a distinct entity. Maximum sensitivity to the *e*-vector is proved to lie in vertical dorsoventral axis of the eye as well as in horizontal rostocaudal axis in *Cardisoma* (Waterman and Horch, 1966), and in the crayfish (Yamaguchi, personal communication). The ommatidia of the crayfish has a square facets with their diagonal axes run dorsoventral and rostocaudal directions. The polarization planes of maximum sensitivity run parallel to them. Both the geotactic and optokinetic responses described in this paper are effective to maintain and stabilize this sensitive planes in reference to the direction of the gravitational field. The reduction of the drift of the image is thus guaranteed when the bodily displacement is imposed either by external or internal causes. Of course, the whole crayfish body also shows geotactic and optokinetic reactions as described by Bethe (1897) and Kühn (1914), but the response is of rather long time course and, meanwhile, the eyecup response is likely to be serving as the primary compensation.

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