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THE CONTROL OF EYESTALK MOVEMENTS IN THE MYSID SHRIMP *PRAUNUS FLEXUOSUS*

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SUMMARY

The compensatory eyestalk movements of intact and statocystless mysid shrimps *Praunus flexuosus* have been measured under a variety of light conditions. The results indicate that the statocyst organs in the uropods are the major gravity receptors, and that they are both necessary and sufficient to produce sinusoidal compensatory eyestalk movements. The addition of visual cues (vertical light beam, optokinetic stimuli) modifies the eyestalk response to some extent, but does not alter its general form. When the statocysts are removed, however, light stimuli become important orientational cues, and the eyestalks perform a tracking response which is considered to be the experimental counterpart of the dorsal light reaction of the free-swimming animal.

INTRODUCTION

Among the many equilibrium reactions displayed by higher crustaceans, compensatory eyestalk movements have received most attention (Cohen & Dijkgraaf, 1961). Early behaviour experiments (Kreidl, 1893; Clark, 1896; Bethe, 1897) demonstrated the important contribution made by the gravity-sensitive statocysts to the control of compensatory eyestalk movements in decapod crabs and shrimps. More recently the influence of light direction (Schöne, 1961) and optokinetic stimuli (Horridge, 1966) on eyestalk position has been demonstrated. Also the interaction of gravitational and visual stimuli in the control of compensatory eyestalk movements has been studied using behavioural measurements (Hisada, Sugawara & Higuchi, 1969) and electrophysiological recordings (Wiersma & Oberjat, 1968). Thus a picture is beginning to emerge of the complex neuronal mechanisms which must underlie the integration of signals from statocysts and eyes for the control of eyestalk position.

By comparison with the decapods, studies of the equilibrium reactions of opossum shrimps (Order Mysidacea) are few in number, and in no case is there a systematic account of eyestalk movements or the factors which control them. The majority of reports derive from observations of free-swimming animals (Delage, 1887; Bethe, 1895; Bauer, 1908; Foxon, 1940) and lead to the conclusion that pitch and roll are under the joint control of the dorsal light reaction (whereby the dorsal body surface is directed towards the light source) and orientation transverse to gravity. Further

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than this only one report (Jander, 1962) gives quantitative data concerning the relative effectiveness of visual and gravitational inputs as orientational cues.

Other lines of evidence suggest that vision and a gravitational sense both make important contributions to the behavioural responses of mysids:

(i) The visual ability of mysids is well established. The large compound eyes are borne on mobile stalks and have a complex receptor structure (Debaisieux, 1944) matched by a high degree of development of the optic ganglia, (Mayrat, 1956). Fraenkel (1940) showed that vision is a major factor in rheotaxis, and De Bruin (1956) found that the mysid *Praunus flexuosus* exhibits a very well developed optomotor response. We might therefore expect a large visual component in the eyestalk compensatory responses of mysids.

(ii) Opossum shrimps have prominent statocysts which, despite their unusual position in the uropods, are built on the standard crustacean plan (Bethe, 1895; Debaisieux, 1947) and function in the same way as antennular statocysts (Neil, 1975*b*). Their role in gravity perception and equilibrium control has long been established (Delage, 1887) and is considered by von Buddenbrock (1914) to be a dominant one.

The aim of the present study has been to determine in a quantitative manner the relative contributions of sensory inputs arising from visual and gravitational stimulation to the control of eyestalk position in mysid shrimps. The eyestalk is uniquely appropriate for a study of the interaction of these two sensory modalities because (*a*) it is the final effector for both visual and gravitational inputs; (*b*) compensatory eyestalk movements represent the 'simple dependable response' necessary for quantitative behavioural measurements (Adler, 1962); (*c*) the eyestalk equilibrium control system lends itself to analysis based on the engineering principles of servo-control.

MATERIAL AND METHODS

The chameleon shrimp *Praunus flexuosus* (Müller), the largest and probably most abundant mysid around British shores, was used in all the experiments. Animals were collected in the estuaries of Plym and Tamar and kept in holding tanks at the Department of Zoology, University of Cambridge, for up to three weeks. Experiments were performed as soon after collection as possible. Individuals of both sexes were used and no difference was observed in the manner of their responses.

The experimental animal was secured to a 'Perspex' rod by glueing the dorsal carapace with a drop of a warm solution of gelatin in sea water. This fixative had the advantages of being quick-setting, strong and non-toxic, and it allowed release of the animal after the experiment. It was applied in such a way that the respiratory currents of the animal were affected as little as possible.

The 'Perspex' rod was mounted on a rotating device in a bath of sea water, as illustrated in Fig. 1 (*a*). The animal could be rotated in a controlled manner about its longitudinal axis (i.e. body roll), and this was accomplished either manually or, more often, by a pulley drive device operated by a Palmer 'Electric Twelve' kymograph. This latter method provided continuous smooth rotation at a constant speed of 2°/sec in a clockwise or an anticlockwise direction.

Eyestalk positions during body roll were measured with the apparatus shown in Fig. 1 (*b*). The eyes were viewed from the front through a binocular microscope and

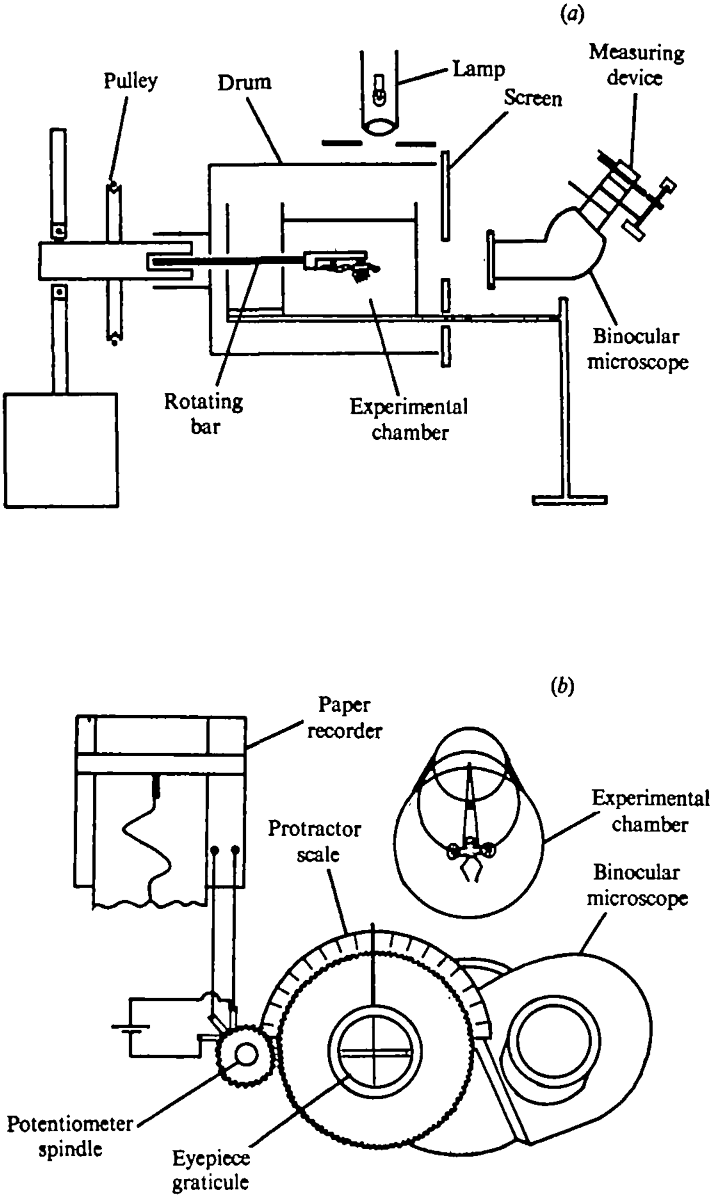

Fig. 1. Experimental apparatus for measuring compensatory movement. (*a*) Apparatus for producing controlled rotations and presenting standard visual stimuli. For certain experiments a circular fluorescent lamp replaced the microscope lamp. (*b*) Apparatus for measuring and recording eyestalk positions.

a graticule mounted in one eyepiece was aligned with the dorsal edge of one eyestalk. Alignments were made on each eyestalk in turn and their positions could be read off a protractor scale mounted on the eyepiece tube. This procedure was used in conjunction with manual rotation between body positions, and in order to standardize the measurements 30 sec were allowed to elapse between reaching a particular body tilt and reading off eyestalk position.

Alternatively, eyestalk position could be monitored continuously by linking the microscope eyepiece through a series of cogs to a potentiometer. The procedure of eyestalk alignment changed the resistance in the potentiometer circuit and the resulting d.c. voltage change operated a Smith 'Servoscribe' pen recorder. Thus, when used in conjunction with kymograph-driven rotation, this continuous recording technique provided a complete record of eyestalk movements throughout a full body rotation. It also facilitated the testing of a single specimen with up to four different stimulus combinations within a short space of time, and so overcame the problem of failing responsiveness of mysids subjected to prolonged experimentation.

For experiments conducted in darkness flash photography was employed to record eyestalk positions, the flash being directed from in front of the animal. Appropriate measurements were made from the projected negatives.

Three different light stimuli were used in the course of this work:

(i) Directional light was provided by a microscope lamp placed at a distance of 6 in. from the preparation.

(ii) Diffuse uniform lighting was produced by mounting a 14 in. diameter circular fluorescent lamp (Philips 'Warm White') around a 6 in. diameter 'Perspex' drum which had been covered with a layer of 'Kodatrace' tracing paper. (The possibility was not excluded, however, that the gap in the lamp might have acted as a weak optokinetic stimulus.) The animal was mounted at the centre of the apparatus.

(iii) Striped patterns were manufactured by sticking lengths of $\frac{1}{2}$ in wide black insulation tape on to transparent cellophane sheets. These could be mounted on the Perspex drum and when illuminated through diffusing paper a black/white pattern was produced, the repeat period of which subtended 19° at the eye of the mysid. The drum could be held stationary while the animal was rotated inside it, or it could be clamped to the rotating device so that the stripes turned with the animal.

To ablate the statocysts the mysid was immobilized on a damp tissue with its ventral side uppermost and the inner uropod rami were cut off at their bases with a pair of sharpened needles. The animal was quickly returned to a tank of aerated sea water and the reappearance of swimming was used as a criterion for post-operational recovery.

RESULTS

The results are presented graphically. Three readings of eyestalk position have been averaged and subtracted from the body position to give the amount of compensatory movement. In most cases the data for the two eyestalks are combined to give a measure of the deviation of a line bisecting the eystalks from the dorso-ventral body axis. Compensatory movements, expressed either as deviations of individual eyestalks or as deviations of the bisector line, are plotted on the ordinate against body position on the abscissa.

(1) *Intact animal*

In order to determine the control exerted by visual stimuli over eyestalk movements, an intact mysid was rotated under different light regimes.

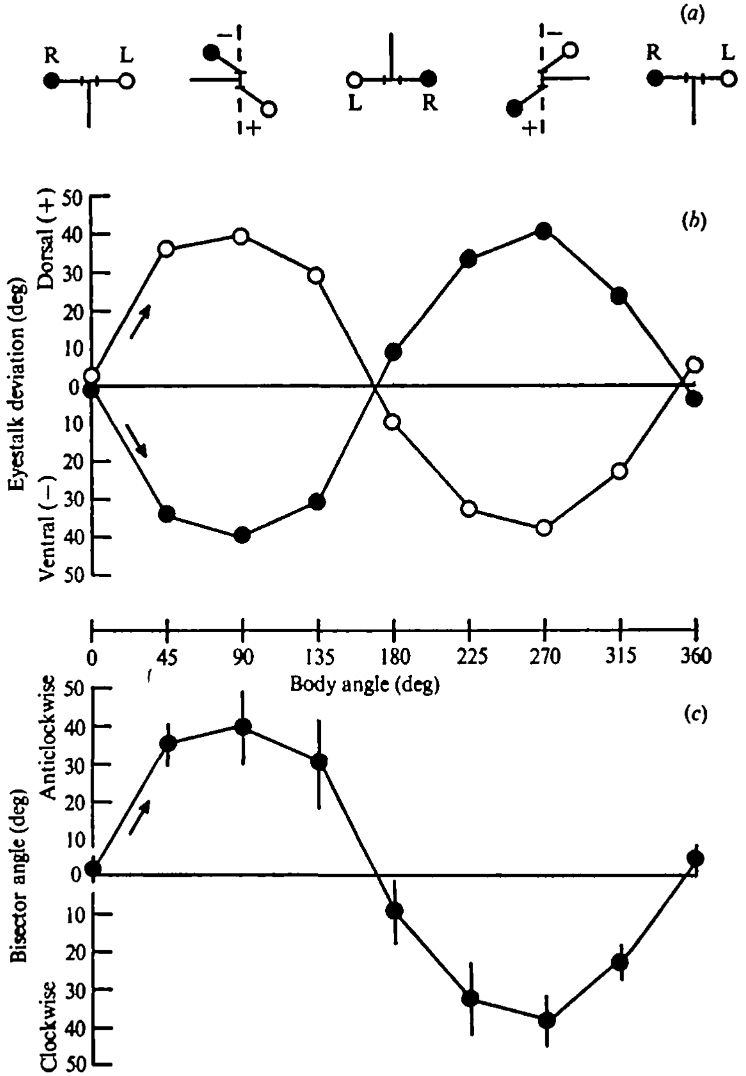

Fig. 2. Compensatory eyestalk response of intact *Praunus* rotated in a vertical light beam. (*a*) Diagrammatic representation of eyestalk deviations during rotation, as viewed from the front of the animal. Deviations of the left eyestalk (○) and the right eyestalk (●) from the transverse body axis (- - -) in a dorsal (+) and a ventral (——) direction are indicated. (*b*) Plot of eyestalk deviations against the angle of body tilt for a clockwise rotation from 0° to 360° (left side leading). Mean values for 15 animals. (*c*) Same data, expressed as deviations of the eyestalk bisector line from the dorso-ventral body axis (i.e. the bisector angle). Note the relation between the direction of the compensatory response (i.e. clockwise or anticlockwise) and the deviations of the two eyestalks (i.e. dorsal, +, and ventral, −). The vertical bars represent two standard deviations.

Vertical light

Fig. 2 shows the compensatory eyestalk response curve of intact mysids rotated clockwise in a vertical light beam. When upright the eyestalks are held out horizontally, but when the body is rotated they deviate in such a way as to compensate for the imposed tilt. The response curve follows a sine function with maximum values when

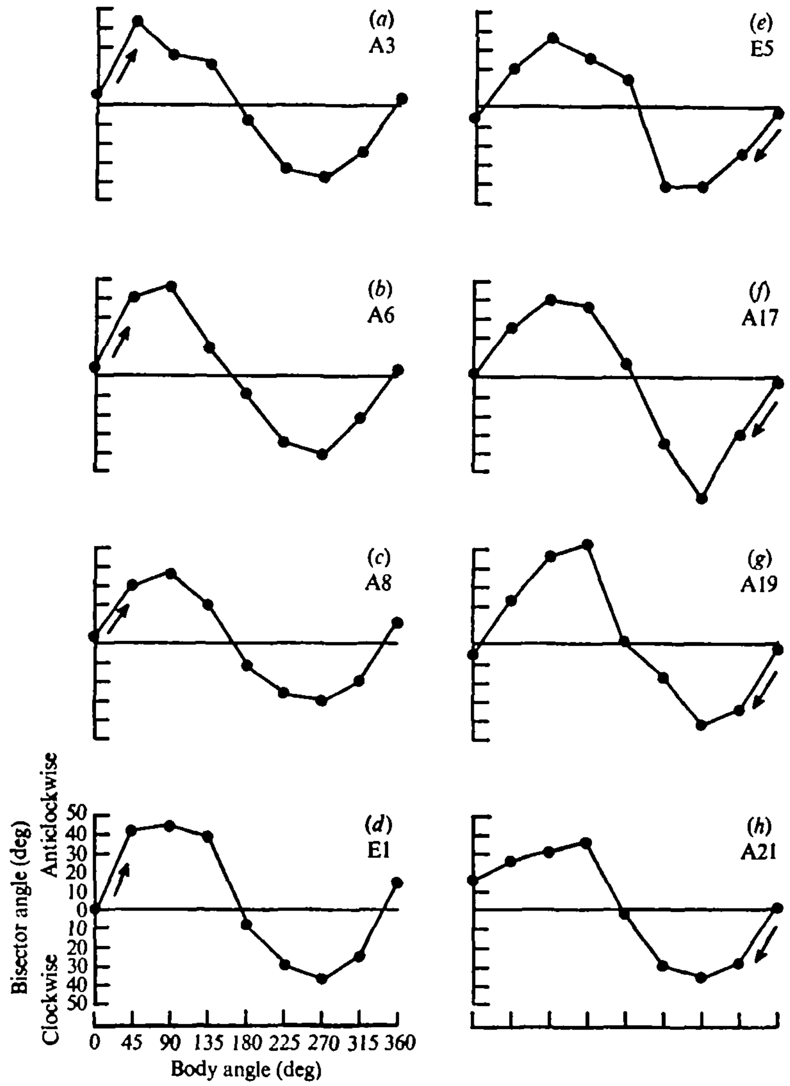

Fig. 3. Individual variability in the compensatory eyestalk response of intact *Praunus*. (*a*)–(*d*) The responses of four mysids to a clockwise rotation in a vertical light beam. (*e*)–(*h*) Anticlockwise rotation of four different individuals, under the same light conditions. For a given direction of rotation the responses share certain common features (see text).

the animal is turned onto its left and right sides. Around the origin the graph is straight and has a slope of 0·65, which gives a measure of the overall gain of the eyestalk compensatory mechanism. This value represents good compensation by *Praunus* and compares with values of 0·55 for *Carcinus* (Horridge, 1966), 0·4 for *Palaemonetes* and 0·16 for *Crangon* (calculated from data in Schöne, 1954) when rotated about their longitudinal axes.

There is some variability in the amount of eyestalk compensation shown by different individuals, and maximum deviations up to 65° have been measured. However, for a given direction of rotation the general form of the response curve is very similar from animal to animal (Fig. 3). Two features appear consistently:

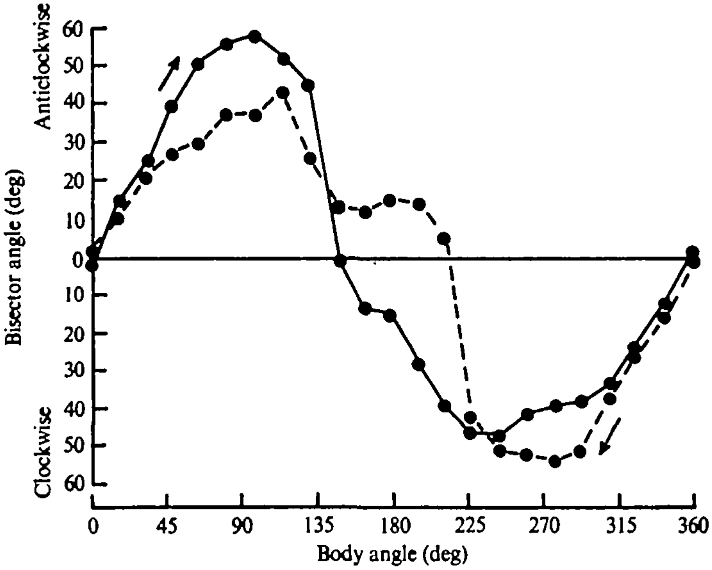

Fig. 4. Hysteresis in the compensatory eyestalk response. Eyestalk deviations, expressed as bisector angles, of an individual mysid rotated clockwise (——) and anticlockwise (---) in a vertical light beam. There is a systematic shift of the null point from 180° body angle towards a point earlier in the rotation.

(i) An amplitude difference between the maximum deviations at body tilts of 90° and 270°. The eyestalks move further when the lateral position is approached from the upright. (For a clockwise rotation, at 90° tilt $\bar{X} = 40°$, S.D. $= 12°$, $n = 36$; at 270° tilt $\bar{X} = 35°$, S.D. $= 9{\cdot}5°$, $n = 35$. A t test on these results shows that the difference between the two deviations is significant at the level $P = 0{\cdot}05$).

(ii) A shift in the position of the null point (i.e. the point where the eyestalk bisector line crosses the abscissa line) away from the point of symmetry towards a point earlier in the rotation. (At the 180° body position, for a clockwise rotation $\bar{X} = -15°$, S.D. $= 13°$, $n = 26$; for an anticlockwise rotation $\bar{X} = +12°$, S.D. $= 15°$, $n = 9$. A t test on these results shows that the difference between the two deviations is significant at the level $P = 0{\cdot}01$).

The direction of body rotation has a systematic effect on the form of eyestalk movements, and the response curves for clockwise and anticlockwise turns are mirror images of one another. Together they form a hysteresis loop in which the eyestalks take up different positions when a particular angle of body tilt is approached from opposite directions (Fig. 4). Asymmetrical stimulus cues would not produce such an effect, which must therefore reside in some directional property of the eyestalk movement control system. Without affecting the essential compensatory nature of the eyestalk response, this directionality may enable the mysid to distinguish between rolling over to the inverted and rolling back to the upright.

The vertical light stimulus acts synergistically with gravitational force to produce the observed eyestalk responses, and so this stimulus combination reveals little about the relative effectiveness of light and gravity in equilibrium control. More information can be obtained by removing the directional light stimulus (darkness, uniform illumination) or by causing the light to be directed from a different angle (horizontal light).

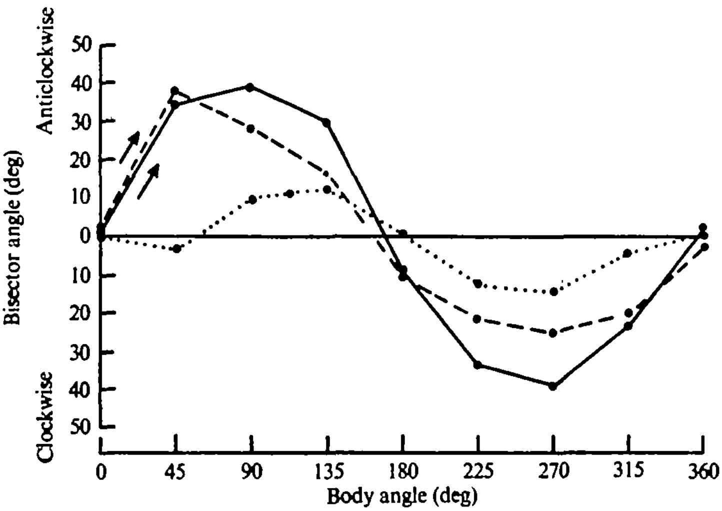

Fig. 5. The influence of directional light on the compensatory eyestalk response. Measurements taken during clockwise body rotation in darkness (●– – –●) and in a vertical light beam (——) (mean values for five animals). The contribution of the light cue to the response is derived by subtraction (. . . .).

Darkness

Specimens of *Praunus* were rotated between nine body positions first in darkness and then in a vertical light beam. In the upright body position the eyestalks are held out horizontally when light is present, but they are both directed upwards by 10° in darkness. This difference is not seen in Fig. 5 where deviations of the bisector line, rather than of individual eyestalks, are presented.

The response curve in darkness retains its sinusoidal form, and at positions close to the upright the eyestalks compensate as much as they do in the light. The contribution of vision to the response in the region 315°–45° is therefore minimal (Fig. 5, dotted curve). However at body tilts far from the upright the amplitude of the response curve is reduced by approximately one third when the light is removed. Therefore in the region 45°–315° one-third of the compensatory eyestalk response is produced by the action of the vertical light beam, and the remaining two-thirds of the response can be attributed to the action of gravity. Thus, under the experimental conditions employed here, vertical light is approximately half as effective as gravity as an orientational cue.

Another feature of the compensatory eyestalk response of *Praunus* which persists when the light stimulus is removed is the hysteresis between rotations in opposite directions (Fig. 6). This suggests that, as well as its sinusoidal form, the observed hysteresis of the eyestalk response can also be attributed to properties of the gravity-sensitive system.

Uniform illumination

Under these conditions directional light cues are eliminated. The results of an experiment in which a specimen of *Praunus* was subjected in turn to directional light and uniform illumination during rotation are shown in Fig. 7. In the vertical light beam there may be a slightly enhanced eyestalk response, as compared with uniform light, when the mysid is first tilted onto its side (90° in a clockwise turn). Otherwise

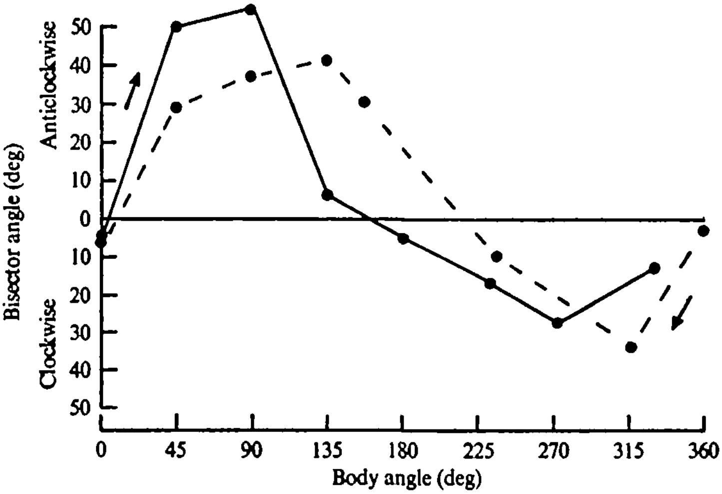

Fig. 6. Hysteresis in the absence of visual cues. Eyestalk deviations of an individual mysid rotated clockwise (——) and anticlockwise (- - -) in darkness. A systematic shift in the null point remains when visual cues are removed.

there are no differences between the eyestalk responses obtained under the two light conditions. This demonstrates the relatively minor role played by the directional visual cue in eyestalk movement control of intact mysids.

Horizontal light

In order to provide additional information on the interaction of stimuli in eyestalk movement control, a conflicting stimulus situation was produced by conducting the experiment in a horizontal light beam. In a single sequence a mysid was rotated in both directions with light incident first from above, and then in turn from the left and the right sides. The compensatory eyestalk movements under these various light conditions are shown in Fig. 8, where the abscissae represent the sign of body rotation relative to the direction of light. This relationship determines, to a large degree, the form of the eyestalk movements.

When rotation takes the eyes initially away from the lateral light beam (Fig. 8*a*) the position of the null point is not affected, compared from the equivalent curve in vertical light. However a difference is apparent approaching the upright, where the eyestalks tilt towards the lateral light source. Here the effect of the horizontal light beam is greater than predicted from the results of experiments in vertical light (Fig. 8*b*).

When the eyes are turned first towards the lateral light (Fig. 8*c*) the first phase of compensation is prolonged and the null point is delayed by approximately 50°. This represents a shift to the compromise position between those dictated by the gravitational and visual stimuli. Therefore the horizontal beam again produces a greater turning tendency than predicted, but in this case the enhancement occurs through most of the rotation (Fig. 8*d*).

These results suggest that horizontal light provides a better orientational cue than does vertical light. The different responses obtained with turns away from the light

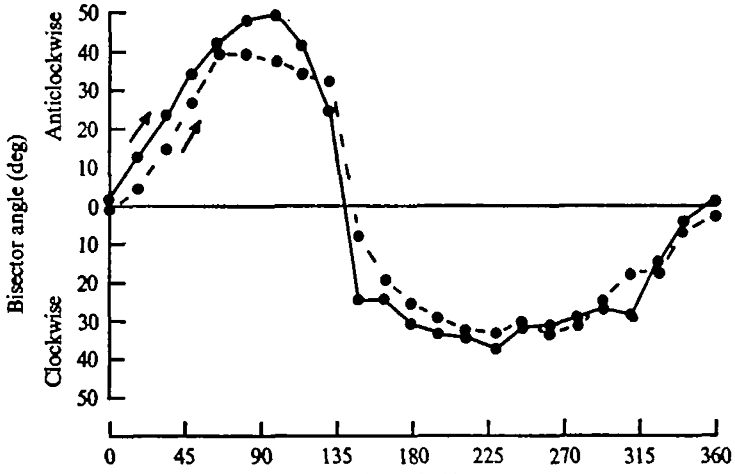

Fig. 7. Compensatory eyestalk responses in a vertical light beam (——) and with uniform diffuse illumination (– – –). Results for an individual specimen of *Praunus* rotated clockwise under both light regimes.

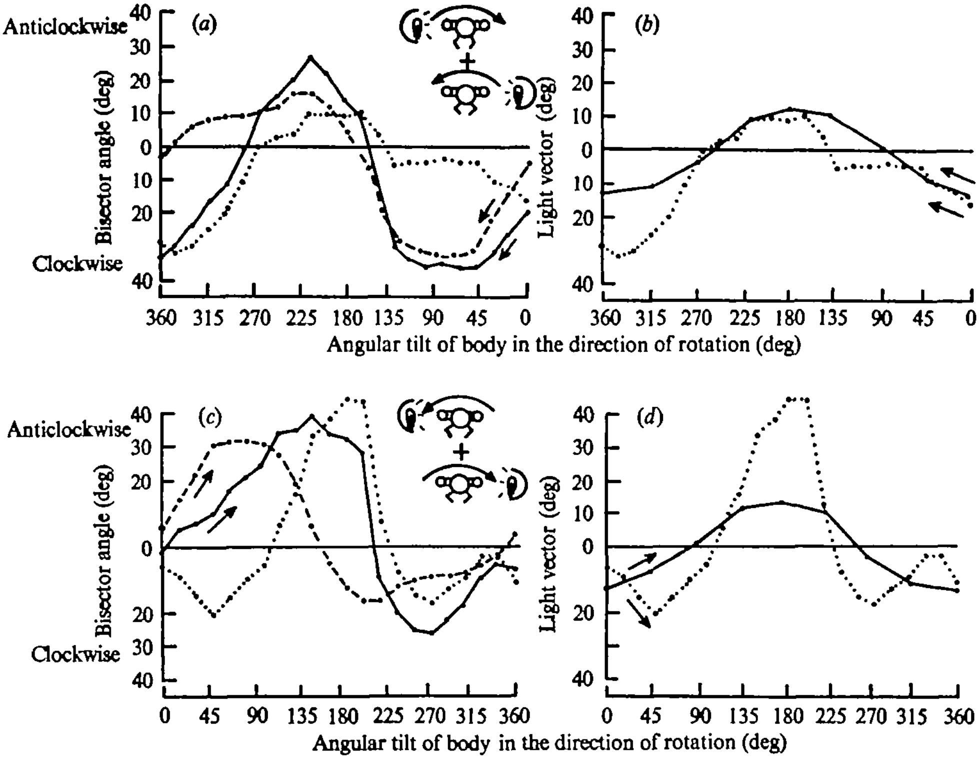

Fig. 8. The influence of horizontal illumination on the compensatory eyestalk responses of *Praunus*. Data from rotations of an individual mysid with light incident from the left side and from the right side have been combined, and are expressed relative to the direction of rotation, i.e. as turns first away from the light (*a*, *b*) and turns first towards the light (*c*, *d*). (*a*) and (*c*). From the response in horizontal light (——) the horizontal light vector (....) is derived by subtracting the gravity vector (– – –) (calculated as two-thirds of the values obtained in vertical light, see Fig. 5). (*b*) and (*d*) The horizontal light vector (....) is compared with the predicted value (i.e. the vector for vertical light, Fig. 5, phase-shifted through 90°) (——).

and turns towards the light may reflect the operation of a visual motion detection system which initiates the following of the directional light source by the eyestalks. This system seems to involve only the more dorsal ommatidia since, for each direction of rotation, distortion of the eyestalk response curve is greatest when the dorsal body surface, and hence the more dorsal ommatidia of the compound eyes, pass through the light beam. Evidence in support of this suggestion is provided by the finding that rotation of a black and white sectored disk below a mysid fails to elicit an optomotor reaction, whereas a strong following response occurs if vertical stripes are turned around the animal (De Bruin, 1956).

Optokinetic stimuli

These were used to produce further stimulus conflict situations. In addition to a strong optomotor response (De Bruin, 1956) *Praunus* also shows eyestalk movements in the transverse vertical plane in response to appropriate moving stripe stimuli (Neil, 1975*a*). The strength of this optokinetic response in relation to the influence of the gravitational input has been gauged in experiments with two optokinetic stimuli.

No relative stripe movement. A striped drum was clamped to the spindle which rotated the animal so that they turned together. During rotation there was no relative movement between the stripes and the animal, and the expectation was that closed loop optokinetic feedback would operate to reduce eyestalk movements.

The results of such an experiment show that when the eyes see 'stationary' stripes the first phase of eyestalk compensation (0°–180° in Fig. 9*a*) is reduced in amplitude by about 20%, compared with the response in vertical light, and the null point is delayed. Beyond this point the response curves for the two stimulus conditions are closely similar. In this respect the striped pattern is a little more effective in modifying the eyestalk response curve than uniform illumination (compare Fig. 9(*a*) with Fig. 7, which are the results for the same animal). However the optokinetic system is far less effective in dictating eyestalk position than the one based on gravitational input.

Relative stripe movement. Rotation of a mysid inside a stationary striped drum generates relative movement between the stripes and the eye. The animal sees a pattern of stripes moving in a direction opposite to its own rotation throughout the whole revolution. However eyestalk compensatory movements are sinusoidal in form and one eyestalk moves in opposite directions on the two sides of the null point. Therefore optokinetic effects will reinforce gravitational ones in the first half of the rotation, but they will counteract them in the second half of the turn. This will tend to produce an exaggerated difference between the amplitudes of the eyestalk movements in the two halves of the turn. The magnitude of this effect can be estimated from the fact that rotation of the striped pattern around a stationary upright mysid at an equivalent speed (2°/sec) induces the eyestalks to move through an angle of 15° in the direction of stripe rotation (Neil, 1975*a*).

Typical results of this experiment are shown in Fig. 9*b*, where the eyestalk response curves of a specimen rotated in a vertical light beam and with relative moving stripes are plotted. In the first phase of the turn (0°–180° clockwise) the reinforcing effect of the optokinetic stimulus is no greater than that of the vertical light. In the second phase (180°–360° clockwise) the predicted effect of relative stripe movement, namely a reduction in the amplitude of the eyestalk movements, does not occur. Therefore

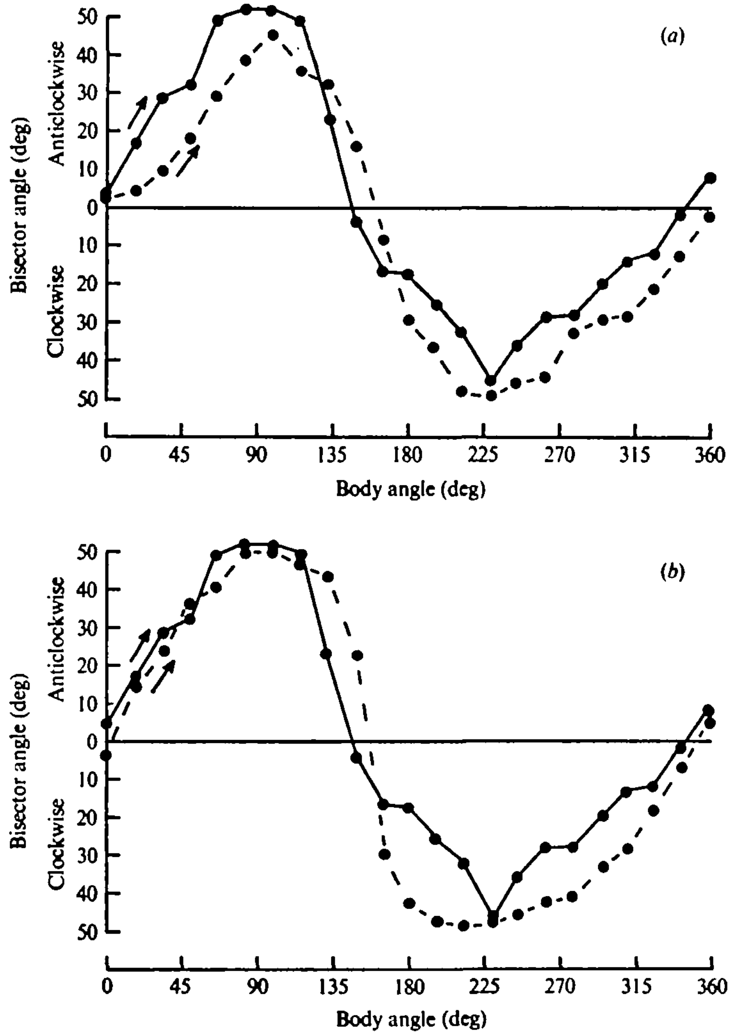

Fig. 9. The influence of optokinetic stimuli on the compensatory eyestalk responses of *Praunus*. (*a*) Response in a vertical light beam (——) compared with that to 'no relative stripe movement' (– – –). (*b*) Response in a vertical light beam (——) compared with that to 'relative stripe movement' (– – –).

this optokinetic stimulus fails to produce any significant effect on compensatory eyestalk movements.

The experiments under various light regimes indicate that visual stimuli can reinforce, or modify to a greater or lesser degree, the compensatory eyestalk movements of *Praunus*, but that they are not essential for the response and therefore not primarily responsible for it. The major contribution to eyestalk movement control has been attributed to the action of a gravity-sensitive system, and further evidence about the nature of this system has been obtained from experiments with statocystless mysids.

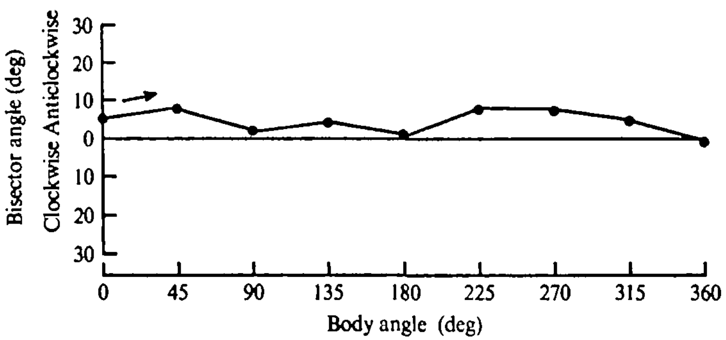

Fig. 10. Compensatory eyestalk responses of a statocystless *Praunus* rotated in darkness. Eyestalk movements are much reduced.

(2) *Animal with both statocysts removed*

In order to estimate the influence of gravitational input, and in particular its statocyst component, on compensatory eyestalk movements and to determine what effects visual stimuli produce when gravitational ones are removed, mysids with both statocysts removed were tested with a variety of light stimuli.

Darkness

Compensatory eyestalk movements are virtually absent when a statocystless mysid is rotated in darkness (Fig. 10). A residual response of less than 10° may remain, but is often not sinusoidal. That reduced eyestalk movements are not due to fatigue can be demonstrated by adding a light cue, for eyestalk deviations then appear. The absence of a compensatory response must therefore be attributed to a reduced sensory input, and indicates that the statocysts furnish the major proportion of information to the animal about its position in the gravitational field.

Vertical light

When a statocystless mysid shrimp is rotated in a vertical light beam its eyestalks move in an attempt to keep the retinal surfaces pointing towards the light source (Fig. 11*a*). Deviations up to 45° are reached. The tracking response continues through three-quarters of the rotation, so that the eyestalks maintain their original deviations until far beyond the inverted body position. It is possible that a non-involvement of ventral ommatidia in eye tracking contributes to this maintained response. In the final quarter of the turn the eyestalks move through a small angle in the opposite direction, so that the graph has the appearance of a much distorted sine curve. However it bears little resemblance to the eyestalk response curve of an intact mysid under the same light conditions (Fig. 2), especially with regard to the position of the null point. The hysteresis between the response curves for opposite rotations has the opposite sign, and is also much exaggerated.

Taken together with the fact that the statocyst gravity response alone can generate normal sinusoidal eyestalk movements, these results suggest that the influence of the visual system is suppressed in the intact mysid and that light stimuli become more important as orientational cues when the statocysts are removed. This conclusion is similar to the one reached by von Buddenbrock (1914) with regard to the dorsal light

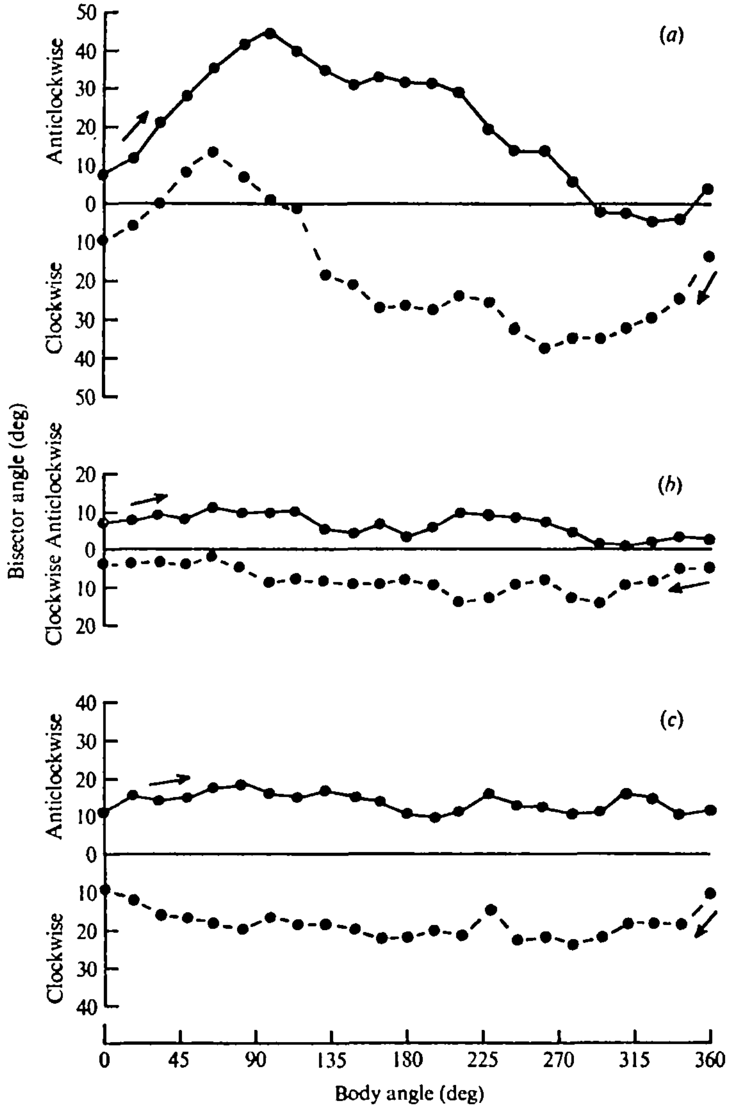

Fig. 11. The influence of visual cues on the compensatory eyestalk response in the absence of static gravity input. A statocystless *Praunus* subjected to clockwise (——) and anticlockwise (– – –) rotations with (*a*) vertical light, (*b*) 'no relative stripe movement' and (*c*) 'relative stripe movement'.

reaction of mysids, and it seems appropriate to identify the eye tracking response observed in controlled rotations with the dorsal light reaction of free-swimming statocystless mysids.

Optokinetic stimuli

Mysids with both statocysts removed were tested with the two standard stripe stimuli in order to see if the optokinetic system operates more effectively when the gravitational input is absent.

No relative stripe movement. The eyestalks show minimal deviations from their rest positions when stripes are rotated together with the animal (Fig. 11*b*). The eyes see 'stationary' stripes and closed-loop optokinetic feedback prevents drift of the eyestalks away from their original positions. This control is not absolute, however, for a small directional component remains (compare the curves for clockwise and anticlockwise turns in Fig. 11*b*). This residual response may be due to input from receptors, other than the statocyst, which respond to movements relative to gravity.

Relative stripe movement. As indicated above, operation of an optokinetic response in this stimulus situation is expected to induce eyestalk movements of the order of 15° in a direction opposite to the imposed rotation throughout the whole turn. This expectation is completely fulfilled in the experiment (Fig. 11*c*), for when rotation commences the eyestalks make initial deviations of the predicted amount in the direction of apparent stripe movement. The magnitude of this response remains constant throughout the rotation. Therefore this result reinforces the suggestion that visual processes take on a more important role in dictating eyestalk position when the statocyst signal is absent.

DISCUSSION

Two important conclusions which emerge from the present study are that gravitational stimulation alone can produce the typical sinusoidal eyestalk responses, and that the statocysts are the major gravity receptors. In both these respects, as well as in other aspects of statocyst function (Neil, 1975*b*), mysids resemble decapods. It therefore seems likely that, as previously demonstrated in decapods (Schöne, 1971), shearing force is the adequate stimulus for mysid statocyst sensory hairs and that linearity exists between this force and the eyestalk deviations.

The asymmetrical nature of statocyst-mediated compensatory eyestalk movements is clearly evident in the responses of *Praunus*, where it is expressed as a hysteresis between the response curves for opposite turns. Asymmetry is also apparent in the eyestalk responses of the decapods *Astacus* (Lyon, 1900) and *Palaemonetes* (Schöne, 1954). However in his graphical presentation of eyestalk movements Schöne (1954) eliminates asymmetries by summating the response curves obtained in clockwise and anticlockwise turns. Although this is a useful analytical procedure, it nevertheless conceals the asymmetries which constitute the true response of the animal, and which reflect the ambiguous response characteristics and directional properties of statocyst sensory hairs (Cohen, 1955, 1960). Electrical recordings from the statocyst hair receptors of *Praunus* have also revealed a directionality in receptor firing which has the same sign as the observed eyestalk hysteresis (Neil, 1972). This correlation reinforces the conclusion that there is strong drive from the statocysts to the eyestalks.

The residual eyestalk movements which remain after statocyst ablation may be due to the action of gravity on other receptors. Enteroceptors, sensitive to the displacement of internal organs, may play a part but it is more probable that limb joint proprioceptors are involved. Among the decapods, leg movements exert a large degree of control over eyestalk movements in rock lobsters (Dijkgraaf, 1956; York, Yanagisawa & Wiersma, 1972), and a smaller drive from limb proprioceptors to eystalk muscles has been demonstrated in footboard experiments with a crayfish (Stein & Schöne, 1972). The method of mounting mysids for rotation allowed free movement of the

Table 1

Visual stimuli		Eyestalk responses	
		Intact	No statocysts
Directional light	Vertical beam	Sinusoidal	Eye tracking
	Horizontal beam	Dislaced sinusoidal response	
No directional light	Darkness	Sinusoidal	Small residual movement
	Uniform diffuse illumination	Sinusoidal	
Optokinetic stimuli	No relative movement	Sinusoidal	Small residual movement
	Relative movement	Sinusoidal	Eye tracking

limbs, and it is possible that the shearing force on the limb joints was reponsible for the observed residual eyestalk movements.

The results of experiments in which different stimuli were combined with gravity stimulation are summarized in Table 1. The sinusoidal statocyst-mediated compensatory eyestalk response persists in all but horizontal light (where it appears in a distorted form). This finding is in accord with behavioural measurements of free-swimming mysids (Jander, 1962), but is opposite to the predictions of servo-control theory applied to a simplified model of the eyestalk control system. Under the conditions of the experiment the control by the statocysts is open-loop because they are borne on the fixed body and receive no change in stimulus when the eyestalks move in compensation. On the other hand visual control involves a negative feedback loop because information about eyestalk movement is available down the visual channel from the relative movement of images over the surface of the compound eye. Control theory predicts that a closed-loop visual servo-system will dictate eyestalk position more strongly than a straight feed-forward gravity sensitive system, assuming that the two inputs are treated equally in the central nervous system. Hisada *et al.* (1969) report that in the crayfish *Procambarus clarki* the eyestalk movement control system about the pitch axis behaves in a manner exactly predictable from control theory. However this theory does not hold good for the eyestalk behaviour of *Praunus*, as reported here.

The failure of servo-control theory to describe the eyestalk movement control system of mysids may be due to a difference in the relative importance of the sensory inputs from eyes and statocysts for the production of motor output to eyestalk muscles. Electrophysiological evidence from a number of decapod species supports the suggestion that there are differences in the firing rates of optomotor fibres produced by visual and gravitational inputs. It also indicates that there are differences in this respect between the effects of stationary light stimuli and striped patterns. In the crayfish *Procambarus clarki* Wiersma & Oberjat (1968) find that optokinetic stimuli have a greater influence than stationary light, but that changes in the firing frequencies of optomotor fibres produced by either visual stimulus are less than half those produced by statocyst stimulation. The rock lobster *Panulirus interruptus* resembles the crayfish with regard to the relative efficacy of statocyst and visual inputs, but in this case light distribution on the eyes is more important than optokinetic input (York *et al.* 1972).

Another possible reason for the small effect of visual stimuli on optomotor fibre discharge is that there is a direct inhibition of visual units by statocyst input. A closely similar effect has been suggested as the basis of the well documented space-constant phenomenon in crustacean visual systems (Wiersma, 1966). In *Praunus*, modulation of the output of visual units by the statocyst signal may be the basis of position-dependence in the optokinetic response to moving stripe stimuli (Neil, 1975*a*). Similar results are described by Schöne (1961) for *Palaemonetes* with one statocyst removed and with a single light as the visual stimulus.

Inhibition by the statocyst is also indicated by the fact that light stimuli assume a much greater importance as orientational cues when the statocysts are removed. In controlled rotations the eyestalks of statocystless mysids show a following response to moving light source or striped pattern, whereas in the intact animal eyestalk positions are determined to only a small degree by visual stimuli. Since the purely visual eyestalk responses of statocystless *Praunus* involve tracking by the motion detection system of the compound eyes, the statocyst inhibitory influences may act directly on visual movement detection units to suppress their effect on optomotor fibre discharge.

The eyestalk movements of *Praunus* in horizontal light do not fit a picture of statocyst dominance over these equilibrium reactions. The directional light stimulus is of equal importance to the gravitational force in determining eyestalk position. Measurements of the orientation of free-swimming mysids of the species *Mysidum gracile* confirm that phototaxis is stronger in horizontal than in vertical light (Jander, 1962). In horizontal light these mysids take up compromise body positions between those dictated by the light and gravitational stimuli. To account for the differences observed in the two light conditions Jander (1962) invokes a reciprocal inhibition between the visual and gravitational systems in which the direction as well as the strength of the difference turning forces is taken into account. The test of such a model, and the elucidation of the interactions between the various sensory inputs in the control of eyestalk position in mysids, await electrical recordings from the appropriate nervous elements.

The present findings add to the accumulating body of information about the eyestalk control systems of higher crustaceans. It is evident that there is a great species variation in the relative contribution of different sensory modalities to the control of eyestalk movements. For example, in rock lobsters, in addition to the statocyst signal, sensory inputs from legs (Dijkgraaf, 1956), antennule joints (Schöne & Schöne, 1967), antennae and eyes (York *et al.* 1972) all exert considerable control over eyestalk position. In mysids, on the other hand, the statocyst signals are more important for eyestalk position control than the sensory inputs from other potential position detectors.

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