

EYE MOVEMENTS OF THE CRAB *LEPTOGRAPSUS VARIEGATUS* ELICITED BY IMPOSED LEG MOVEMENTS

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SUMMARY

1. The horizontal component of eyestalk movements elicited by moving the legs of blinded crabs is described.

2. The animals' bodies were fixed to a stand and the legs were supported on either a sphere or platform and subjected to movement around the three major axes (yaw, pitch, and roll). Both sinusoidal and stepped movements of the legs were studied.

3. The effect of moving the legs on one side only, homolateral or contralateral to the eyestalk was also studied.

4. The eyestalk excursion elicited by sinusoidal leg excursion around the vertical axis (yaw) is a nearly linear function of the leg excursions over the range of 1-40° peak to peak at 0.1 Hz. The amplification of the system is about 0.4 when the animal's legs are supported on a ball, and 0.8-1.0 when the legs are supported on a platform.

5. The frequency response of the system to yaw is nearly flat for eye excursions of 16° peak to peak, over the range of 0.005-0.1 Hz.

6. The visual system has a powerful braking effect on the eye rotation, when this is generated by the imposed leg movements.

7. Eyestalk responses to yaw can be interpreted to be compensatory in that they stabilize the eyes in space in freely moving animals.

8. Eyestalk movements to pitch and roll are complex. In roll, their horizontal component indicates the presence of considerable rectification in the leg proprioceptor-eye system.

9. The functional significance of the eyestalk movements in the horizontal plane is discussed.

INTRODUCTION

The stalk-eyed crustaceans exhibit characteristic eye movements when they turn or are turned about their vertical axis. These eye movements consist of a slow or 'compensatory' phase, during which the eyes remain stationary relative to the environment, and a rapid phase (saccade) in which the eyes are moved quickly in the same direction as the body rotation.

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Eyestalk movements in the horizontal plane in the spiny lobster and in the crayfish are known to be evoked by the visual system (the optokinetic response), and by proprioceptors in the legs (Dijkgraaf, 1956; Mellon & Lorton, 1977; Olivo & Jazak, 1979, 1980; Olivo & Mellon, 1980). In crabs, eyestalk movements are similarly produced by the visual and the leg proprioceptive inputs (Dijkgraaf, 1955) but also by the statocysts (Dijkgraaf, 1955; Sandeman & Okajima, 1972; Janse & Sandeman, 1979).

Horizontal eye movements controlled by the visual input are well described in the Australian rock crab, *Leptograpsus*, and consist of the usual optokinetic responses as well as scanning movements of the eyes in freely walking animals (Sandeman & Erber, 1976; Sandeman, 1978). The eye movements produced by the leg proprioceptors have not been investigated in *Leptograpsus*. We report here the nature of the horizontal component of the eye movements produced by moving the legs of these animals in the absence of inputs from the eyes and statocysts.

MATERIALS AND METHODS

Crabs with carapace widths ranging from 30 to 42 mm were caught on the rocky shores of the New South Wales coast near Bateman's Bay, and kept in the laboratory in a circulating sea water aquarium. Before using an animal for an experiment it was induced to autotomize its chelae.

The experiments involved measuring the horizontal component of eye movements of blinded animals fixed in a stand so that their legs rested either on a polystyrene ball, or a platform, which was rotated about the vertical, transverse or longitudinal axis of the animal (yaw, pitch and roll, Fig. 1).

The animals were blinded by covering the corneal surfaces of their eyes with a water soluble opaque paint, designed for retouching photographic plates (Kodak opaque). In animals which are able to see, leg movements elicit very small eye movements. By comparing the size of the responses in the dark with those in light, we could test for complete occlusion of the visual system before starting a series of experiments.

Eye movements were measured with a capacitive sensing device which requires a light-weight wand to be cemented to the eye (Sandeman, 1968). The wands we used were thin glass tubes (less than 0.3 mm outside diameter, 36–47 mm long) containing a fine silver wire, and weighing at the most 0.005 g. They were glued to the tops of the crab's eyes so as not to impede the eye movement in any way.

The transducer was calibrated for each experiment by correlating its voltage output with an observed excursion of the wand against a millimeter scale placed beneath it. Errors in the measurement of the eye excursion could have been introduced, because the proximal end of the wand did not always exactly intersect the axis of rotation of the eye. This error can be calculated to amount to a maximum $\pm 5\%$ for a 2 mm offset of a 40 mm-long wand, and is too small to affect the interpretation of our results significantly.

The ball (10 cm in diameter), or the platform (16 cm across) on which the animal rested its legs was driven sinusoidally at different frequencies and amplitudes by a

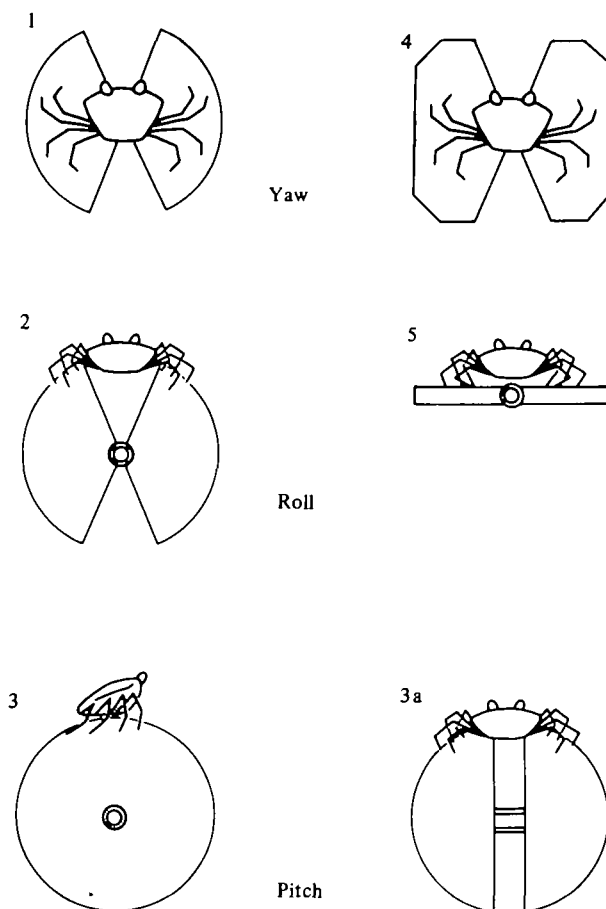


Fig. 1. The various stimulus situations used to evoke horizontal eye movements in the crab. The animals are shown from above (1, 4); from the side (3); and from behind (2, 3a, 5). Unilateral stimulation was achieved by moving one half of the divided ball (1, 2, 3, 3a) or platform (4, 5) while holding the other half still. The axis of rotation is perpendicular to the plane of the drawing in all cases but one (3a).

electric motor and an eccentric wheel. The movements of the ball or platform were monitored with a potentiometer and registered simultaneously with the eye movements on a chart recorder.

In some experiments the legs of one side rested on a fixed platform, or half ball, while the legs of the opposite side were moved. Stepped changes of the ball or platform position were made by hand.

In most experiments, the frequency of oscillation of the ball or platform was not intentionally varied, and was set at the beginning of each session to 0.1 Hz. During the course of the experiment however, the frequency drifted away from the preset value and had to be adjusted. In the following text, therefore, 0.1 Hz means that the frequency of oscillation lay between 0.07 and 0.14 Hz.

Throughout this paper we refer to the eye movements being 'in phase' with the legs when the horizontal component of the angular displacement of the eyes is in

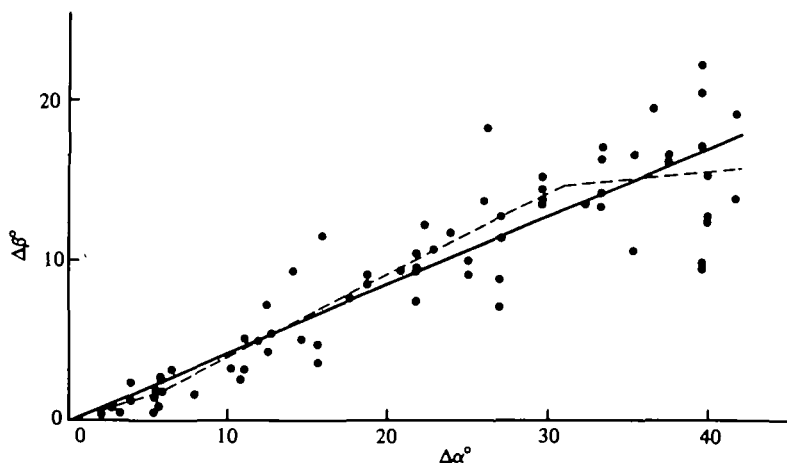


Fig. 2. The excursion of the eye ($\Delta\beta$) plotted against the excursion of the legs ($\Delta\alpha$) which were supported on a ball and oscillated around the vertical axis (yaw) at a frequency of 0.1 Hz. The solid line represents the linear regression fitted to all the points. The broken lines represent the linear regressions fitted to the points over the ranges $\Delta\alpha = 1-10^\circ$; $10-30^\circ$; $30-40^\circ$.

the same direction as that of the legs, and in 'antiphase' whenever the eyes move in the opposite direction to the legs. By 'phase lead' we mean that for a maintained sinusoidal oscillation of the legs, the eye reaches its maximum angular excursion ahead, in time, of the legs. 'Phase lag' means that the eyes reach their maximum angular excursion after the legs.

The amplitudes of the eye excursions were obtained by measuring the subsequent peak to peak differences in the recordings. These were averaged and the result plotted as a single point in the graphs in Figs 2-4 and 6. About 15 measurements were obtained in one run, and the variance was typically 10-20%. For the lower frequencies (Fig. 6) the points represent fewer measurements (a single cycle for 0.001 Hz) because of the relatively long times needed to complete a single cycle.

RESULTS

(1) *Rotation about the vertical axis (yaw)*

The movements of the legs relative to the body induced by yawing the supporting ball or platform may be compared with those occurring when the freely moving animal turns itself about its vertical axis. The imposed motion at the tip of each leg is restricted to the horizontal plane regardless of whether the animal rests on a ball or a platform.

(a) *Sinusoidal movements of the ball.* The eyes of a blinded animal move in phase with the legs when these are oscillated about the vertical axis at 0.1 Hz with a peak to peak excursion of 2-40°. The eye response is approximately linearly related to the stimulus amplitude over this range, the amplification (i.e. the slope of the regression line in Fig. 2) being 0.43 on the average.

The relationship between the peak to peak leg excursion ($\Delta\alpha$) and the eye excursion

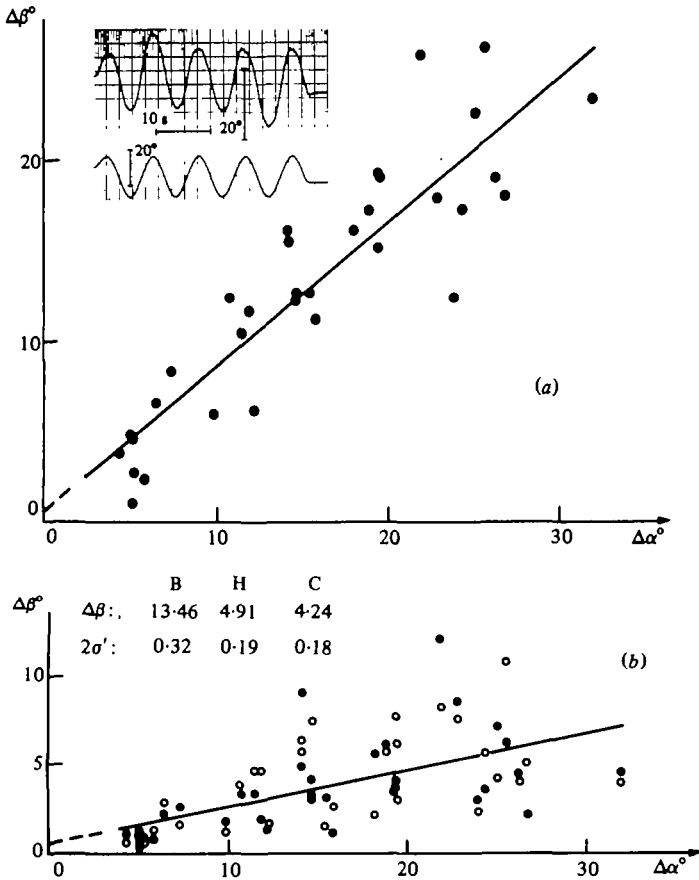


Fig. 3. The response of the eye ($\Delta\beta$) to yaw of the legs ($\Delta\alpha$) supported on a platform. (a) Both legs oscillated. The solid line represents the linear regression fitted to the points and its slope gives the amplification (0.8) of the system. The inset shows a sample of the recordings of the eye response (upper trace) and the platform excursion (lower trace). Positive going (upward) traces of the response correspond to rotation of the monitored eye toward the animal's right side. This convention holds for all figures. Positive going (upward) traces of the stimulus correspond to clockwise rotation of the substrate (as seen from above) around the vertical axis (yaw). (b) The legs of only one side oscillated. Filled circles represent the response of the eye when only the legs homolateral to it are oscillated, \circ , when only the contralateral legs are oscillated. The solid line represents the linear regression fitted to all the points. The amplification of the system when driven unilaterally from either side is reduced to about 0.2. The Table contains the average values of $\Delta\beta$ for 4 different animals where $\Delta\alpha$ remained at 15° and the frequency was about 0.1 Hz. (B: legs on both, H: on the homolateral, C: on the contralateral side moved). The data in the table represent the total of more than 400 amplitude measurements. ($2\sigma'$ denotes the twofold standard deviation of the means.)

($\Delta\beta$) might be represented more accurately by fitting three separate line segments to the points in Fig. 2 over the ranges of $\Delta\alpha$ values $0-10^\circ$, $10-30^\circ$, $30-40^\circ$. Together these three segments now resemble the course of a slightly sigmoid curve, but the fit is not significantly improved.

(b) *Sinusoidal movements of a platform.* When the legs are supported on a platform the eye responses are also in phase with the leg movements, for oscillations of about 0.1 Hz and over peak to peak leg excursions of $4-30^\circ$ (see inset in Fig. 3a).

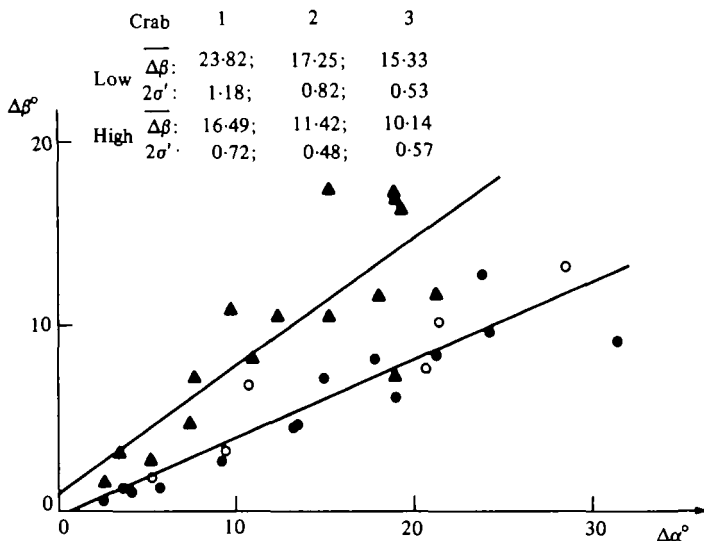


Fig. 4. The response of the eye ($\Delta\beta$) plotted against the excursion of the legs ($\Delta\alpha$) supported on either a ball or a platform and rotated about the vertical axis (yaw). The animal was first placed on the ball (●) then on the platform (triangles) and then back on the ball (○). The slopes of the regression lines give the amplification of the system. On the platform this is 0.68, and on the ball 0.42. The table contains the results of an experiment in which three different animals were supported at different distances above the platform which rotated their legs about the vertical axis (yaw). $\Delta\alpha$ was kept constant at 16° . $\Delta\beta$ is always larger when the animal is closer to the platform. ($2\sigma'$ denotes the twofold standard deviation of the means.)

The linear relationship between the leg displacement and the eye response persists but the amplification is significantly increased to about 0.8 on average (Fig. 3*a*).

To confirm the above result and control for differences between animals, the experiments were repeated and two animals were tested first on the ball, then on the platform, and then again on the ball. The result (Fig. 4) clearly indicates that the amplification of the system is consistently higher when the animal stands on the platform instead of the ball.

The essential difference in the two situations is that the legs are more extended when the animal is supported on the ball: the joints between the merus and the carpus are opened, and the merus is lower in relation to the body (Fig. 5).

The legs can be similarly flexed or extended by raising or lowering the platform and the possibility that the amplification is influenced by these postural changes has been tested in this way. It should be noted that raising the animal usually causes it to move the tip of the legs nearer to the axis of rotation of the platform. The distance between the ventral surface of the animal and the platform was set to a minimum of about 5 mm, and a maximum of between 25 and 27 mm. The excursion of the platform ($\Delta\alpha$) was kept at 16° and the frequency held at 0.1 Hz.

The results from three separate animals (five runs each) are given in the table in Fig. 4 and show that when the body of the animal is close to the platform the amplification of the system is significantly increased.

The conclusion which can be drawn from these experiments is that the amplification

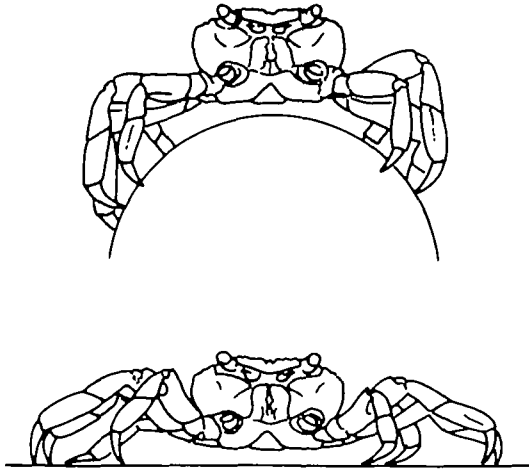


Fig. 5. Differences in the geometry of the legs of a large crab which stands on a ball and on a platform. (Traced from photographs.)

of the response is affected by the positions of the leg segments in relation to each other and to the body.

Our photographs show that all the joints are affected when the ball is replaced by the platform, or when the platform is raised or lowered, and at this stage we cannot assess whether the result is due to an integrated effect of all the joint receptors or whether it is caused primarily by one particular set of receptors which are differently stimulated if the geometry of the legs is changed.

(c) *The effect of unilateral leg movements.* In these experiments the legs of each side were supported on separate platforms which could be rotated independently so that the legs contralateral or homolateral to the monitored eye moved while those on the opposite side remained stationary. Coupling the platforms together allowed the movement of all the legs as before. The experiments were carried out in the following sequence:

- (1) Contralateral legs oscillated, homolateral legs stationary.
- (2) Both contralateral and homolateral legs oscillated.
- (3) Contralateral legs stationary, homolateral legs oscillated.

The measurements were then repeated in the reverse order, i.e. 3, 2, 1 and so on for $\Delta\alpha$ values ranging from 4° to 30° and at a frequency of 0.1 Hz. The results (Fig. 3b) show that the eye response ($\Delta\beta$) and the slope of the regression lines (amplification) are about the same, no matter whether the contralateral or homolateral legs are moved. However, the amplification of the system with unilateral leg stimulation is 0.21 compared with the 0.8 amplification obtained with bilateral stimulation.

To establish the above phenomenon more securely, the experiments were repeated with $\Delta\alpha = 15^\circ$ and the oscillation frequency kept as before at 0.1 Hz. Five runs (contralateral; both; homolateral) each with four separate animals, yielded the results in the table in Fig. 3(b) and confirm that the legs of one side are less than half as effective as those from both sides in eliciting the eye movements. The explanation of this phenomenon requires further investigation and at this stage we

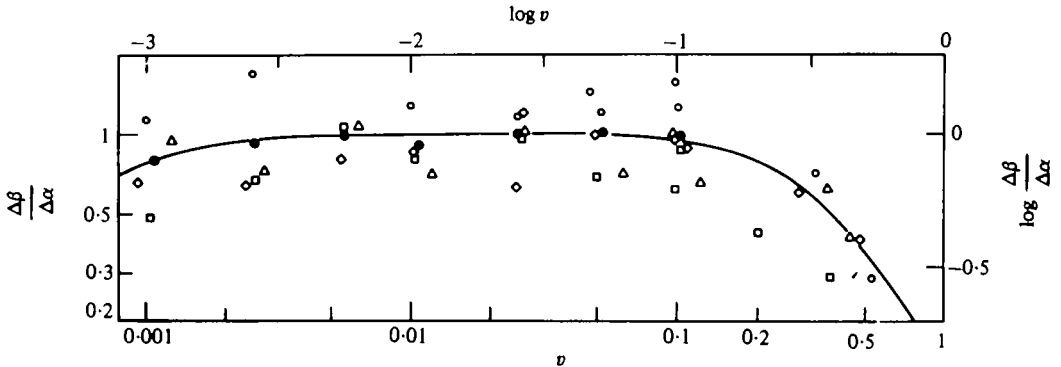


Fig. 6. The frequency response of the system to oscillation of the legs about the vertical axis (yaw). The amplification ($\Delta\beta/\Delta\alpha$) is plotted against the frequency of the platform oscillation. The data were obtained from four different animals. Solid circles are the average values for points occurring at one mean frequency. The solid line represents the amplitude/frequency response of a band pass filter containing a first order high-pass, and a second order low-pass filters in tandem, with time constants of 200 s and 0.42 s respectively. The amplification of the crab leg-eye system is about 1 over a broad range of frequencies.

can only suggest that either the stationary legs exert an inhibitory influence, or that the signals from either side enhance one another. Also in these experiments, the legs homolateral to the monitored eye are marginally more effective than the contralateral legs, in producing the eye movements.

(d) *Frequency responses.* The results above show that the leg-eye reflex may stabilize the eyes relative to the environment within a large range of active body turns about the vertical axis. To serve this purpose, the reflex also needs to be effective over a reasonably wide range of angular velocities. We therefore measured the dependence of the system on the frequency of platform oscillation. We were limited to an upper frequency of about 0.5 Hz by our apparatus. Our lower frequency limit was set by the length of time the animals would remain still. Thus oscillation frequencies ranged from 0.001 to 0.5 Hz and the peak to peak excursion was kept constant at between 14° and 16° . Each frequency run was covered in a single session, finishing with a repeat of the first used frequency to control for trends. At the lowest frequencies the run was limited to one full period (1000 s). The curve is flat over a range from about 0.005 to 0.1 Hz (Fig. 6) and the amplification $\Delta\beta/\Delta\alpha$ is approximately 1 within this range.

The upper frequency limit set by our apparatus prevents us from making accurate statements about the filter properties of the system. Also, the low frequency portion of the curve could not be well established, due to the long duration of a single period. Nevertheless at 0.001 Hz there is apparently a real decrease in the response. The continuous curve is the amplitude frequency response of a band-pass filter, consisting of a first order high-pass filter with a time constant of 200 s, and a second order low-pass filter with a time constant of 0.42 s, in tandem (Fig. 6).

In experiments in which we measured the eyestalk responses to changes in the frequency of leg oscillations, we found no significant changes in the phase between the stimulus and response. Considering the flat amplitude frequency curve, this

to be expected for the frequencies we used. A possible source of phase lag in the system, that of a fixed delay due to latency, would be too small to be detectable at such a low oscillation frequency.

(e) *Stepped movement of the platform.* Sinusoidal movement of the legs reveals a relatively slow linear system which operates with high amplification between 0.005 and 0.1 Hz. There is evidence for a more rapid eye movement system in *Carcinus* and *Leptograpsus* linked to the optokinetic system (Sandeman, Erber & Kien, 1975) and related to the eye scanning which occurs when the animals walk (Sandeman, 1978) or struggle when they are suspended (Fleischer, 1980). To explore the response of the proprioceptors to faster movements we abruptly changed the angular position of the platform beneath the animal by hand.

We tested the response of the animals with the following stimuli, applied to the legs relative to the monitored eye:

- (A) Homolateral legs rotated backwards.
- (B) Homolateral legs rotated forwards.
- (C) Contralateral legs rotated forwards.
- (D) Contralateral legs rotated backwards.
- (E) All the legs rotated clockwise.
- (F) All the legs rotated counterclockwise.

Sample records of the eye movements are shown in Fig. 7 where a number of step responses have been redrawn from the records and superimposed in each trace. In this and subsequent figures responses are shown to stimuli of different size, and recorded with different sensitivities of the plotter. Our conclusions must therefore remain strictly qualitative. Here we show only the responses from the right eye. The conclusions we draw have been verified by monitoring the step responses also from the left eye.

A significant feature of the eye motion is its asymmetry related to the direction in which it moves. The response of the right eye to moving the homolateral legs back, contralateral legs forwards, or both clockwise, is characterized by a fast initial rotation away from the midline. This is followed by a slow movement of the eye either toward or away from the midline. The slow phase of this and subsequently described responses are extremely variable and our sample records do not show the entire spectrum of the eye movements we observed (Fig. 7*a, c, e*).

Responses of the right eye to moving the homolateral legs forward, contralateral legs back, or both counterclockwise are more complex: the movements often (but not always) start with a small, fast rotation of the eye away from the midline. The most consistent part of the responses is a fast movement of the eye toward the midline, followed by the lower variable phase during which the eye can rotate in either direction (Fig. 7*b, d, f*). A comparison of Figs 7(*a, c, e*) and (*b, d, f*) reveals that the fast lateral-to-medial eye movements are about three times slower than the fast medial-to-lateral movements.

Recordings obtained with hand-controlled steps do not allow the responses to be precisely quantified, but we estimate that the amplification during the fast phases is considerably less than 1; values for two animals being 0.2 and 0.1 respectively.

The asymmetry is probably not of sensory origin since it is correlated with the

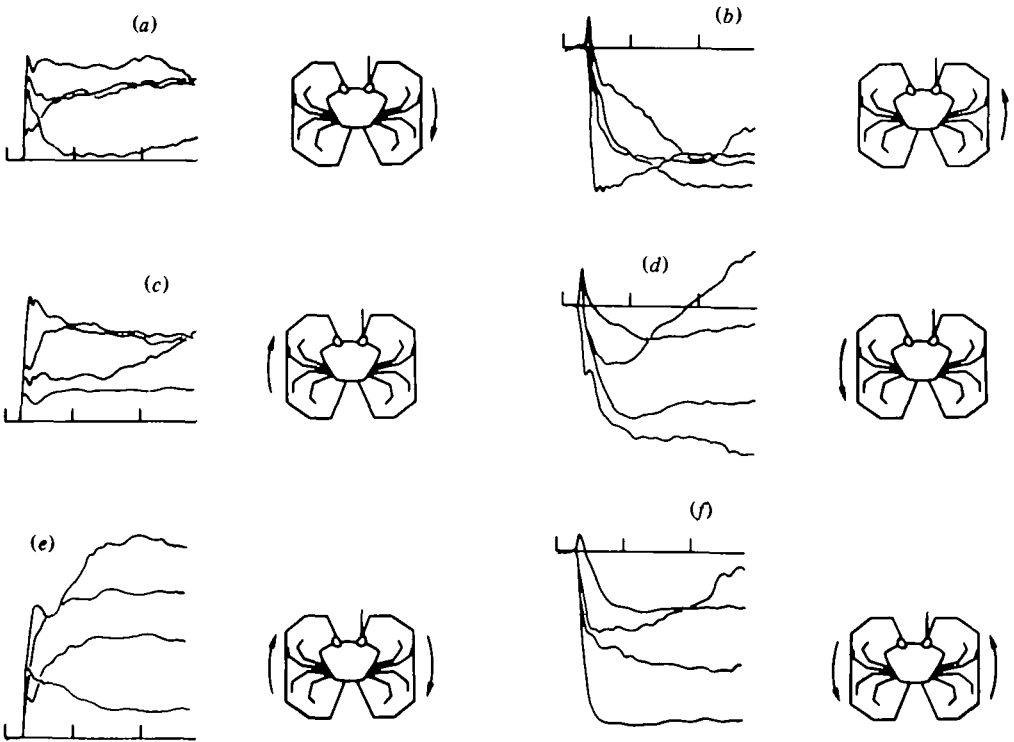


Fig. 7. Eye rotation elicited by stepped movement of the platform around the vertical axis (yaw). The traces are the superimposed recordings of several responses from different crabs. The distance between neighbouring vertical bars along the time axis corresponds to 5 s here and in subsequent similar figures. The six different stimulus situations are symbolized by the pictograms in which the projection of the leg movement in the horizontal plane is indicated by the arrows. The right eye was monitored in each case.

direction in which the eye moves relative to the midline and not with the particular set of legs which are moved. Such asymmetries are also known to occur in the optokinetically evoked eye movements of *Carcinus*. There, the eye movements away from the midline are also faster than those towards the midline, and this is attributed to asymmetries in the eye muscles (Burrows & Horridge, 1968; Sandeman *et al.* 1975).

It may be asked why the asymmetries in the system do not affect the response to sinusoidal stimulation. The explanation lies in the fact that asymmetries revealed by the step stimuli are confined to a rapid component of the response. Thus while the slow system, which is active during the sinusoidal movement, is reasonably linear, the fast system, which we assume to be activated like in *Carcinus* during rapid movements (Sandeman *et al.* 1975), is not.

(f) *The effect of vision on the eye response to leg movements.* In our experimental situation the visual system acted as a powerful brake on the eye movements elicited by rotating the legs, and animals able to see contrasting objects in their visual field showed little or no eye movements in phase with imposed leg movements. If the bright white ambient illumination was changed to dim red light (Ilford safelight

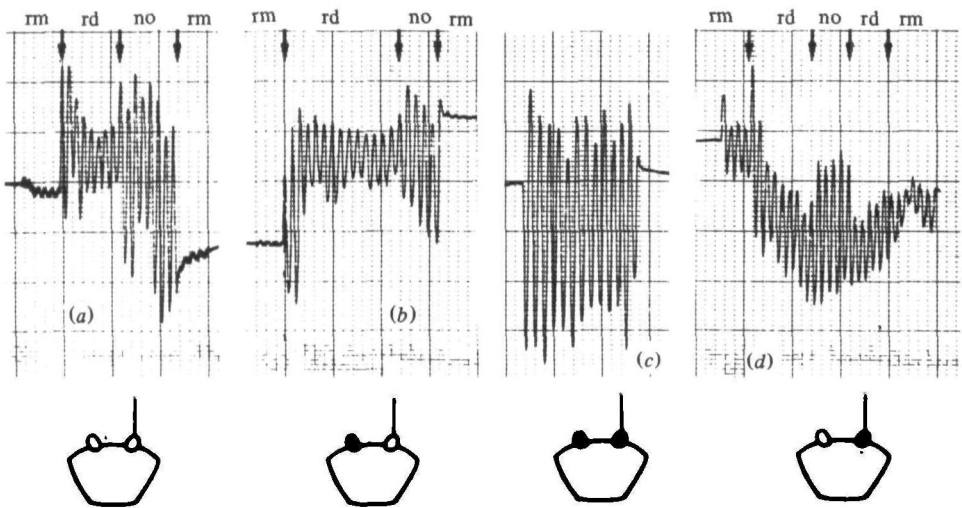


Fig. 8. The influence of ambient light and binding on the eyestalk response to oscillation of the platform around the vertical axis (yaw). In the pictograms, black denotes blinded, and the right eye was monitored in each case. rm = light from an overhead incandescent lamp; rd = light from an incandescent lamp covered with an Ilford filter (No. 4 red); no = lights out. Some light still filtered through gaps around the door in this case, so that the animal was never in complete darkness. Changes in the light conditions during the course of the experiment are marked by arrows. The traces show that light reduces the amplitude of the leg-induced eye movements, and that in the unilaterally blinded animals the visual feedback from an eye has a greater braking effect on its own movement than on that of its contralateral partner.

No. 4), the eye responded to the imposed leg rotation, but as dark adaptation proceeded the optokinetic response again increased and reduced the eye excursion (Fig. 8). Thus the optokinetic input dominates the leg proprioceptive input.

(2) *Rotation about the transverse and longitudinal axes (pitch and roll)*

It has been adequately demonstrated that for both crabs and crayfish, muscles which produce eye movements in the horizontal plane are also active when the animal's body is tilted about the transverse or longitudinal axes (Burrows & Horridge, 1968) or when the legs are tilted about the longitudinal axis (Mellon & Lorton, 1977). Although the response to these stimuli might have stronger components in the vertical plane, the horizontal component is an output and a measure of the leg proprioceptor-eye movement system, and has consequences for the animal, even if it cannot be interpreted as compensatory in the same sense as the movements elicited by rotation of the legs about the vertical axis. In the present study we confine ourselves to the horizontal component of the response.

(a) *Simusoidal movement of the ball about the transverse axis (pitch)*. Three different stimulus situations were tested:

- (A) Homolateral legs oscillated.
- (B) Contralateral legs oscillated.
- (C) Legs on both sides oscillated in phase.

The frequency of the ball oscillation was always about 0.1 Hz and the excursion

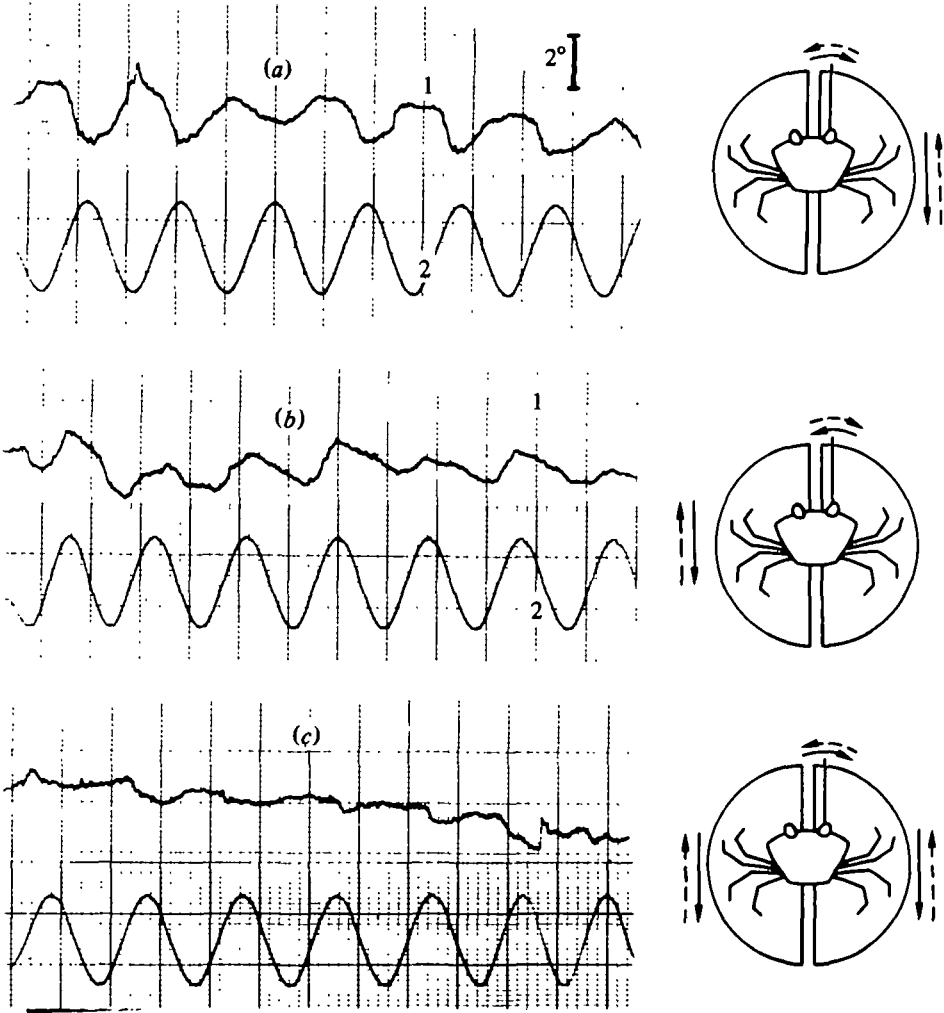


Fig. 9. The responses of the eyestalk (horizontal component) to oscillating the ball supporting the legs, around the transverse axis (pitch). The experimental conditions are illustrated by the pictograms in which the arrows indicate the projection of leg and corresponding eye movements in the horizontal plane. Upper traces: eye response; lower traces: ball excursion. Due to the complex relationship between the angular leg and ball excursion these traces are taken to indicate only the phase relationship between stimulus and response. Upward deflexion of the traces denotes an eye movement to the animal's right side, respectively a forward rotation of the upper surface of the ball. The eye rotates away from the midline if the homolateral legs are moved backward or the contralateral legs are moved forwards. If the legs on both sides are moved simultaneously and in the same direction, little or no eye response occurs, depending on the relative contribution of the legs on either side. ($\Delta\alpha = 19.25$; frequency = 0.1 Hz.) The vertical bar indicates 2° of eye excursion.

varied between 12° and 19° . The excursion of the horizontal eye movements was never more than a few degrees.

Oscillation of the homolateral legs produces the strongest response. The eye moves periodically and in phase with the legs. Thus when the legs move backwards, the eye moves away from the midline (Fig. 9a).

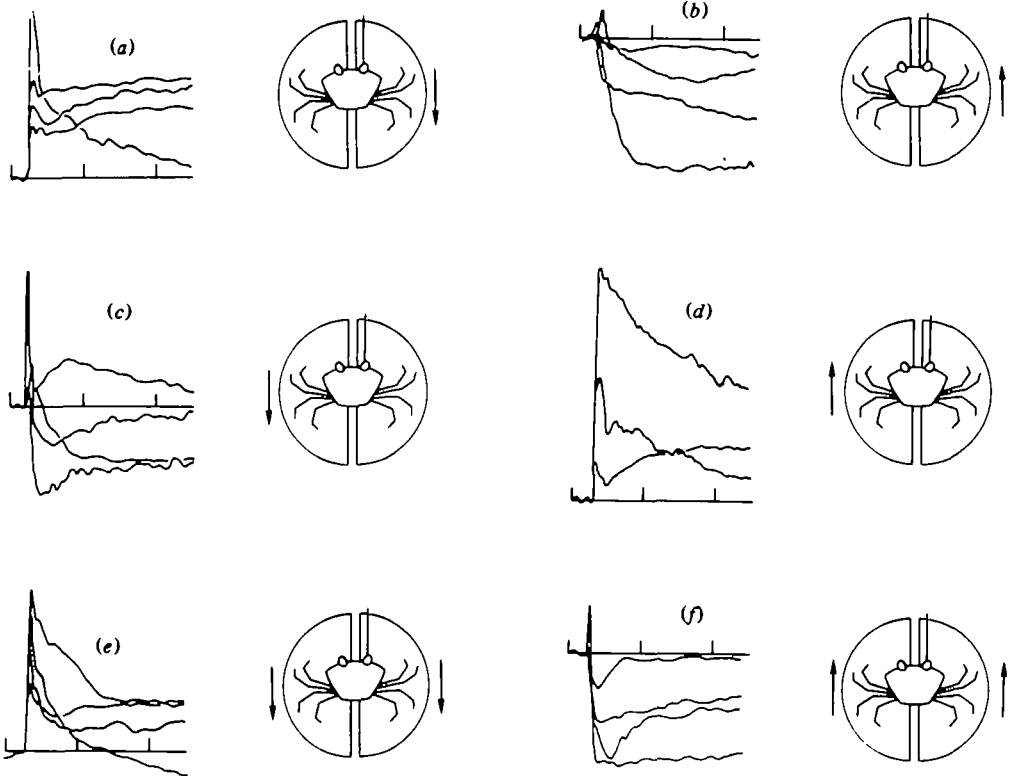


Fig. 10. The response of the eyestalk to stepped movements of the ball supporting the legs, around the transverse axis (pitch). The traces are the superimposed responses from different crabs. Directionalities and pictogram convention as in Fig. 9.

When the contralateral legs are oscillated the eye movements are again in phase with the legs; when the legs move backwards, the eye moves towards the midline (Fig. 9b).

If the legs on both sides are oscillated simultaneously their effects are antagonistic. Either the homolateral input dominates, or the eye movements are too small to be reliably measured (Fig. 9c).

(b) *Stepped movements of the ball about the transverse axis (pitch)*. Step movement of the ball were applied under six different conditions:

- (A) Homolateral legs shifted backwards.
- (B) Homolateral legs shifted forwards.
- (C) Contralateral legs shifted backwards.
- (D) Contralateral legs shifted forwards.
- (E) Legs of both sides shifted backwards.
- (F) Legs of both sides shifted forwards.

The responses have time courses similar to those elicited by rotating the ball around the vertical axis and show the same asymmetry.

Stepping the homolateral legs back produces a rapid movement of the monitored eye away from the midline, followed by a slow and variable movement in either direction (Fig. 10a).

Stepping the homolateral legs forwards results in a bi- or triphasic response. A small fast movement (often absent) of the eye away from the midline precedes a slightly slower movement of the eye toward the midline, which is in turn followed by a much slower movement of the eye in either direction (Fig. 10*b*).

The responses to stimulus situations (C) and (D) are like those to (B) and (A) respectively, except that they are usually weaker. The direction of the eye rotation to stepped movement of the legs is therefore consistent with that obtained with corresponding sinusoidal movement.

Stepping the legs on both sides backwards gives a result which is a mixture of stimuli (A) and (C); stepping the legs on both sides forwards is expected to give a result which is a mixture of the responses to stimuli (B) and (D) (Figs. 10*e, f*). The responses depend on the contribution of the legs of both sides, and here again the homolateral legs usually dominate (cf. Figs 10*a, e* and *b, f*).

(*c*) *Sinusoidal movements of the ball about the longitudinal axis (roll)*. Three different stimulus situations were tested:

- (A) Homolateral legs oscillated.
- (B) Contralateral legs oscillated.
- (C) Legs on both sides oscillated simultaneously.

The results in Fig. 11(*a-d*) show that in all cases the eyes move conjugately and in *antiphase* to the movements of the legs; for example when the ball forces the left legs up and to the right, both eyes move to the left.

(*d*) *Sinusoidal movements of the platform about the longitudinal axis (roll)*. The same three stimulus situations were applied. The responses elicited by tilting the platform are complex and confirm our results obtained in yaw which showed that leg geometry exerts an important control on the amplification of the system.

Oscillating the homolateral legs elicits the same type of response as obtained with the ball in that the eye moves toward the midline when the legs move down, i.e. in antiphase to them. However, when the homolateral legs are pushed above the horizontal on their upward cycle, the response of the eye is much weaker or absent. The result is a truncated or half-rectified sine wave (Fig. 11*e*).

Oscillation of the contralateral legs provides an unexpected result. When the legs are moving downwards, the eye moves in a lateromedial direction. This is opposite to the result obtained with the ball. In addition, when the legs move up above the horizontal during the upward phase of their cycle, the eye does not respond. The result is again a truncated sine wave and if anything the 'rectification' is more marked with the contralateral than with the homolateral legs (Fig. 11*f*).

Oscillation of the legs on both sides at the same time can be expected to, and does, elicit a bizarre response. Sometimes the eye movement is either very similar to that when only the homolateral legs are stimulated, and has the same basic frequency as the stimulus but also contains higher harmonics (Fig. 11*g*). The homolateral leg appears to dominate. When the homolateral and the contralateral legs both contribute to the response in an equivalent manner, the two truncated sine waves (which are in antiphase) add to one another and the eye moves back and forth at twice the frequency of the platform oscillation (Fig. 11*h*).

At the same time, oscillation of the legs elicits a DC shift in the eye position

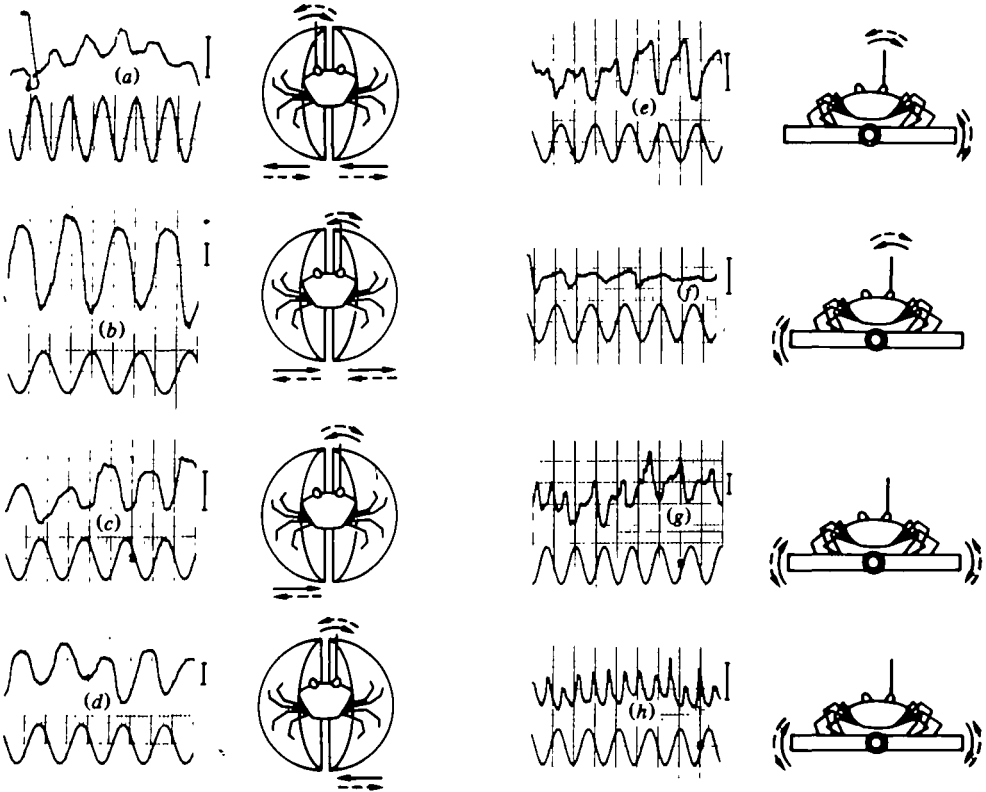


Fig. 11. Responses of the eyestalk to oscillating the ball or platform supporting the legs, around the longitudinal axis (roll). The pictograms symbolize the stimulus situations. The arrows indicate the projection of the leg movement in the horizontal (*a-d*) and in the vertical (*e-h*) plane, and the corresponding horizontal component of the eye movement. Upper traces: eye excursion; lower traces: ball or platform excursion. Upward deflexion of the trace indicates movement of the monitored eye to the animal's right, rotation of the upper surface of the ball to the right, or the right side of the platform down. During oscillation of the ball the eye movements are conjugate and always move in the direction opposite to the ball (*a-d*). Oscillation of the legs of one side with the platform produces a complex rectified signal (*e, f*). When the legs on both sides are oscillated simultaneously on the platform the frequency of the response can be twice that of the stimulus. The bars represent an eye response of $\Delta\beta = 2^\circ$. $\Delta\alpha$ was 12.8° in *a*, 21.5° in *b-d*, and 20.2° in *e-h*. See text for details.

towards the animal's midline. This is best demonstrated with rapid oscillation (0.5 Hz) of the legs on both sides. Examples are shown in Fig. 13. The possible source of this nonlinearity is considered in the discussion.

(*e*) *Stepped movements of the ball about the longitudinal axis (roll)*. Stepped movements about the longitudinal axis of the animal elicit eye movements comparable to those produced by stepped movements about the vertical and transverse axis. The following stimulus situations were tested:

- (A) Homolateral legs moved down and away from the body.
- (B) Homolateral legs moved up and toward the body.
- (C) Contralateral legs moved up and towards the body.
- (D) Contralateral legs moved down and away from the body.

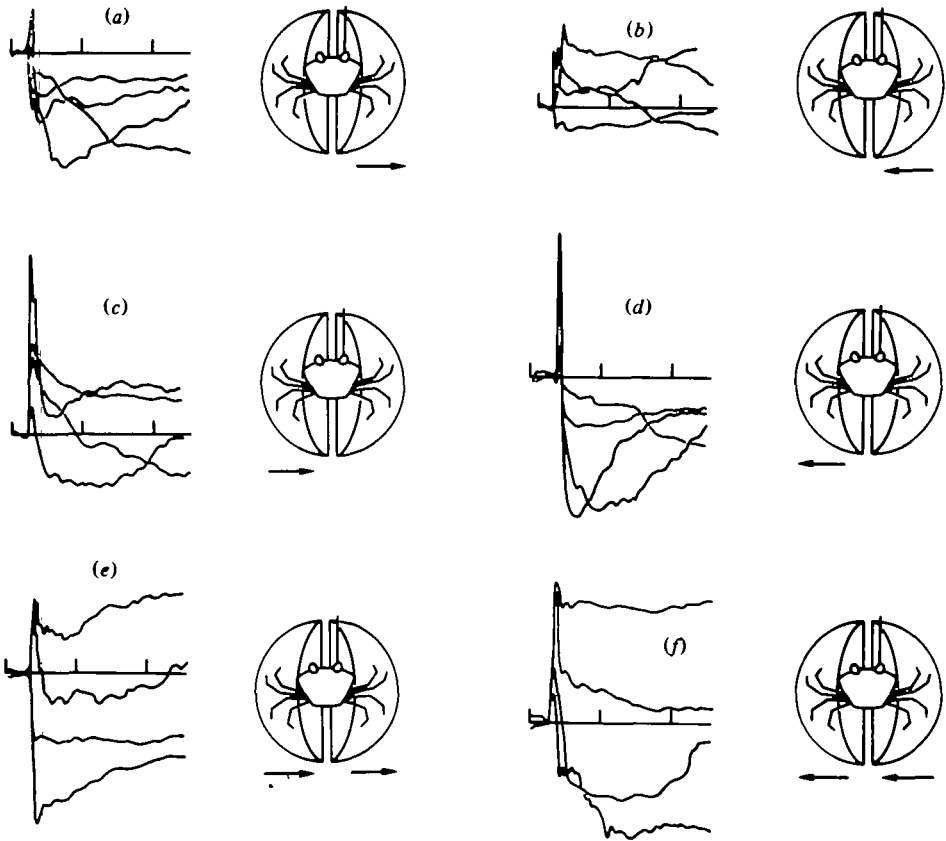


Fig. 12. The responses of the eyestalk to stepped movements of the ball supporting the legs, around the longitudinal axis (roll). Traces are the superimposed responses from different crabs and the pictograms symbolize the stimulus situations (as in Fig. 11 *a-d*). The extremely variable responses can differ qualitatively, especially if the legs on either side are moved toward the body (*b, c*). The responses to moving the legs on either side away from the body are more reproducible; in both *a* and *d* the right eye moves toward the midline. The responses to moving the legs on both sides in either direction are very variable and can differ from time to time in the same animal and from animal to animal (*e, f*).

(E) Both sets of legs moved (homolateral down and away, contralateral up and toward the body).

(F) Both sets of legs moved (contralateral down and away, homolateral up and toward the body).

The time courses of the responses are comparable to those obtained in other step response experiments.

If the homolateral legs are moved down and away from the body there is a fast eye rotation towards the midline, which can be preceded by a short and less extensive eye movement away from the midline. A slow eye rotation in either direction follows (Fig. 12 *a*). The principal part of the response, therefore, is an eye rotation against the direction of the leg movement.

Moving the contralateral legs down and away from the body causes the same

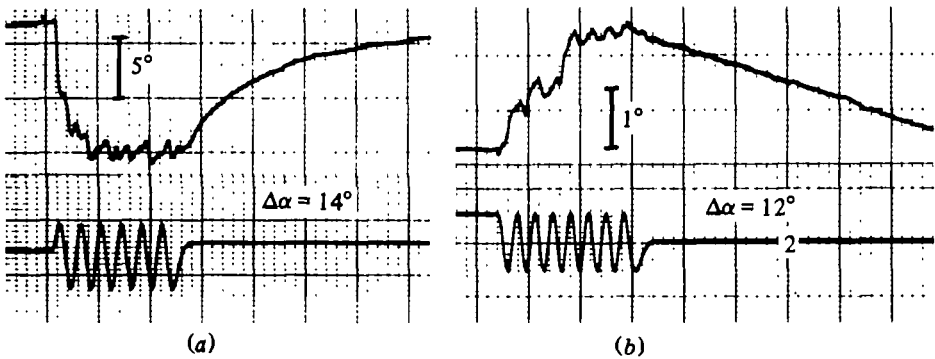


Fig. 13. The platform was oscillated around the longitudinal axis (roll) with a frequency of about 0.5 Hz. In (a) the right eye and in (b) the left eye of different animals were monitored. The main effect of the relatively high frequency oscillation is a DC shift of the eyestalk toward the animal's midline.

type of response (Fig. 12d) except that here the eye moves in the same direction as the legs during the principal part of the response.

If the homolateral legs are moved up and towards the body, in most cases the principal part of the response is an eye rotation away from the midline (Fig. 12b), and again in the opposite direction to the legs.

The same type of responses are obtained while moving the contralateral legs towards the body (Fig. 12c).

Responses to movements of the legs up and towards the body are always significantly more variable than when the legs are moved down and away from the body.

When the legs of both sides are moved simultaneously, one expects a combination of both inputs (which are antagonistic). Since there is often also a dominance of the homolateral input, the responses can be expected to be still more variable than that obtained by moving the legs of only one side, and this is the case (Fig. 12e, f).

In summary, we might conclude that the great variability of these responses is the consequences of the complexity of the stimuli, in which both lateral and vertical movements are combined. As a result a large number of receptors will be simultaneously activated and their relative contributions are probably influenced by changes in the geometry of the legs and also by the state of the animal.

(f) *Stepped movements of the platform about the longitudinal axis (roll)*. The same six stimulus situations used with the ball, were used with the platform. Time courses are qualitatively the same as with the ball. The responses are usually triphasic, the principal part being a fast movement of the eye toward the midline in all cases. This can be preceded by a fast movement of the eye away from the midline and is always followed by a slow rotation of the eye which can be in either direction but which is most frequently away from the midline (Fig. 14a-f).

The angular velocity of the eye rotation toward the midline was always the same regardless of how the legs were stimulated.

DISCUSSION

Three systems control the movements of the eye in crabs: the visual, the statocyst, and the leg proprioceptors. All work to the same end, which is to stabilize the eye position in space. The eye itself has a single feedback controlling its movements, operating through the sensitivity of the visual system to the motion of an image across the retina. The statocyst and the leg proprioceptor inputs are not altered by movements of the eye itself and are therefore open loop systems in this regard. The visual system, because of its feedback, exercises, under proper input conditions, the final control over the eye movements and has received most attention from research workers (Sandeman, 1977). The statocysts because of their easily quantifiable directional properties have also been well investigated as initiators of eye movements (Dijkgraaf, 1956; Sandeman & Okajima, 1972).

(1) *The proprioceptors*

The leg proprioceptors have received less attention as directional inputs to the eye movement system, although studies on the crayfish show them to play a major role in the generation of eye movements in those animals (Mellon & Lorton, 1977; Olivo & Jazak, 1980). Of all the systems, the input from the leg proprioceptors is the most difficult to quantify. The action of the leg proprioceptors alone on the eye movements can be demonstrated easily enough; the visual control is removed by blinding, and the statocyst influence by fixing the animal's body. But the animals have eight walking legs, each leg has six joints, and each joint is known to be monitored by one or more proprioceptive systems (Clarac, 1977). There is also ample evidence from studies on locomotion in the decapods that the leg proprioceptors at each joint, and even for each leg, do not work in isolation. Instead there are complex interactions between the receptors monitoring the joints of each leg, and also between the receptors of different legs (Ayers & Davis, 1978).

In spite of the above complications and the scope for an almost unlimited number of positions in which the legs can be held, moving them in relation to the body produces eye movements which are consistent in their direction for a given leg movement. Some conclusions about the system can be drawn from the experiments we have performed and described in this paper. Changes in the posture for example have a clear effect on that part of the system which transduces leg rotation about the vertical axis to eye movements in the horizontal plane. This effect is only quantitative however and the sensitivity to direction is never altered.

An explanation for the relative consistency of the eye movements elicited by the legs is that either very few proprioceptive systems are involved, or that all are involved, some controlling the directional movements of the eyes, and others having a regulatory or gain control effect. This perhaps focuses attention on the more proximal joints as sources for the directional inputs during rotation of the substrate around the vertical axis, because no matter what the attitude of the distal part of the leg, the motion imposed at these joints can be resolved into movements of the legs about the vertical or longitudinal axes.

Movements of the ball about the longitudinal axis affect the more distal joints

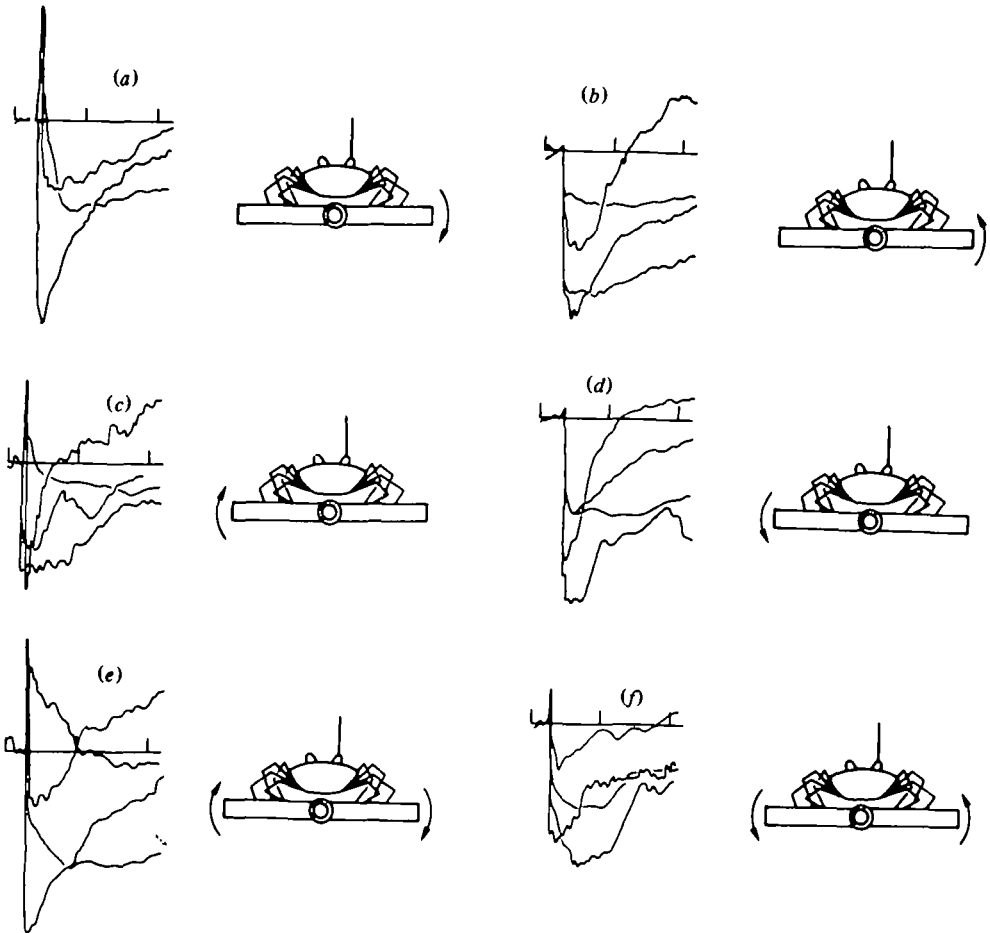


Fig. 14. Responses of the eyestalk to stepped movements of the platform supporting the legs, around the longitudinal axis (roll). The pictograms symbolize the stimulus situations (as in Fig. 11 (e-h)). The eye movements usually exhibit the same qualitative properties no matter on which side, or in which direction the legs are moved. The principal movement is a fast rotation toward the midline followed by a slower return of the eye toward a more lateral position.

particularly the M-C joint, and the interpretation of the eye movements is, as to be expected, more difficult. Tilting a platform on which the animal stands also involves the more distal leg joints, and the horizontal component of the complex eye movements which follow cannot be described as compensatory.

These results do provide, however, some insight into the underlying mechanisms. The most striking property is the considerable rectification within the system, apparent in both the responses to sinusoidal (Fig. 11 e-h) and step stimuli (Fig. 14); in the latter case the principal part of the response brings the eyes towards the animal's midline independently of the direction in which the platform is tilted. If these results are manifestations of the same non-linear property of the system, one would expect sinusoidal stimulations to cause not only periodic eye movements but

also a shift in the average angular position of the eye. Such a result is in fact obtained, as demonstrated in Fig. 13. Responses of this type are frequently observed in biological systems (e.g. Varjú, 1964).

It has however to be considered that these response properties might be partially artefacts. The wand glued to the eye is not colinear and not even parallel to the eye's own axis. If the eye makes vertical excursions or twists around its own axis, the tip of the wand describes an arc in the vertical plane, and the horizontal projection of this arc would appear as a horizontal eye movement. As estimated on the basis of eye and wand geometry, this apparent horizontal eye movement could amount in the worst case to some tenth of a degree. The measured excursions are several degrees. We believe, therefore, that our results are of physiological origin, even if more convincing evidence has to be obtained, e.g. by investigating also the vertical component of the eye movement.

Since the DC shift persists also at high stimulus frequencies which cause no considerable eye oscillation, one has to conclude that the nonlinear signal transformation precedes essential low-pass filtering and is caused by early stages in the system, possibly by the receptors themselves. In fact leg proprioceptors responding to movements in both directions by increasing their firing rate have already been reported in insects (Bässler, 1977).

(2) *The relationship of imposed leg movements about the vertical axis to active turns and eye movements in the horizontal plane*

When an unrestrained animal turns about its vertical axis, it does so by moving its legs in a particular sequence. The legs are raised and rotated forward or back in relation to the body, and then set down. At the same time, the body rotates relative to the legs which have remained in contact with the substrate. The standing legs, and those which are moved, therefore rotate in opposite directions relative to the body. The question then arises as to why rotation of the raised legs does not elicit eye movements. We have no final answer to this problem, but it is possible that the action of the proprioceptors is switched off if the legs are actively raised. Contact between the most distal segments of the legs with the substrate might be a powerful controlling factor here.

The eyes of actively turning crabs often exhibit a fast forward saccade at the beginning of turns about the vertical axis, which is followed by a slow compensatory movement in the opposite direction. Since these rapid saccades frequently anticipate the turns in unrestrained animals, they are regarded as 'voluntary' movements (Dijkgraaf, 1956). It has been suggested that in the crayfish the initial saccades are in fact reflexes stemming from the leg proprioceptors (Mellon & Lorton, 1977). Our observation is that fast saccades in the direction in which the body would turn if free to do so, are very seldom related to an imposed rotation of the legs about the vertical axis. Large amplitude rotations of the legs were often accompanied by saccades in the direction opposite to the slow 'compensatory' eye movement, but these were almost invariably preceded by a slow phase eye movement. We conclude that at least under the conditions of our experiments, the proprioceptors are not responsible for the fast anticipatory saccades.

Conceivably the rapid movements of the eyes following stepped leg movements are produced by the same system responsible for eye saccades, but we have no evidence to support or deny this speculation, nor any real grounds for a comparison. On the other hand we believe that the small rapid motions of the eyes away from the midline, frequently seen with the stepped stimuli, are the result of discharges in the eye-withdrawal neurones, which are known to mediate the rapid and protective withdrawal of the eyes into their sockets rather like the eye blink of the vertebrates (Sandeman, 1969). All the results support this conclusion: If the eye response to leg movement is a lateromedial movement, then this and the withdrawal reflex are opposite to each other, and the initial part of the withdrawal reflex appears as a fast peak. If the leg reflex moves the eye away from the midline, both responses have the same direction, and we cannot say to what extent the withdrawal reflex contributes to the reaction. It could be that the differences in the velocity during the principal part of the step responses, e.g. in Fig. 7 (*a, c, e*) on the one hand and (*b, d, f*) on the other hand is entirely due to the withdrawal reflex, the contribution of which increases the velocity in (*a, c, e*) and reduces it in (*b, d, f*).

Any consideration of the variability of the slow phase of the stepped responses must take into account that the muscle system responsible for eye movements is a complex one. There are eleven eye muscles involved and these are divided in their function of maintenance of eye position and eye movement (Burrows & Horridge, 1968). The position in which the eye rests is therefore, in the absence of any proprioceptive feedback (Sandeman, 1977) controlled by a tonic discharge in the motoneurones of some eye muscles, and the elastic properties of the eyestalk joint. A stepped response disturbs this equilibrium resulting in a consistent initial eye movement, but followed by a variable one caused by the varied responses of the tonic muscle systems to the step input, and the absence of the stabilizing visual feedback. This continues until activity in the eye muscle systems has returned to its new equilibrated state. Another possibility to consider here is the effect of the activation of resistance reflexes in the legs when they are suddenly rotated. The slow movements of the eyes following the initial fast rotation may reflect the waning (or increasing) influence of these reflexes.

(3) *The functional significance of leg-driven eye movements*

During the day, stabilization of the eye in space may be adequately achieved by the visual system because field observations show that apart from short rapid dashes for cover at the approach of birds or humans, most of the time the movements of the crabs are relatively slow. There is no need to propose the existence of a 'fast' eye stabilizing system, and we therefore suggest that the eye movements produced by leg proprioceptors are of critical importance when there is very little light and the optokinetic system is no longer able to operate at a high gain. *Leptograpsus* is active at night, and like a number of arthropods (Blest, 1980) resynthesizes the rhabdoms of the retinula cells each evening (Stowe, 1980). The night-eye has a rhabdom with a diameter almost twice that of the day-eye. Having a more sensitive eye for night vision however would be of little advantage unless, like during the day, there was a mechanism for keeping the eye stabilized in space to prevent blurring of

the image. Image blurring caused by motion is related to the finite time taken for receptors to respond, and to stop responding, to the changes in light intensity produced by an image moving across the retina (Srinivasan & Bernard, 1975). Time constants of the retinula cell responses are known to be significantly increased during dark adaptation leading to an increased blurring of moving objects (Howard, 1981). Thus, stabilizing the eye in space at night could be as important as during the day for the preservation of the image quality, and could also perhaps compensate for slow processing in the visual system. It can be argued however that the angular velocities of the eyestalk movements during body rotations are much too slow to cause blurring of the image at the receptor level. Instead, the function of the proprioceptively elicited eye movements may be to improve the signal-to-noise ratio by ensuring that in conditions of very low light intensity as many photons as possible are concentrated into as few photoreceptor cells as possible, and not spread over the entire eye.

The possession of movable eyes has yet another possible advantage for the crab: when foraging out of water, the animals depend entirely on vision to detect the approach of predators (mainly birds). Evidence from studies on the fly shows that moving objects are, under certain conditions, not seen if they are viewed against a moving background (Reichardt & Poggio, 1979). This has still to be demonstrated to be the case in crabs but the result nevertheless leads to the suggestion that the main function of crab eye movements is to secure a stable visual field against which any movement can be acutely seen. For body turns of more than $10-15^\circ$ of arc the eye is repositioned relative to the body with a fast saccade. This interrupts vision for only a few milliseconds.

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