THE MECHANISM OF STATOCYST OPERATION IN THE MYSID SHRIMP *PRAUNUS FLEXUOSUS*

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SUMMARY

Analysis of the compensatory eyestalk responses of mysid shrimps before and after the removal of one statocyst has revealed, in the light of statocyst anatomy, that the two statocysts co-operate in their action at all angles of body tilt. Many features of statocyst operation in mysids are shared by decapod crustaceans, but an important difference exists between the geometries of the two statocyst systems. The consequences of this difference highlight the structural constraints on systems of statolithic gravity receptors for which shear magnitude is the adequate stimulus.

INTRODUCTION

Opossum shrimps of the Order Mysidacea have prominent statocysts at the bases of their uropod endopodites. This is an unusual position for balance organs, which in the losely related decapod crustaceans are found in the basal segments of the antennules. Despite its unconventional site, however, the mysid statocyst was the first such organ in the crustacea to be assigned a role in equilibrium control rather than in hearing (Delage, 1887). Morphological and histological studies (Bethe, 1895; Debaisieux, 1947, 1949) have indicated that the mysid statocyst resembles that of the decapod, but it has not yet been established whether or not caudal statocysts and antennular statocysts operate in the same way.

The behavioural investigations of Schöne (1952, 1954) have demonstrated that in decapods the bending of statocyst hairs is the adequate stimulus for statocyst stimulation, and that a linear relationship exists between this stimulus and the final behavioural response of eyestalk movements. Utilizing this relationship, Schöne (1954) determined the mechanism of statocyst operation from an analysis of the eyestalk response of animals with one statocyst removed. He concluded that the two statocysts of a decapod such as *Palaemonetes* co-operate in their action, and that there is a simple algebraic summation of the afferent signals from the two organs.

A linear relationship between statocyst hair bending and eyestalk deviations is also evident in the responses of the mysid shrimp *Praunus* (Neil, 1975 a). The measurements of eyestalk movements can therefore be used to give a direct indication of the stimuli acting on the statocyst sensory epithelia. This facilitates a parallel study to that of

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Schöne (1954) and the results of this investigation are reported here. They indicate that statocyst operation in *Praunus* exhibits many of the features found in *Palaemonetes*, but nevertheless represents a variation on the decapod scheme.

MATERIAL AND METHODS

Praunus flexuosus (Müller) was used in all the experiments. Animals were collected in the estuaries of the Plym and Tamar, and kept in holding tanks for up to three weeks.

In an experimental chamber animals were rotated in controlled manners about their longitudinal axes and eyestalk deviations were recorded at different body positions. The rotating apparatus, light stimuli and recording techniques employed here were as described in Neil (1975a). For experiments in darkness flash photography was employed, and appropriate measurements were made from the projected negatives.

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

For the anatomical studies material was fixed in Bouin's solution and embedded in paraffin wax. Serial sections were cut at 4 μm and stained with iron haematoxylin. Some material was fixed in a glutaraldehyde-formaldehyde mixture, post-fixed in osmium tetroxide solution and embedded in Araldite. Sections were cut at 1 μ and stained with methylene blue solution.

RESULTS

The results are presented graphically, eyestalk position (expressed relative to the transverse body axis) providing a measure of compensatory movement. In most cases the data for the two eyestalks are combined to give a measure of the deviation of the eyestalk bisector line.

(1) *The mechanism of statocyst operation*

It has been shown (Neil, 1975a) that light stimuli modify, to some extent, the compensatory eyestalk movements of *Praunus*. In the absence of visual cues eyestalk movements reflect the gravitational input, the major component of which is statocyst stimulation. Therefore rotations in darkness provide appropriate data for an analysis of the mechanism of statocyst operation: those presented here being for clockwise rotations of intact mysids and of animals with one statocyst removed.

Intact animal

The compensatory eyestalk movements of an intact mysid rotated in darkness follow a sine function, with maximum values when the animal is turned onto its left and right sides (Fig. 1). The graph is not a perfect sine curve, but is slightly asymmetrical (Neil, 1975a). However the asymmetries are consistent with the known directional properties of crustacean statolith hairs (Cohen, 1955), and the eyestalk response curve can be regarded as an accurate reflexion of the statocyst signal.

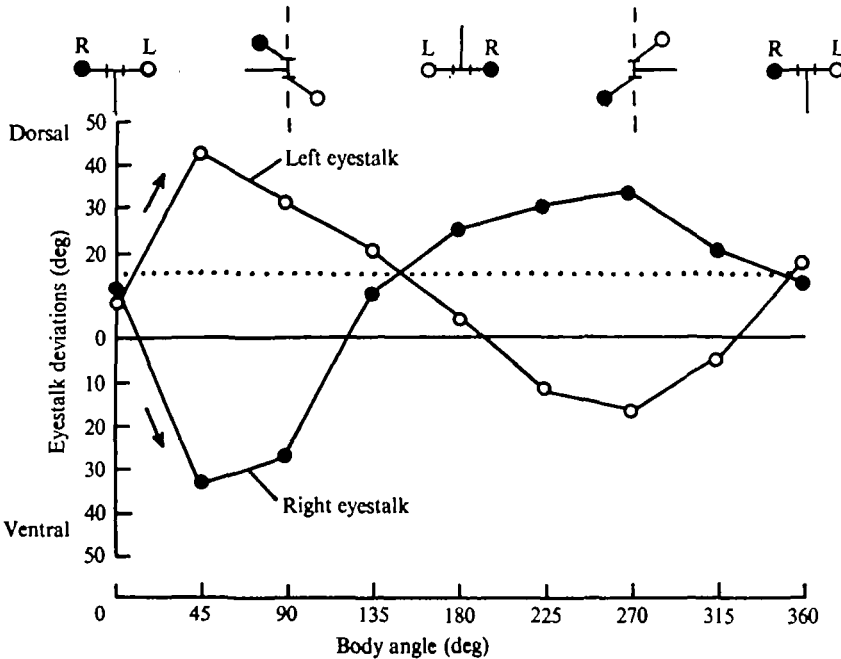Both eyestalks are directed upwards by an average of 12° in the upright animal, and

Fig. 1. Compensatory eyestalk response of intact *Praunus* in darkness. Deviations of the left (O) and right (●) eyestalks from the transverse body axis are plotted against the angle of body tilt. Mean values for three animals rotated in a clockwise direction (0° → 360°). The line of symmetry of the response curve lies 12° above the abscissa (– – –).

the whole response curve is symmetrical about a line through this point on the ordinate (dotted line in Fig. 1). The upward drift of the eyestalks occurs only in the absence of visual cues, for when light is present the eyestalks are held out horizontally in the upright animal (Neil, 1975 a).

Single statocysts control

Unilateral statocyst ablation causes spiral swimming and continual rolling about the longitudinal axis towards the deficient side. Such abnormal swimming behaviour continues with decreasing strength for a number of days. It affects the form of the compensatory eyestalk movements and consequently must be taken into account in analyses of the responses of unilaterally deficient animals. Rotation experiments were, therefore, conducted at a constant time (24 h) after the operation. In darkness the animals were rotated clockwise (i.e. left side leading), typical results for the two conditions being shown in Fig. 2. Well-defined movements of up to 40° persist in both eyestalks when one statocyst is removed. The upward drift of the eyestalks, caused by the absence of visual cues, is again evident, and the line of symmetry (dotted lines in Fig. 2) lies between 10° and 15° above the abscissa. The remaining statocyst thus controls the movements of both eyestalks, producing a simultaneous ventral deviation of one eyestalk and a dorsal deviation of the other. The eyestalk response differs considerably from that obtained when both statocysts are present; prolonged eyestalk deviations occurring towards the deficient side, the opposite deviations being virtually absent. This distortion occurs with respect to the operative condition, not the direction
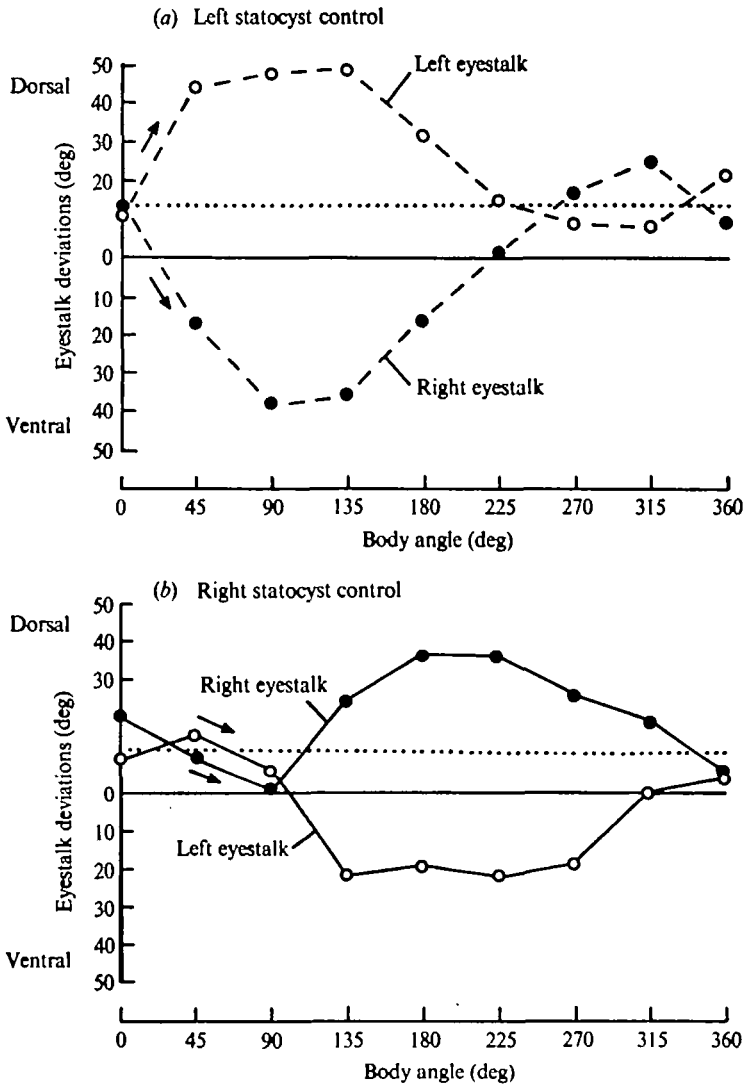
Fig. 2. The effect of unilateral statocyst ablation on the form of the compensatory eyestalk response. (a) Control by the left statocyst alone (– – –), (b) control by the right statocyst alone (———). Both results represent typical responses of individuals to a clockwise rotation in darkness. Deviations of the left (O) and right (●) eyestalks from the transverse body axis are plotted against the angle of body tilt. The lines of symmetry of the response curves lie 10–15° above the abscissa (. . . .).

of rotation (which is the same for both single statocyst conditions), and indicates that the turning reaction produced by one organ is predominantly in one direction.

An analysis of the mechanism of statocyst operation based on the eyestalk data for single statocyst control requires the linear relationship between the stimulus on the statocyst and the eyestalk movements to persist when one statocyst is removed. The anatomy of the statocyst provides important evidence on this matter.
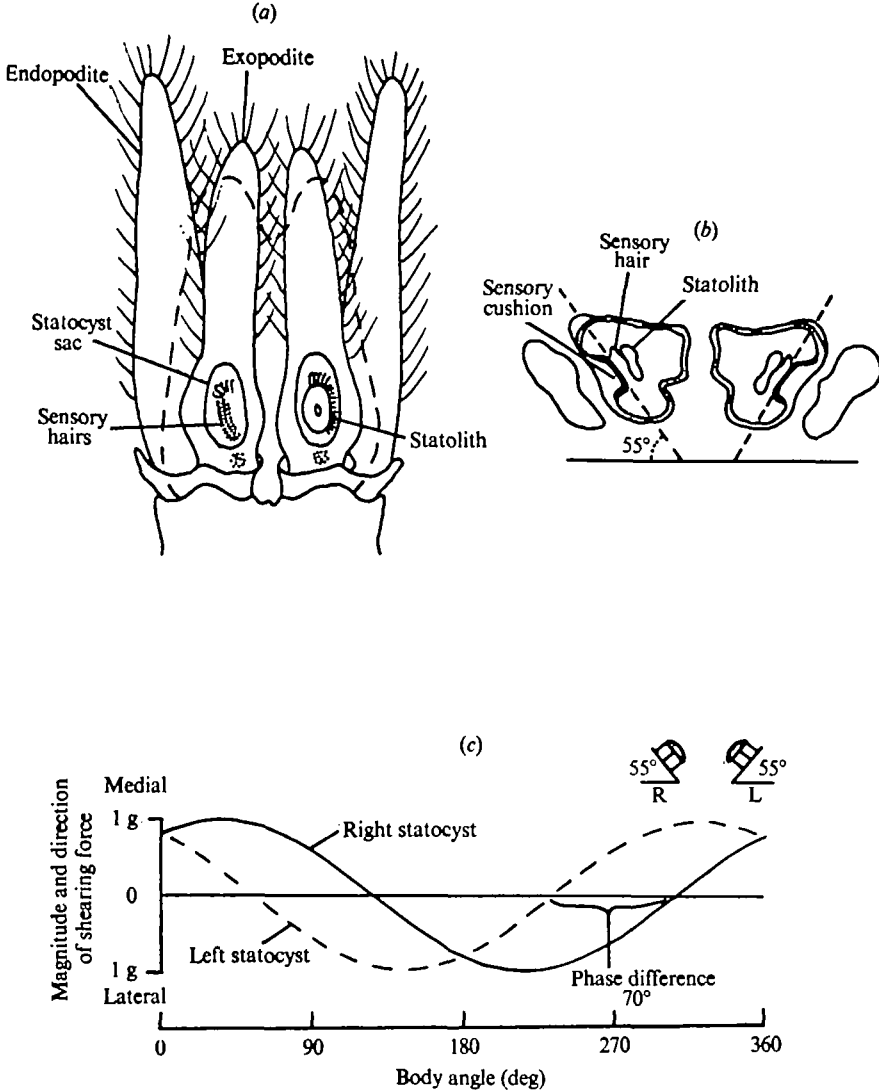
(a)

(b)

(c)

Fig. 3.(a) Dorsal view of the uropods of *Praunus* showing the position of the statocysts in the endopodites. The position of the telson is indicated by the dashed line. (b) Transverse section through the uropods at the level of the statocysts. The sensory epithelium is in the form of a raised cushion which lies at an angle of approximately 55° to the transverse body axis. (c) The shearing stimuli imparted upon the right statocyst (———) and the left statocyst (– – –) of *Praunus*. With statocyst epithelia tilted by 55° to the TV body axis the shearing stimuli are out of phase by 70°, and the sensory hairs of each organ are subjected to medial bending when the mysid is upright.

Anatomy of the statocyst

The mysid statocyst is a swollen vesicle at the base of the uropod endopodite. The statolith, which is secreted by the animal itself, is composed of a protein matrix surrounded by a calcareous shell rich in calcium fluoride (Bethe, 1895). The lith rests over the latero-ventral wall of the sac, suspended by the 50–60 statolith hairs which insert into its central matrix. These hairs are arranged in two or three rows along the length of a raised sensory cushion, forming a crescentric array.
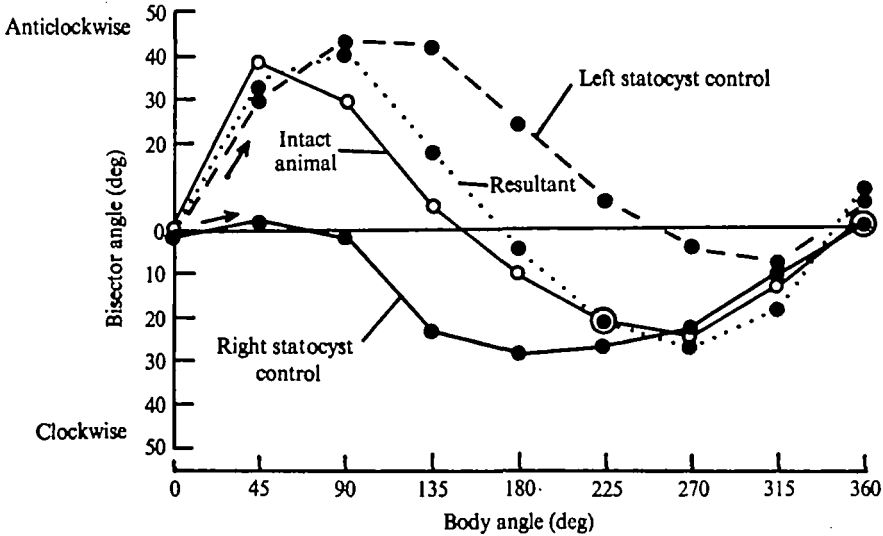
Fig. 4. Analysis of the mechanism of bilateral statocyst interaction using eyestalk data. The component eyestalk response curves for control by the right statocyst (●——●) and the left statocyst (●– –●) (data from Fig. 2, expressed as bisector angles) have been summed to produce a resultant (●·· ·●). This resultant is compared with the eyestalk response curve for the intact animal (O——O) (data from Fig. 1, expressed as bisector angles).

Transverse sections through the statocyst reveal that the elevated sensory cushion is inclined ventro-medially from the dorso-lateral margin of the sac (Fig. 3). Each sensory epithelium makes an angle of 50–55° with the transverse body axis, so that a medial shearing force is imposed upon the statolith hairs of both statocysts when the animal is on an even keel. The geometry of the system suggests that during rotation the shearing forces on the two statocysts are out of phase with one another by 80–70°. Plots of the shearing stimuli on the left and right statocysts are sine functions centred about the body positions in which the corresponding statocyst sensory epithelia are horizontal (Fig. 3).

Comparison of the curve for the shearing stimulus acting on one statocyst (Fig. 3c) with that for the eyestalk movements released by this organ alone (Fig. 4) shows that two significant conversions occur in the transformation from initial stimulus to final behavioural response. First, shearing in a given direction over the statocyst epithelium (i.e. medial or lateral) is converted to opposite turning tendencies (i.e. clockwise or anticlockwise) by the two statocysts. Secondly, each eyestalk curve for single statocyst control (Fig. 4) is displaced vertically along the ordinate, compared with the equivalent curve for shearing stimulus (Fig. 3c). These shifts occur in a side-symmetrical manner, so that the two curves lie almost entirely on opposite sides of the abscissa line, and represent the release of predominantly unidirectional turning tendencies from the two statocysts. The small eyestalk movements in the opposite direction may be the result of a partial central compensation, since the measurement were taken on the day following statocyst ablation (see pp. 693–4).

Despite the two conversions performed by the statocyst control system the eyestalk response released by a single statocyst retains a linear relationship to the shearing stimulus, thus providing appropriate data for the analysis of bilateral statocyst interaction.
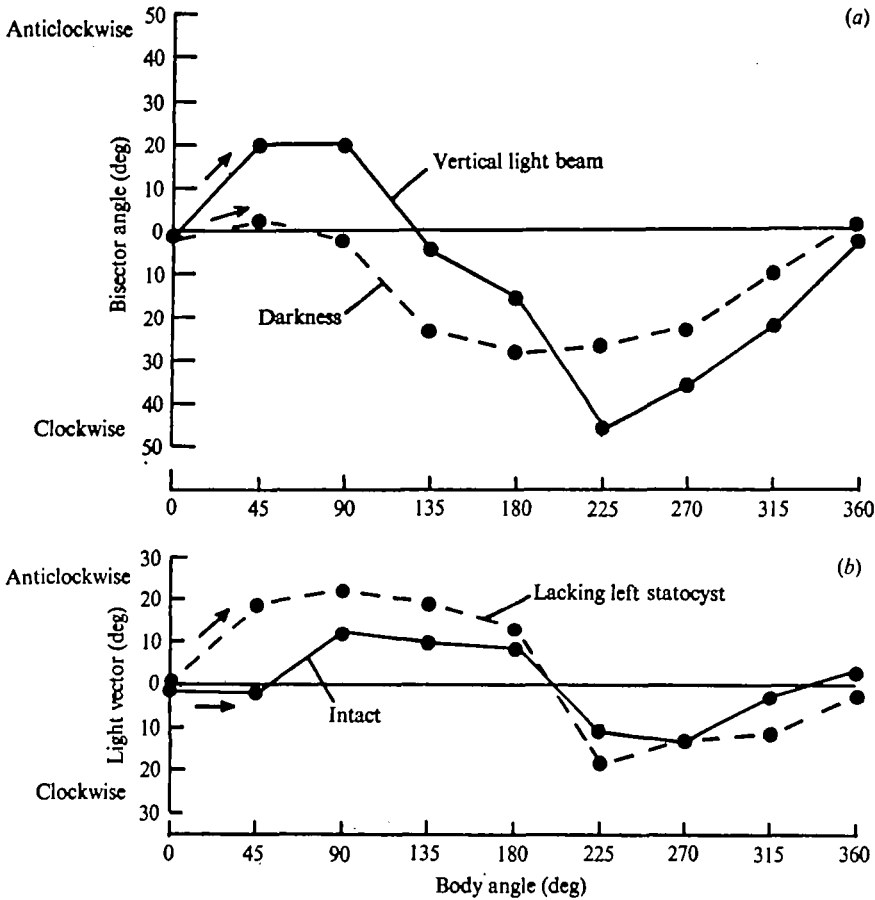
Fig. 5. The influence of vertical light on the compensatory eyestalk response of *Praunus* with one statocyst removed. (a) Successive rotations of a mysid with only the right statocyst intact in a vertical light beam (————) and in darkness (— — —). (b) Comparison of the light vector for the unilaterally deficient animal (— — —) with that for the intact animal (————) (data from Neil, 1975a).

Analysis of bilateral control

The simplest hypothesis of bilateral statocyst interaction involves an algebraic summation of the signals from the two organs at all body positions. A test of this possibility is provided by adding together the eyestalk response curves for control by each statocyst alone (Fig. 4), and comparing the resultant with the actual response curve of the intact mysid (Fig. 4). There is a good fit between the theoretical resultant and the measured response of the intact animal over the whole range of body tilts. This analysis, therefore, indicates that the two statocysts co-operate in their action at all body positions, and that their afferent signals sum in a simple manner.

(2) The influence of visual cues

Rotations of *Praunus* with one remaining statocyst were performed to determine whether visual cues make a more important contribution to eyestalk position control when only one statocyst remains than they do when both are present (Neil, 1975a).
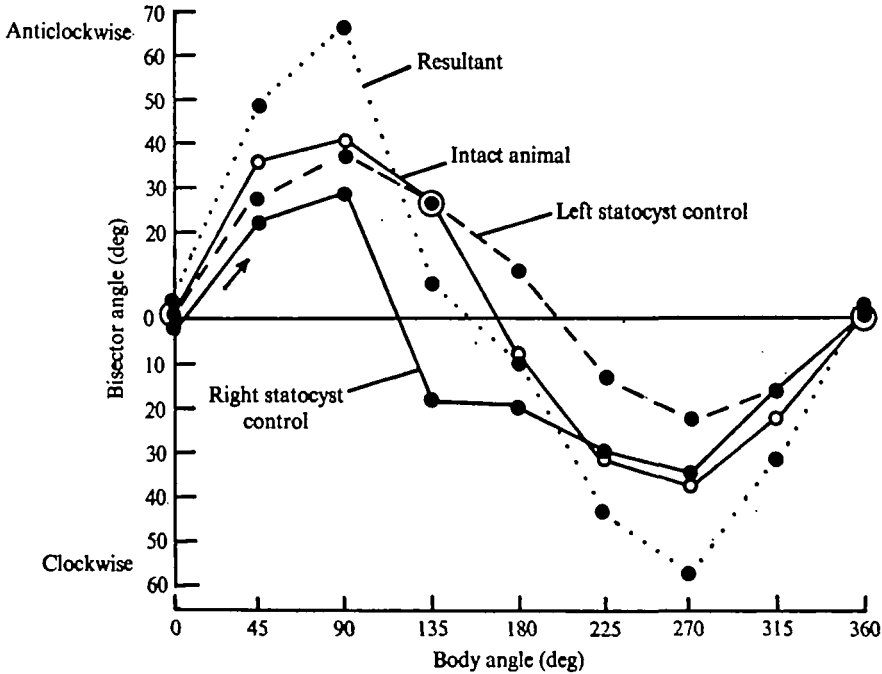
Fig. 6. Algebraic summation of the eyestalk response curves of mysids lacking one statocyst, rotated clockwise in a vertical light beam. The component curves for control by the right stato-cyst (●——●) and the left statocyst (●– – –●) are the means for 5 animals, and the resultant curve (●···●) is their algebraic sum. This resultant is compared with the eyestalk response curve for intact *Praunus* under the same stimulus conditions (O—O) (mean of 15 animals).

Mysids with one statocyst removed were rotated clockwise in darkness and in a vertical light beam (Fig. 5). When the light stimulus is added the eyestalk response increases in amplitude and regains a bidirectional form. The light vector which produces this effect is larger than its counterpart in the intact mysid (Fig. 5*b*), suggesting that the light stimulus plays a more important role in eyestalk position control when one statocyst is removed.

Fig. 6 demonstrates that the visual stimulus influences eyestalk position under both conditions of single statocyst operation. Summation of the two eyestalk response curves produces a resultant which is greater in amplitude than a component, and reaches higher values than those recorded in the intact mysid (Fig. 6). This departure from the simple algebraic relationship is a consequence of an equal enhancement of the two component turning tendencies by the light stimulus.

In the eyestalk responses of intact *Praunus* a hysteresis has been demonstrated between rotations in opposite directions, both in darkness and under various light conditions (Neil, 1975*a*). It was argued that directional properties of statocyst hairs were responsible for the hysteresis effect. A similar hysteresis occurs in single statocyst control (Fig. 7). The magnitude of eyestalk deviations in the shortened compensation phase is greater when the initial tilt is towards the deficient side (i.e. clockwise turn in Fig. 7). This direction of rotation also displaces the null point of the response curve further from its normal position close to 180°. These asymmetries have the same directionality as the hysteresis in the eyestalk responses of intact mysids, but are opposite in direction to those induced by light in statocystless animals (Neil, 1975*a*).
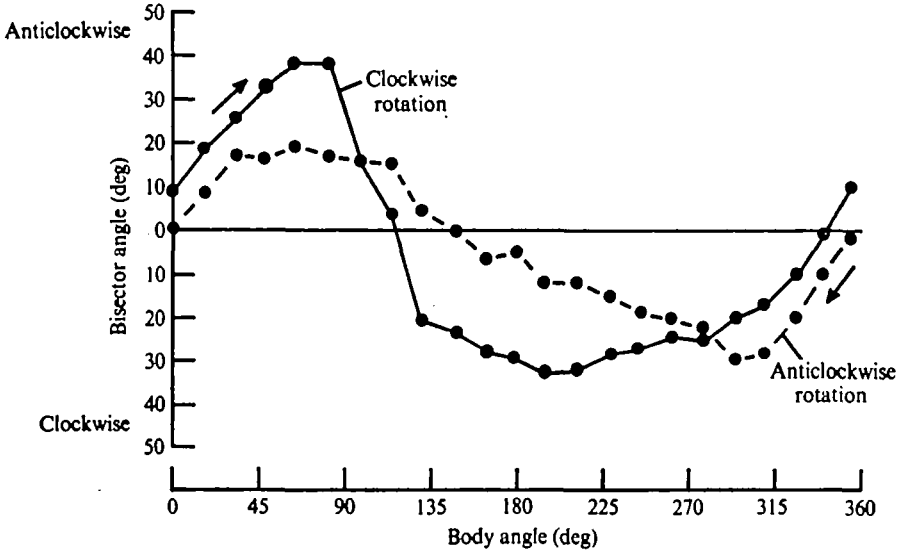
Fig. 7. Hysteresis in the eyestalk responses controlled by a single statocyst of *Praunus*. Eyestalk response curves of a mysid with the left statocyst removed, rotated clockwise (——) and anticlockwise (– – –) in a vertical light beam.
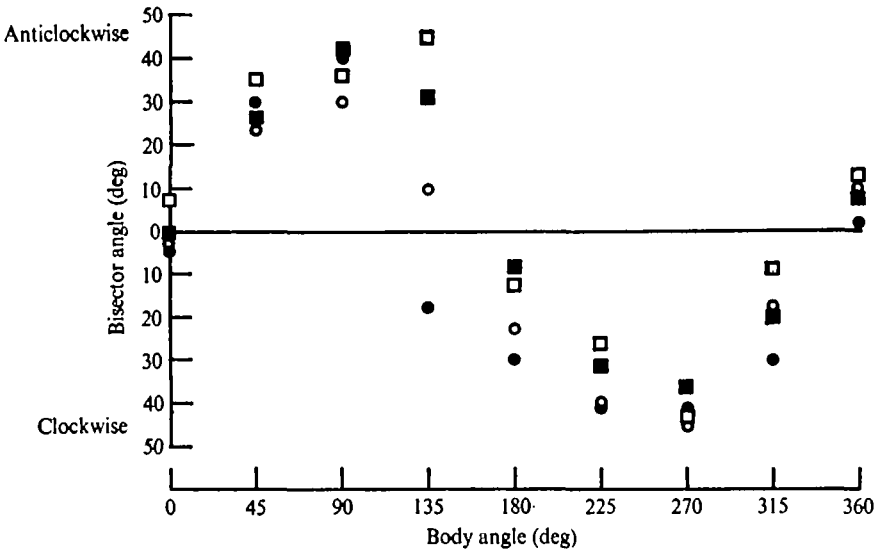

Fig. 8. The effect of central compensation on the compensatory eyestalk response of a mysid with the left statocyst removed. Dyestalk positions were measured at nine body positions immediately following the operation on day 0 (●), and on three succeeding days, day 1 (○), day 2 (■) and day 3 (□).

It is probable, therefore, that the hysteresis in the eyestalk responses of *Praunus* with one statocyst removed has the same basis as in intact animals, and reflects the directional properties of the sensory hairs of the remaining gravity-sensitive organ.

(3) *Central compensation*

The post-operative rolling and spiralling of mysids with one statocyst removed occur consistently towards the injured side, but over a number of days more normal

swimming behaviour reappears. This recovery of apparently normal equilibrium
responses suggests that the inappropriate turning force is cancelled, perhaps by some
central nervous mechanism. Post-operative changes also occur in the eyestalk responses
of *Praunus*, and these have been followed by taking measurements on the day of the
operation and on each of the three following days. The most complete series of results
has been obtained for experiments conducted in a vertical light beam, the presence
of which, however, caused the eyestalk response to assume a bidirectional form
(cf. Fig. 5).

The mysid was mounted into the apparatus in dim red light so that no asym-
metrical visual cues influenced the initial eyestalk deviations. Typical changes in the
form of the eyestalk response over a period of three days following the operation are
shown in Fig. 8. There is a gradual change in the direction of the initial eyestalk devia-
tion from a 5° deviation to the injured side on the day of the operation, day 0, to a
7·5° deviation to the intact side of day 3. A similar change is evident in the general
form of the response curve. Thus the changes in the eyestalk responses of *Praunus*
over a period of time after unilateral statocyst ablation correspond to the changes in
behaviour of free-swimming mysids, and are consistent with the theory that a central
mechanism cancels the tendency of the animal to look (or, if free, roll) to the injured
side.

DISCUSSION

Four major features of the mysid statocyst control system have emerged from the
present study:

(1) Anatomical studies have revealed that the statocyst epithelia of *Praunus* are
tilted. This finding, first reported by Bethe (1895) but until now overlooked, provides
an essential key to the interpretation of the eyestalk responses of mysids with only one
intact statocyst. In addition, an interesting comparison can be drawn between the
statocyst geometry of mysids and that of decapod crustaceans (Schöne, 1952), for the
two systems differ with respect to both the magnitude and the direction of tilting of
the organs.

(2) A linear relationship is maintained between the initial shearing stimulus on the
sensory hairs of one statocyst and the final movements of the eyestalk. This finding
has facilitated the use of eyestalk data in an analysis of bilateral statocyst interaction,
which in turn has revealed that the two statocysts of *Praunus* co-operate in their
action at all body positions through a simple summation of their afferent signals
(Fig. 4).

(3) A given shearing stimulus (i.e. medial or lateral) over the sensory epitheliatis of
the two statocysts produces opposite turning reactions (Fig. 3). This finding is con-
sistent with the observed polarization of sensory elements in the *Praunus* statocyst
(Debaisieux, 1949; personal observation), and with our current understanding of the
mechanism of transduction in crustacean statolith hairs (Schöne & Steinbrecht, 1968).

(4) The bidirectional input to the statocyst control system (i.e. the shearing stimu-
lus, Fig. 3) is converted into an essentially unidirectional output (i.e. the eyestalk
movements, Fig. 4). This conversion is represented in the vertical displacements of
the eyestalk curves in Fig. 4, but these shifts, being symmetrical, in no way affect the
arithmetical treatment of the eyestalk data.

The consistent rolling of the free-swimming mysid to the injured side, observed immediately after the ablation of one statocyst, is a further expression of the unilateral turning tendency released by the remaining balance organ. Similar initial turning follows the removal of one balance organ in decapod shrimps (Schöne, 1952) and in fish (von Holst, 1950), and its basis has been expressed by these authors as unmatched firing from sensory receptors of the remaining intact organ. Some support for this idea comes from the electrophysiological demonstration of a continuous resting discharge in the utricular receptors of elasmobranch fish (Lowenstein & Roberts, 1950) and in the statocyst receptors of the lobster (Cohen, 1955). Preliminary studies (Neil, 1972) suggest that there is also continuous firing in mysid statocyst units. It has also been shown that during rotation of the organ about the longitudinal axis the resting discharge increases for a lateral shear of the sensory hairs (and of the majority of utricular hair cells) and decreases for a medial shear. Thus it is possible to interpret the behavioural response of a fish or crustacean during body rotations in terms of a modulation of the continuous discharge from the statocyst receptors by the shearing stimulus. The precise changes in turning tendencies released by the two organs for a given body tilt are determined by the particular geometries of the fish, decapod and mysid statocyst epithelia (Fig. 9).

The scheme in Fig. 9 corresponds closely to the one discussed by Schöne (1959), but differs from previous interpretations (von Holst, 1950; Schöne, 1952) in that 'spontaneous' and 'reflex' component turning tendencies are replaced by a single turning component, the magnitude of which is modulated by shear. The single turning component generated by one statocyst is always in one direction, but this appears as a unidirectional eyestalk response only if the opposite cyst is completely ablated (Fig. 10). If the lith of one statocyst is removed, but the organ otherwise left intact, as in the experiments of Schöne (1954), the continuous discharge from the lith hairs of the empty sac produces an opposite turning tendency, upon which the modulated output of the intact organ is superimposed. The final eyestalk response is therefore bi-directional (Fig. 10, dashed curve). Complete cyst ablation was the only procedure employed in the experiments on *Praunus* reported here because it proved difficult to remove the secreted lith without also tearing away the sensory hairs from the epithelium. The inherent unidirectionality of the signal from the remaining statocyst is therefore revealed in the eyestalk responses of unilaterally deficient mysids (Fig. 4).

The function of tilted statocysts

The difference in the geometry of the statocysts of mysid and decapod crustaceans raises interesting questions concerning the functional significance of such tilted arrangements. In *Praunus* each statocyst epithelium makes an angle of 55° with the transverse body axis in a manner which imparts a medial bending force on the statolith hairs when the mysid is in an upright position. In *Palaemonetes* the statocyst epithelia make angles of 30° with the transverse body axis, imparting lateral bending on the lith hairs when the animal is on an even keel. The different tilt directions of the sensory epithelia in the two groups lead to different strengths of turning tendency in the upright body position (Fig. 9), and to different phase shifts of the eyestalk response curve when a given statocyst is removed (Fig. 11*b*, *c*). The different tilt magnitudes result in different ratios between the amplitude of the eyestalk response of an intact
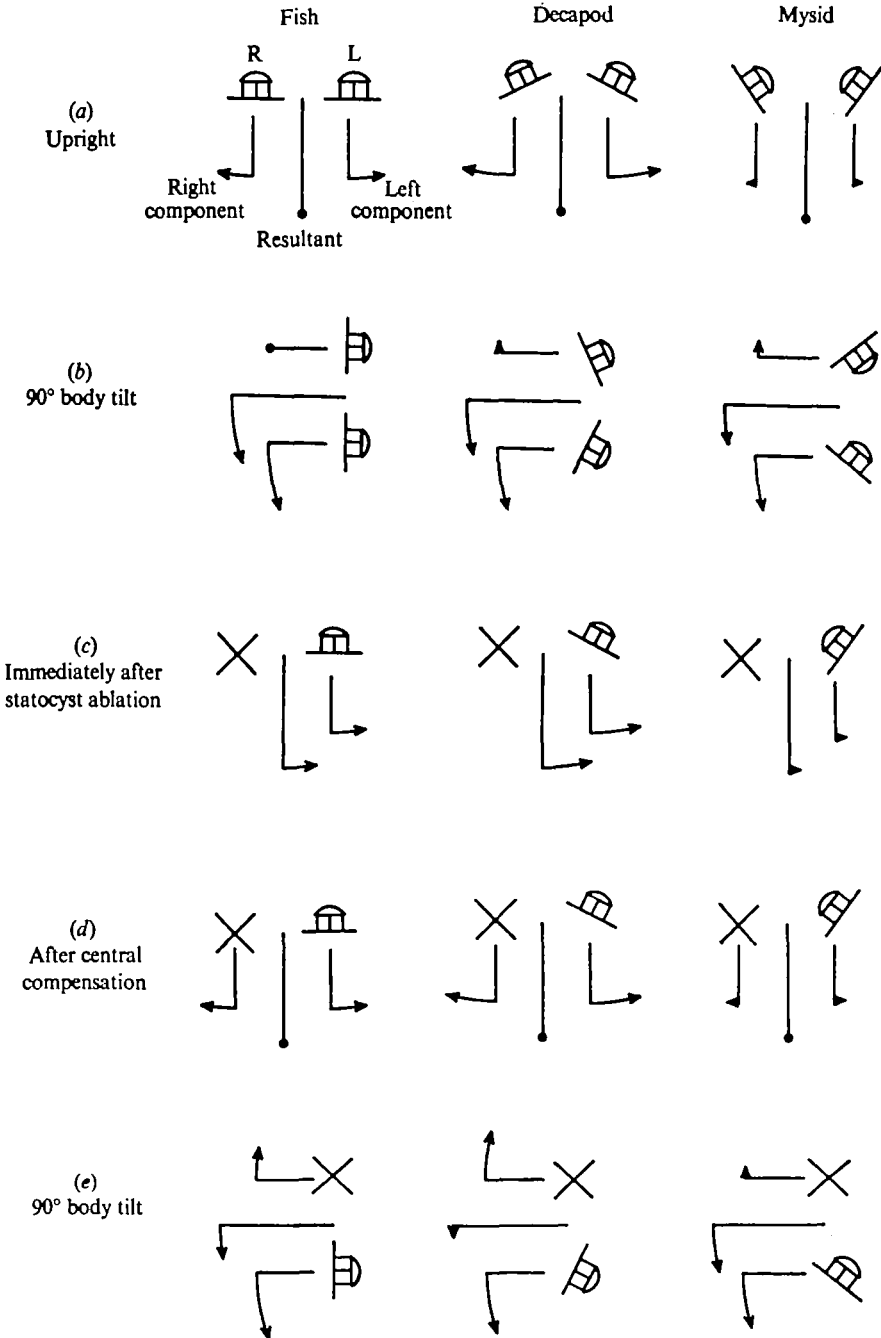
Fig. 9. For legend see facing page.

animal (i.e. resultant turning tendency) and that of a unilaterally deficient one (i.e. component turning tendency) (Fig. 11 b, c). However, more significant than these differences themselves is the fact that any functional advantage conferred by the tilted statocyst arrangement cannot depend on the particular direction of tilt of one organ◄
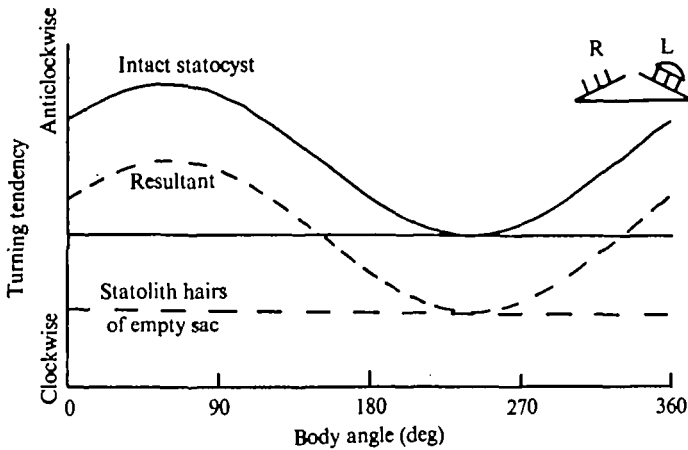
Fig. 10. The basis of the bidirectional eyestalk response in decapod crustaceans after removal of one statolith. The constant turning tendency generated by discharge from the sensory hairs of the empty sac (dashed line) summates with the unidirectional turning tendency released from the remaining organ (solid curve) to produce a bidirectional resultant (dashed curve) (after Schöne, 1959).

which is different in the two crustacean groups, but must be a consequence of the bilateral opposition of tilting between the organs.

Opposed tilting should enhance the response to pure roll, since at all body positions there is always one organ in its region of maximum sensitivity (Fig. 11*b, c*). In addition, the phase-shifted outputs of the two statocysts may improve responses to 'mixed' tilts, e.g. a roll imposed upon an initial pitch, when changes in both the magnitude and the direction of the shearing force are involved, but the amount of change is relatively small. In these and other ways, mutual tilting may reduce the ambiguities inherent in the responses of individual statocysts to linear accelerations. This is analogous to the way in which the responses of canal thread-hair systems in crabs interact to provide unambiguous information about angular accelerations (Sandeman & Okajima, 1972).

The utricular control systems of fish and other vertebrates with horizontal utriculi can also be represented by a breakdown of the resultant turning tendency into components arising from the two balance organs (Fig. 11*a*). During body rotation the

Fig. 9. Diagrams showing the turning tendencies which contribute to the control of equilibrium in fish (left column), decapods (middle column) and mysids (right column). The statocysts are shown in transverse section to indicate the orientation of the sensory epithelia. The sign and strength of the resultant turning force (central vector) and the component turning tendencies are expressed in the direction and the length of the arrows. The turning tendencies released from the two statocysts are directed to opposite sides (a clockwise turning tendency from the right organ, an anticlockwise turning tendency from the left organ), and their strengths are modulated by the shear forces acting on the statocyst epithelia. Different stimulus conditions are shown in rows (*a*)–(*e*). (*a*) In the upright body position opposed tilting of the statocysts (decapod and mysid) introduces a modulation of the statocyst signals. (*b*) At 90° body tilt the magnitude of the resultant turning tendency depends on the statocyst geometry. (*c*) Immediately after removal of one organ there is a turning reaction to the injured side. (*d*) Several days after the operation the inappropriate turning tendency is counteracted by a central compensatory discharge. (*e*) For the centrally compensated animal, the resultant turning tendency at 90° body tilt differs from that of the intact animal (row *b*) because the central compensatory discharge is independent of body tilt.
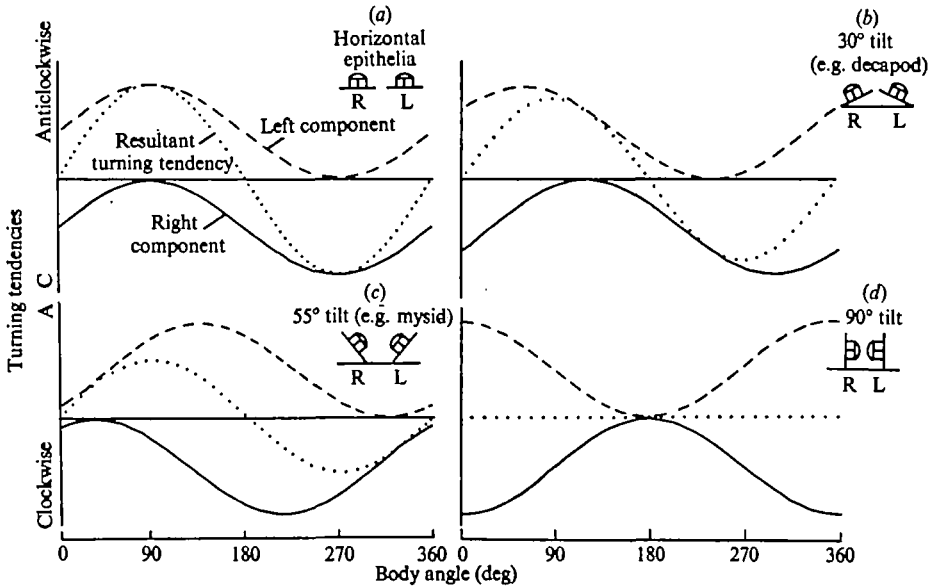
Fig. 11. Component and resultant turning tendencies produced by statocyst systems with different tilted arrangements. The magnitude of the tilt determines the relationship between the amplitude of a component curve (——— for that elicited by the right statocyst, – – – for the left statocyst) and that of the resultant (· · · ·). (a) No tilting, i.e. both statocyst epithelia are horizontal when the animal is upright. The component curved lie in phase, and the resultant is twice the size of a component. This arrangement is found in fish and other vertebrates with horizontal utricular maculae. (b) Statocysts tilted by 30°. The resultant curve is centred about the major body axes, and is greater in amplitude than a component. The decapod crustacean arrangement is represented, with the hairs of both statocysts subjected to lateral bending in the upright body position. (c) Statocysts tilted by 55°. The resultant is here only slightly larger than a component, and is again centred about the major body axes. The geometry of the mysid crustacean statocysts is depicted, with medial bending imparted upon the hairs of both organs when the body is upright. (d) Statocysts tilted by 90°. A system which operates in a manner similar to those of vertebrates and crustaceans would not signal changes in body position relative to gravity, because the resultant turning tendency would be zero at all body positions.

shearing stimuli on the horizontally disposed utricular maculae produce turning tendencies which are coincident in phase. The resultant turning reaction therefore has exactly twice the amplitude of a component. An analysis of the other extreme condition, in which both statocyst epithelia are perpendicular to the transverse body axis is shown in Fig. 11 (d). Such a system, if it involved the same bilateral interactions as found in vertebrates and crustaceans, would not generate equilibrium responses because the resultant turning tendency would be zero at all body positions. It is possible that different patterns of receptor polarization and central connexions could generate appropriate turning reactions, but so far no statocyst system with perpendicular maculae has been found to rely on shear magnitude. Such a geometry is found in the statocyst of *Octopus* (Young, 1960), but in this case the effective stimulus is the direction, not the magnitude, of the shear force (Budelmann, 1970).

Central compensation

The phenomenon of central compensation, which counteracts the inappropriate turning tendency of the unilaterally deficient animal, has been demonstrated in fish (von Holst, 1950) and in decapod crustaceans (Schöne), 1954) as well as in mysids,
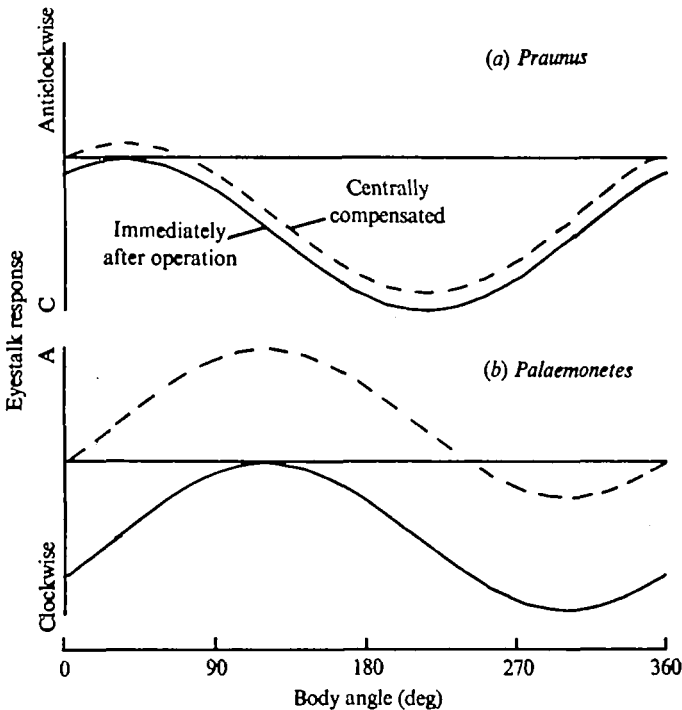
Fig. 12. Comparison of the effects of central compensation on the form of the eyestalk responses of (*a*) *Praunus* and (*b*) *Palaemonetes* after left statocyst loss. These eyestalk responses immediately after the operation (——) are compared with those several days later, after central compensation has occurred (– – –). (Data for *Palaemonetes* from Schöne, 1954.)

In terms of the scheme presented in Fig. 9 central compensation represents the appearance of a constant turning tendency to the intact side which balances out that generated by the continuous discharge of the remaining organ. Therefore, this turning reaction is formally similar to the one produced by continuous discharge from an empty statocyst sac (Fig. 10). From the differences in their statocyst geometry it can be predicted that the central compensatory turning tendencies of fish, decapods and mysids will differ in magnitude. Such differences, however, await direct demonstration.

The function of the central compensatory process in intact animals may be, as suggested by Schöne (1954), to correct for inbuilt asymmetries such as unequal lith size, so that the upright position is held more accurately. Indeed, central compensation for unilateral statocyst removal in crustacea seems to operate specifically with reference to the upright. In bringing the eyestalk and other appendages back to their symmetrical positions in the upright body position, central compensation causes a displacement of the eyestalk responses at all angles of body tilt (Fig. 12). However the eyestalk responses which then occur at large body tilts are to some extent inappropriate as equilibrium responses. It is clear then that central compensation does not involve a complete return to the intact condition, but rather a balance of turning tendencies, and that it is meaningful only with reference to the upright position. This is functionally appropriate because the animal most often has to correct for small deviations from an even keel.

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