

ROLES OF EYES, LEG PROPRIOCEPTORS AND STATOCYSTS IN THE COMPENSATORY EYE MOVEMENTS OF FREELY WALKING LAND CRABS (*CARDISOMA GUANHUMI*)

HERBERT PAUL*, W. JON P. BARNES† AND DEZSÖ VARJÚ*

*Division of Environmental and Evolutionary Biology, Institute of Biomedical and Life Sciences, Graham Kerr
Building, University of Glasgow, Glasgow G12 8QQ, Scotland, UK*

*Present address: Lehrstuhl für Biokybernetik, Universität Tübingen, Auf der Morgenstelle 28, D-72076 Tübingen, Germany

†Author for correspondence (e-mail: J.Barnes@bio.gla.ac.uk)

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Summary

The compound eyes, the canal organs of the statocysts and proprioceptors in the legs all generate compensatory eye movements in the horizontal plane in the land crab *Cardisoma guanhumi*. Frequency analyses of the compensatory eye reflexes elicited by each of these inputs show that visual (V) and proprioceptive (P) reflexes respond best below 0.1 Hz, while statocyst (S) reflexes only achieve a high gain above this frequency. They thus increase the range of frequencies over which compensation can occur.

Eye and body movements were recorded in an arena under all possible combinations of crabs seeing or blind (V+ or V–), with or without statocysts (S+ or S–) and freely walking or passively transported on a trolley (P+ or P–). Intact crabs (V+S+P+) show good stabilisation of the eyes in space, the only movements with respect to external coordinates being saccadic resetting movements (fast phases of nystagmus). The eyes thus compensate well for body turns, but are unaffected by translatory movements of the body and turns that are not accompanied by a change

in the orientation of the long axis of the body in space. In the absence of any one sense, compensation for rotation is significantly impaired, whether measured by the increase in the width of the histograms of changes in the angular positions of the eyes in space ($\Delta\phi_E$), by the mean angular velocity of the eyes (slope of regression line, m_E) with respect to the angular velocity of the body (m_B) or by response gain plotted against angular acceleration of body turn (a). The absence of two senses reduces the crab's ability to compensate still further, with the statocyst-only condition (V–S+P–) being little better than the condition when all three senses are absent (V–S–P–).

Such multisensory control of eye compensation for body rotation is discussed both in terms of making use of every available cue for reducing retinal slip and in making available the information content of the optic flow field.

Key words: *Cardisoma guanhumi*, Crustacea, crab, eye movement, locomotion, multisensory interaction, frequency–response curve.

Introduction

Arthropods have many advantages for the study of visually guided behaviour. They are extremely diverse, having a multiplicity of adaptations of great richness and variety. Also, as stated by Collett *et al.* (1993), they are good subjects for looking at nature's inventive solutions to problems of visual stabilisation in that behaviours are sufficiently stereotyped to allow insights into underlying mechanisms to be gained from a simple behavioural analysis.

Crustaceans are the only arthropod group to have their eyes on mobile stalks. Crabs, unlike mantis shrimps (Land *et al.* 1990), do not fixate and track objects of interest, but they and other decapod crustaceans do exhibit well-developed compensatory eye movements which help to stabilise the position of the eyes in space (for reviews, see Neil, 1982; Nalbach, 1990a; Barnes and Nalbach, 1993). Such eye reflexes compensate for body movements about the pitch, roll and yaw axes. As in vertebrates,

compensatory eye movements can be driven by the eyes (optokinetic responses; e.g. Horridge and Sandeman, 1964), by organs of balance (vestibular responses; e.g. Silvey and Sandeman, 1976) and by proprioceptors (e.g. Varjú and Sandeman, 1982) which, in the case of decapod crustaceans, are located in the legs. In the pitch and roll planes, the strengths of the different reflexes have been shown to vary with the crab's habitat (Nalbach *et al.* 1989). Thus, the eye movements of swimming crabs and other predominantly aquatic crabs are driven mainly by the statocysts, those of semiterrestrial crabs living in a habitat with a well-defined horizon (e.g. a mud-flat) are driven predominantly by the eyes, while crabs living on a solid substratum make strong use of the leg proprioceptor input.

In the horizontal (or yaw) plane, the position is more complex if we also consider that, during locomotion, image movements over the retina are generated not only by turns (rotation about a

vertical axis) but by movements of the animal in a straight line (translation). During rotation, image motion occurs in the opposite direction to the movement at an angular velocity dependent on the vertical position of the objects with respect to the animal ($W^R = R \cos e$, where W^R is the length of the velocity vector, R is the angular velocity of rotation of the animal and e is the elevation of the object with respect to the horizon). In contrast, during translation, the velocity of image motion depends on the object's distance and angle with respect to the animal. Distant objects remain stationary, while closer ones increase their size and velocity as they are approached, decreasing them again when they have been passed by. This visual input, known as the optic flow field, has the potential to provide useful information both about the animal's own movements and about its visual surroundings (Gibson, 1966; Buchner, 1984). The visual input resulting from turns (the rotatory component of the flow field) informs the animal of deviations from a straight path and can thus be used in course control, while that resulting from movement in a straight line (the translatory component of the flow field) provides information on the three-dimensional layout of the animal's surroundings (by motion parallax), as well as information on the animal's speed of movement (you do not need to look at your speedometer to gain an impression of how fast you are driving your car!) and even distance travelled (by integrating velocity over time). In insects, where mechanisms of sensory guidance have been more extensively studied than in crustaceans, there is evidence that the visual flow field is, indeed, used to estimate distance travelled (Esch and Burns, 1996; Schöne, 1996), to control walking speed (Schöne, 1996) or flying speed (Srinivasan, 1992), to initiate landing responses (Srinivasan *et al.* 1996), to gain a three-dimensional view of the world (Lehrer, 1996) and to correct for deviations from an intended path (Egelhaaf and Borst, 1993). To gain all this useful information, however, it is necessary to separate the different components of the flow field from each other, since movement along a curved path defies easy analysis (Koenderink and van Doorn, 1987). Paul *et al.* (1990) and Barnes (1990) have examined the eye movements of freely moving crabs and have shown that walking crabs indeed do this. They carry out an elementary form of flow-field analysis, in that they compensate for the rotatory but not the translatory components of optic flow (i.e. eye movements occur in response to body turns but not to movements along a straight line).

How do crabs distinguish between the rotatory component of the flow field generated by the body turning about its yaw axis and the translatory component of the flow field generated by the body moving in a straight line? Although Barnes (1990) and Paul *et al.* (1990) demonstrated that non-visual inputs (particularly the leg proprioceptors) did contribute to the compensation of rotation in actively walking animals, most studies have concentrated almost exclusively on visual mechanisms. Nalbach *et al.* (1993) studied the effect of differences between the input seen by the two eyes (important for distinguishing rotation and translation in forward-walking animals); Barnes and Nalbach (1993) examined the effect of movement in the anterior and posterior rather than the lateral parts of the visual field (important for distinguishing

rotation and translation in sideways-walking animals); Kern *et al.* (1993) studied the effect of narrow rather than wide spacing of contrasts and Barnes (1990) examined the effect of stationary contrasts. All these factors have been shown to reduce optokinetic gain. Indeed, the role of such mechanisms of whole-field integration for the efficient separation of rotation from translation has been given further support by recent data of Blanke *et al.* (1997), who also failed to find any evidence for mechanisms involving motion parallax effects, systematic variation in the direction and velocity of local vectors in the flow field or any other mechanism involving the detailed analysis of optic flow.

In the present study, we examine the relative roles of all three senses in the generation of compensatory eye movements in the horizontal plane. We have measured the frequency responses of the compensatory eye movements of *Cardisoma guanhumi*, a tropical land crab, in response to visual, statocyst and leg proprioceptive inputs, and systematically analysed the relative roles of these reflexes in generating the compensatory eye movements seen during both active and passive rotation. We find that all three senses are required to act together to elicit accurate compensation for body turns and, contrary to expectations, that the input from leg proprioceptors is as important as that from the eyes. Thus, the control system for the separation of the rotatory and translatory components of optic flow in crabs, like so many other control systems governing the behaviour of arthropods (for a review, see Barnes, 1993), involves multisensory convergence.

Preliminary accounts of some of these experiments have already appeared (Barnes and Paul, 1994, 1998).

Materials and methods

Animals

Land crabs (*Cardisoma guanhumi*) were purchased in local markets in Trinidad by visiting research workers and transported to Britain by air. They were maintained at 20–25 °C in large shallow tanks containing sand and gravel from the sea shore and dishes of copper-free fresh water so that the crabs could submerge themselves. Hiding places for the crabs were provided by stones, slates and pieces of clay guttering. They were fed a varied diet including raw carrots, green vegetables, meat and dry cat food.

For the experiments, we used a total of 28 animals of both sexes, varying in carapace width from 5.2 to 8.1 cm (60–234 g in mass). These experimental animals had all their walking legs and both chelae intact.

Measurement of frequency responses of compensatory eye movements

To measure the compensatory eye movements occurring in response to visual, leg proprioceptor and semicircular canal stimulation, crabs were held firmly in a clamp, while horizontal eye movements were recorded by a capacitive position-sensing device (design of Sandeman, 1968, as modified by Forman and Brumbley, 1980). A 50 mm long wand made of 150 µm diameter steel wire, weighing 1 mg and carrying a low-voltage 34 kHz signal was glued to the peninsula of non-

corneal exoskeleton on the eye and bent back so that its tip moved between two copper plates attached to the dorsal surface of the crab's carapace (Barnes, 1990). In experiments where the movements of both eyes were recorded, the position-sensing devices provided signals of different frequency (25 kHz and 35 kHz) so that cross-talk between the two devices could be excluded by selective filtering. The electrical outputs from these devices, representing the horizontal positions of the eye(s), were digitised and stored in a computer. Additionally, during parts of each experiment, the crabs were video-taped from above at 50 fields s^{-1} , and the angular excursions of the wand were measured. Such measurements were used to produce a calibration factor to convert the digitised values into angular positions. Recordings of the stimuli (see below) were obtained by means of a digital potentiometer and stored alongside the eye movement data.

In all cases, the stimuli were generated by a kymograph motor, whose gearbox allowed a wide range of low velocities. An eccentrically mounted lever arm converted this continuous rotation into sinusoidal oscillation of the stimulus apparatus, whose frequency could be varied within the range 6.2×10^{-5} to 1.28 Hz. For visual (optokinetic) stimulation, a drum of vertical black and white stripes (pattern wavelength 24° , mean luminance 59.8 cd m^{-2} , contrast $>90\%$) was oscillated around the crab which was held in the centre of the drum with its legs making no contact with the ground. For leg proprioceptor stimulation, a circular platform covered by a layer of expanded polystyrene to provide a non-slip surface for the crab's legs was oscillated beneath the animal. Since the crab was firmly fixed by its carapace at the centre of the platform, this stimulus moved the legs to left and right in a sinusoidal manner, most of the movement occurring at the coxo-basal joint (Varjú and Sandeman, 1982). In these experiments, the eyes were painted over with a water-based white paint (Wacofin Mattfarbe, Heinrich Wagner) to exclude any influence of the visual system. The choice of white paint for blinding the crabs was made because, while we wished to exclude form vision, we did not wish to exclude brightness perception. This is because, in complete darkness, crabs often become very passive, with reflex eye movements declining in gain or stopping altogether. For vestibular stimulation, crabs blinded as described above and held in their normal orientation in space were oscillated sinusoidally about a vertical axis across the midpoint of an imaginary line joining the two eyes. The legs of the animals made no contact with the ground. This stimulus would excite the receptors of each horizontal canal but not the statolith organs, which are mainly stimulated by pitch and roll movements (Sandeman and Okajima, 1972).

Measurements of the gain and phase of the responses to each stimulus frequency were made as follows. For the great majority of cases where complete cycles could be obtained, the data were subjected to a computer program that fitted a sine wave by Fourier analysis to both the stimulus and response by minimising the standard deviation of the fitted curve to the data. This excluded both small irregularities and long-term drift. Gain was calculated by dividing the amplitude of the

response by that of the stimulus, while phase represents the phase shift between the stimulus and response sine waves. When the stimulus frequency was very low and responses could only be obtained from part of a stimulus cycle, measurements of phase could not be made, while gains were calculated from regression lines fitted to sections of the data (as described below for arena experiments).

Recording of eye movements in freely walking and passively transported animals

These experiments were carried out in a rectangular arena ($5.6 \text{ m} \times 3.0 \text{ m}$), whose shorter sides were covered by patterns of broad black-and-white stripes and whose longer sides were covered by a plain grey surface. The wooden floor of the arena was marked out in 20 cm squares with white masking tape, each intersection being given a unique reference determined by its row and column number. The luminance of different parts of the arena varied from 65 to 129 cd m^{-2} , owing to the eccentricity of the room lighting. The crabs were filmed from above (at 50 fields s^{-1}) using a video camera (Panasonic) mounted on a trolley so that it was approximately 1 m above the crab. The area covered by the camera image was $35 \text{ cm} \times 25 \text{ cm}$. The trolley was moved by hand to keep the crab within the camera's field of view or, in some experiments, to transport the crab as well. The experiments do not include data from the fastest speeds of which the crabs were capable (escape behaviour), since under such conditions it was not possible to follow the crab with the camera. The long axis of the crab was marked clearly by a dotted line of white paint, while white plastic wands were attached to each eye and bent back over the carapace (see Fig. 1A).

Eight different experimental situations were studied, representing all possible combinations of the following:

crab seeing	V+
crab blinded with white paint	V-
crab with intact statocysts	S+
crab with statocysts destroyed by a needle	S-
crab walking freely so that normal	P+
proprioceptive input was provided by the legs	
crab passively transported on the trolley with	P-
legs free	

Selected sequences from the video tapes were analysed at 100 ms intervals. Coordinates representing each end of the wands attached to the eyes, each end of the line representing the long axis of the body and a number of ground reference points (intersection points of the tape strips) were recorded and digitised for each field analysed. From these data, the orientation of the left and right eyes in space (ϕ_L and ϕ_R) and of the long axis of the body in space (ϕ_B) could be calculated (Fig. 1A). These angular positions of the eyes and body were plotted against time as shown in Fig. 1B, increasing angles with time representing leftward (or anticlockwise) rotations of eyes or body and decreasing angles represent rightward (or clockwise) rotations of eyes or body. The next stage in the analysis was to select by hand the start and end points of each segment of body movement. Two such points are labelled t_1 and t_2 in Fig. 1B. Regression lines for the left eye, right eye

and body were calculated within these limits and drawn on the plots. Their slopes represent the mean angular velocity of the movement of each eye (m_L and m_R) and of the rotation of the body (m_B). Finally, calculations of the angular acceleration of the body were obtained by summing the differentiations of the instantaneous velocities derived from consecutive analysed video frames and dividing by their number n to give a mean acceleration over the segment of data in question.

Results

Frequency response of compensatory eye reflexes

Knowledge of the frequency responses of the different

compensatory eye reflexes is essential to any understanding of the roles of such reflexes in the compensation of body turns during locomotion. Their relative importance varies in crabs from different habitats (Nalbach *et al.* 1989), but no data are available for *Cardisoma guanhumi*. Therefore, we have measured the frequency responses of the eyes of fixed crabs to sinusoidal stimulation in the horizontal plane of the visual system, the leg proprioceptors and the horizontal semicircular canals of the statocysts, making measurements of gain and phase in each case.

Visual system

Visually evoked compensatory eye movements are also known as optokinetic responses and are usually generated by moving a striped drum around a fixed crab. The eyes follow the stripes, flicking back at intervals to their starting position (Horridge and

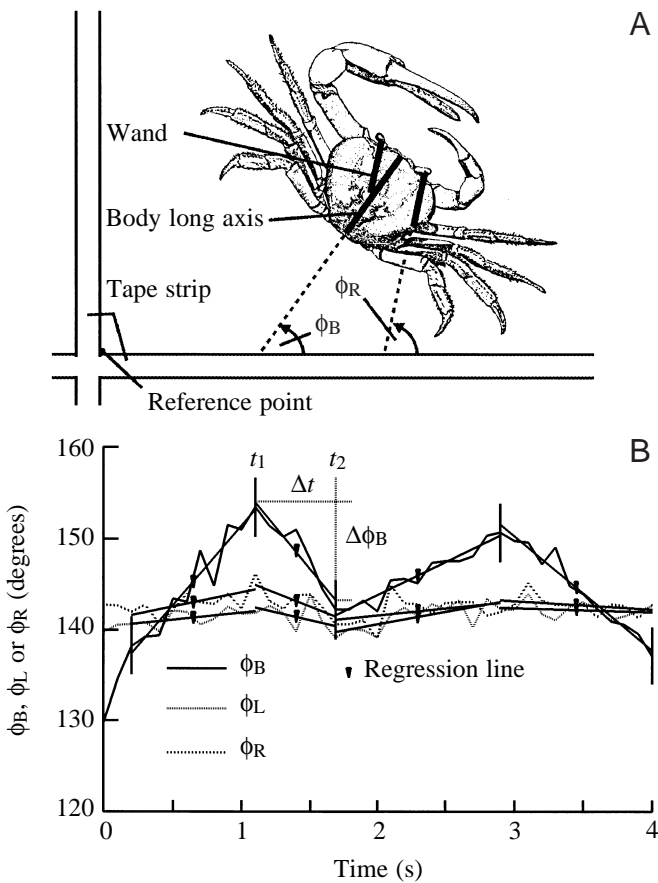


Fig. 1. (A) Diagrammatic representation of a video frame of *Cardisoma guanhumi* in the arena, showing the tape strips that defined the external coordinate system, the paint marks that indicated the longitudinal axis of the body, and the wands attached to each eyestalk. Angle ϕ_B defines the orientation of the body in space, angles ϕ_R and ϕ_L (not shown) define the orientations of the eyes in space. (B) Calculation of the regression lines for ϕ_B , ϕ_L and ϕ_R . Within limits (t_1 and t_2), defined by eye, lines of best fit were calculated separately for the orientation of the long axis of the body and both eyes, making use of all the data points within the limits. $\Delta \phi_B$ is the change in the angular orientation of the long axis of the body, while Δt is the time interval $t_2 - t_1$. The slopes of the regression lines represent the angular velocity of the movement of each eye and the rotation of the body.

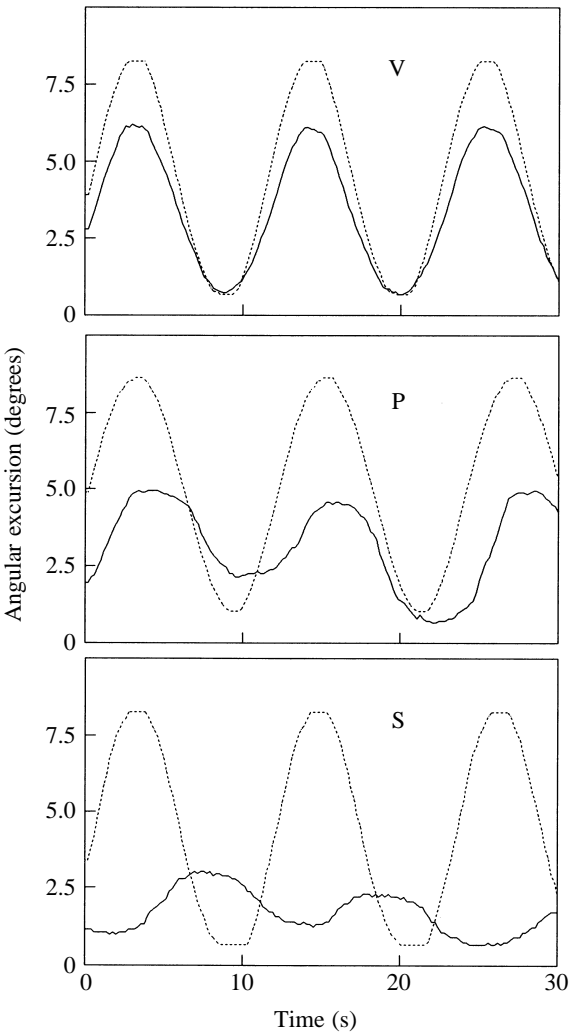


Fig. 2. Examples of the compensatory responses of the left eye of *Cardisoma guanhumi* to visual (V), proprioceptive (P) and statocyst (S) inputs. Angular excursions of the stimulus (dotted lines) and response (solid lines) are plotted against time. In all cases, the stimulus frequency was $8.67 \times 10^{-2} \text{ Hz}$ and peak-to-peak amplitude was 7.6° .

Sandeman, 1964). Such saccadic resetting movements (fast phases of nystagmus) occurred frequently in our experiments, but are absent from the example shown in Fig. 2 (top). Here, at a frequency 8.67×10^{-2} Hz and an amplitude of 7.6° , the eye follows the stripes with negligible phase lag but with reduced amplitude (gain of approximately 0.7).

The results of the frequency analysis are presented as Bode plots in Fig. 3A,B. They represent stabilised values for the responses and thus exclude any influence from the fast-

adapting high-frequency channel that produces good compensation for short-duration fast movements (Nalbach, 1989; see also Fig. 6G of Barnes, 1990). Since responses occurred at the lowest available frequency, they do not identify the lower frequency limit for optokinesis. At all frequencies below 0.1 Hz, the gain is high (>0.6) and the response is approximately in phase with the stimulus. Thus, good compensation occurs over a wide range of low frequencies. At higher frequencies (above 0.1 Hz), the gain falls rapidly and

Fig. 3. Bode plots of the gain and phase of the compensatory eye movements in the horizontal plane of *Cardisoma guanhumi* in response to sinusoidal stimulation at a peak-to-peak amplitude of 7.6° . (A,B) Responses to visual stimulation. (C,D) Responses to leg proprioceptor stimulation. (E,F) Responses to stimulation of the canal organs of the statocysts. Graphs show mean gains (A,C,E) and mean phase relationships (B,D,F) \pm S.D. of the stabilised responses of the eyes; i.e. they exclude any influence from fast-adapting high-frequency channels that exist for both visual and leg proprioceptor stimulation. Horizontal dashed lines in A, C and E represent a gain of one, while those in B, D and F represent a phase lag of zero. In each gain plot, a indicates the number of animals used and c indicates the total number of cycles analysed.

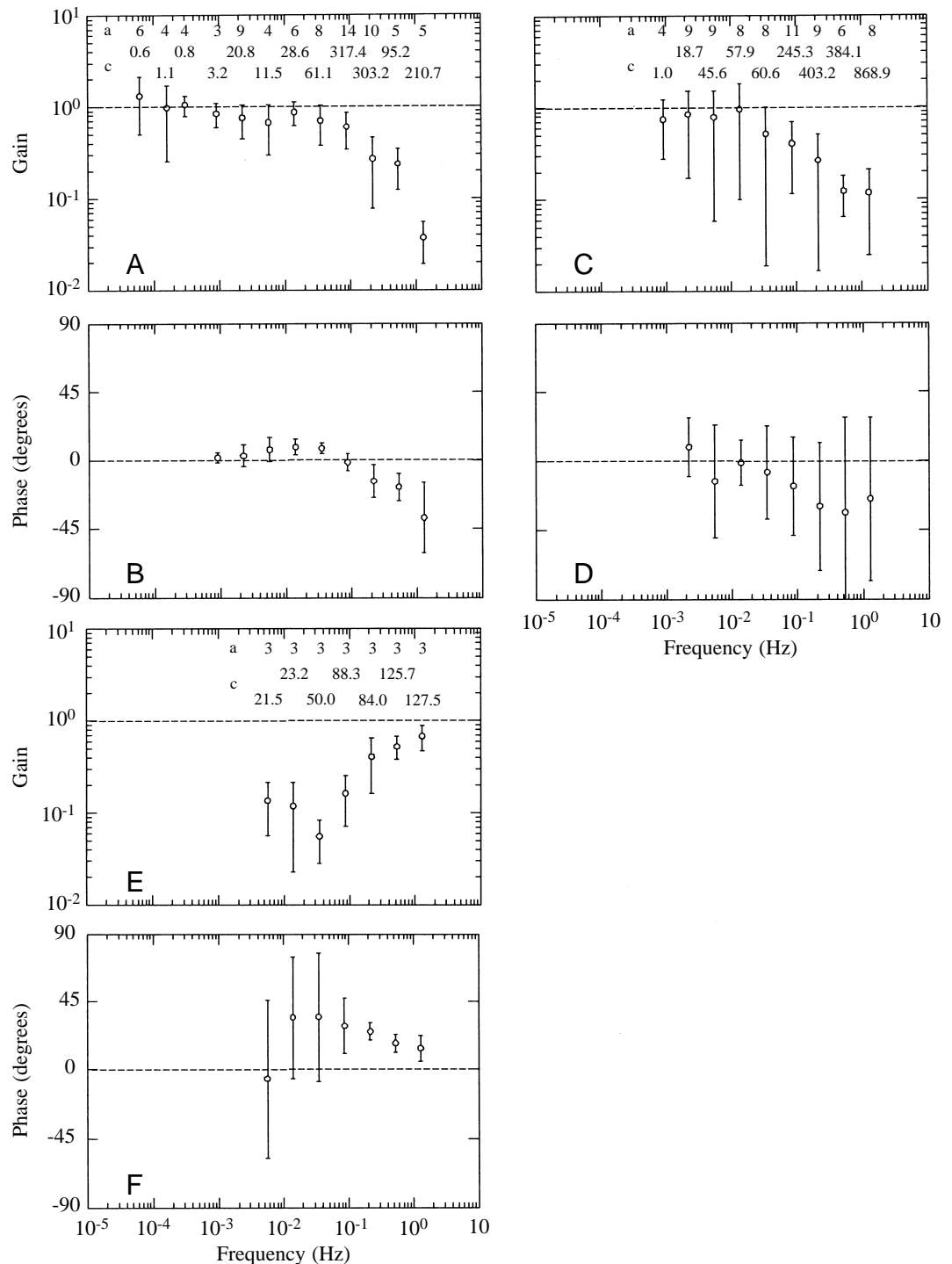
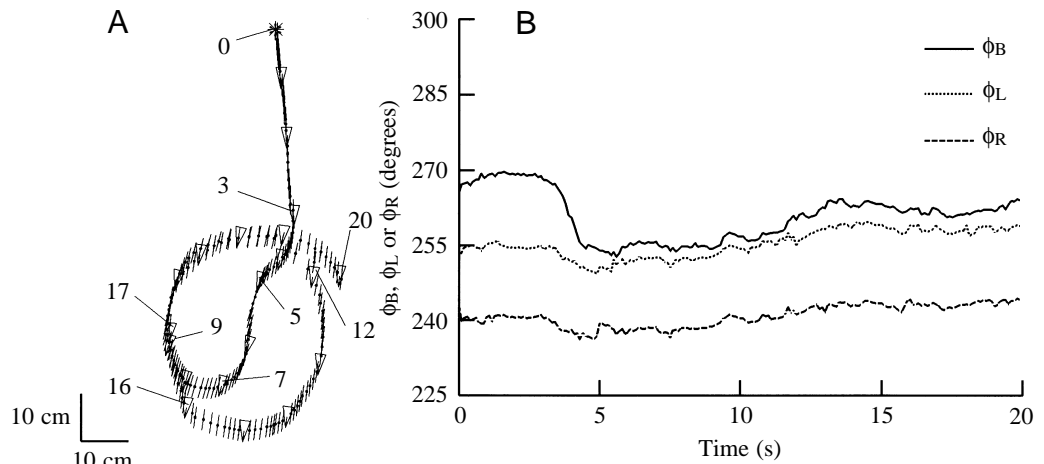


Fig. 4. (A) Passively transported seeing crab with intact statocysts (V+S+P-) in which changes in direction of movement were largely brought about without change in the orientation of the long axis of the body. The orientation of the long axis of the body is drawn at 100 ms intervals, the position of the centre of the body being indicated by a dot and that of the front of the animal by arrowheads, drawn at 1 s intervals. The starting position is indicated by an asterisk. Numbers indicate elapsed time in seconds. (B) Orientation of the long axis of the body (ϕ_B) and of the left and right eyes in space (ϕ_L and ϕ_R , respectively) plotted against time for the sequence shown in A.



the phase lag increases. No responses are seen above 1.28 Hz. At the lowest frequencies, the responses were very variable (high S.D.) and sometimes exceeded a gain of 1. The latter would not be expected because, in such a closed-loop system, if the eyes moved faster than the drum, they would see movement in the opposite direction. Probably the explanation lies in the difficulty of excluding the effects of eye drift (Horridge, 1966a) when analysing very slow responses, but it must be noted that real closed-loop optokinetic gains exceeding 1 have been recorded elsewhere; for instance, in the response of the hawkmoth *Macroglossum stellatarum* to transitory pattern motion (Farina *et al.* 1995).

Leg proprioceptor system

As in humans, where compensatory eye movements occur in response to stimulation of neck proprioceptors (Barlow and Freedman, 1980), proprioceptive inputs generate eye movements in crabs (Varjú and Sandeman, 1982). They have the same direction as the movements of the legs (i.e. if the legs are moved anticlockwise, the eyes move to the left). In the example shown in Fig. 2 (middle), the responses were more irregular, of lower average gain and had a significantly larger phase lag in comparison with the response to visual stimulation at the same frequency and amplitude.

Since responses to oscillating a platform under the animal's legs occurred at the lowest frequency (the crabs struggled too frequently under these experimental conditions for results to be obtained at the lowest frequencies available to us), our analysis (Fig. 3C,D) does not identify the lower frequency limit for proprioceptor-driven eye movements. It does, however, show that good compensation (i.e. a gain near 1 with responses approximately in phase) occurs from below 0.001 Hz to approximately 0.02 Hz. Above this value, the gain declines and the phase lag increases. Thus, the leg proprioceptor reflexes begin to fail at a slightly lower frequency than the visual ones but, like the latter, provide good compensation over a wide range of low frequencies. The responses are, however,

much more variable than those generated by the eyes (note the larger standard deviation in respect of both gain and phase). This happens (at least partly) because, with the eyes painted over, the eye movement control system no longer has a negative feedback loop.

Statocyst system

Eye movements in response to oscillation of a blinded crab about its vertical axis (vestibular responses) are due, as in many other animals including vertebrates, to stimulation of sensory receptors (here thread hairs) within the horizontal semicircular canals (Sandeman and Okajima, 1972). As shown by the example in Fig. 2 (bottom), the eyes move in the opposite direction to that of the body and are therefore compensatory. At this frequency (8.67×10^{-2} Hz), they have a lower gain than either visual or proprioceptor-generated responses and, typically, show a clear phase lead. This is because the thread hairs are stimulated by acceleration rather than velocity.

The frequency analysis (Fig. 3E,F) reveals vestibular responses in the range 0.005–0.03 Hz with decreasing gain and shows that the gain then increases with good compensation (gain approaching 1) above 0.1 Hz. Comparing these data with those obtained by others (*Scylla serrata*, Silvey and Sandeman, 1976; *Mictyris longicarpus*, Nalbach, 1990a; *Pachygrapsus marmoratus*, Nalbach and Paul, 1990), where low frequencies fail to elicit eye movements, suggests to us that those reactions below 0.03 Hz are not due to the statocysts, but (in spite of the fact that the eyes were painted over) are weak visual responses produced by oscillating the crab in front of stationary contrasts in the laboratory. We had attempted to eliminate such contrasts, but the possibility of stray light entering the experimental arena cannot be excluded. We therefore believe that true statocyst responses begin at approximately 0.03 Hz, with the gain increasing thereafter. Since the maximum frequency that could be generated by the kymograph motor was 1.28 Hz, a frequency at which the gain of the vestibular responses was still increasing, the upper limit of the vestibular

responses could not be elucidated. The statocysts thus generate compensatory eye movements at higher frequencies when the other two systems are no longer functioning, but they do so in response to accelerations instead of velocities.

Sensory deprivation experiments

The influences of the visual system, of the canal organs of the statocysts and of the leg proprioceptors in generating compensatory eye movements in walking crabs were studied separately and in all possible combinations in the arena. As described in the Materials and methods section, crabs could be seeing or blind (V+ or V-), could be with or without statocysts (S+ or S-) and could be freely walking or passively transported (P+ or P-).

Eye movements in freely walking and passively transported crabs

We have chosen to display three recordings of our data in order to illustrate different characteristic features of the eye responses (Figs 4–6). In Figs 4A, 5A and 6A, the orientation of the long axis of the body is drawn in space at 100 ms intervals, the position of the centre of the body being indicated by a dot and the front of the animal being indicated by the point of an arrowhead. Arrowheads were placed at 1 s intervals. In Figs 4B, 5B and 6B, the position of the long axis of the body (ϕ_B) and of the left and right eyes (ϕ_L and ϕ_R , respectively) in space are plotted against time.

In Fig. 4, a passively transported crab (V+S+P-) was moved from its starting position (indicated by an asterisk) in a straight line for 3 s along the direction of the long axis of the body (i.e. equivalent to forward walking). Then, following a 20° right turn of the body axis over the time from 3 to 5 s, the body was moved in a circle while maintaining the long axis of the body constant (6–20 s). The eyes compensated for the change in orientation of the body axis at 3–5 s, but otherwise scarcely moved, in spite of the fact that the body had been translated both along a straight line (0–3 s) and along a circle (6–20 s). But although eye compensation for changes in body axis orientation was good, the crab did tolerate both small and slow changes in the orientation of the body. Such failures in compensation have been recorded in intact freely walking crabs (*Pachygrapsus marmoratus*; Paul

et al. 1990), but are greater when, as in this example, the crabs are deprived of part of their normal sensory input.

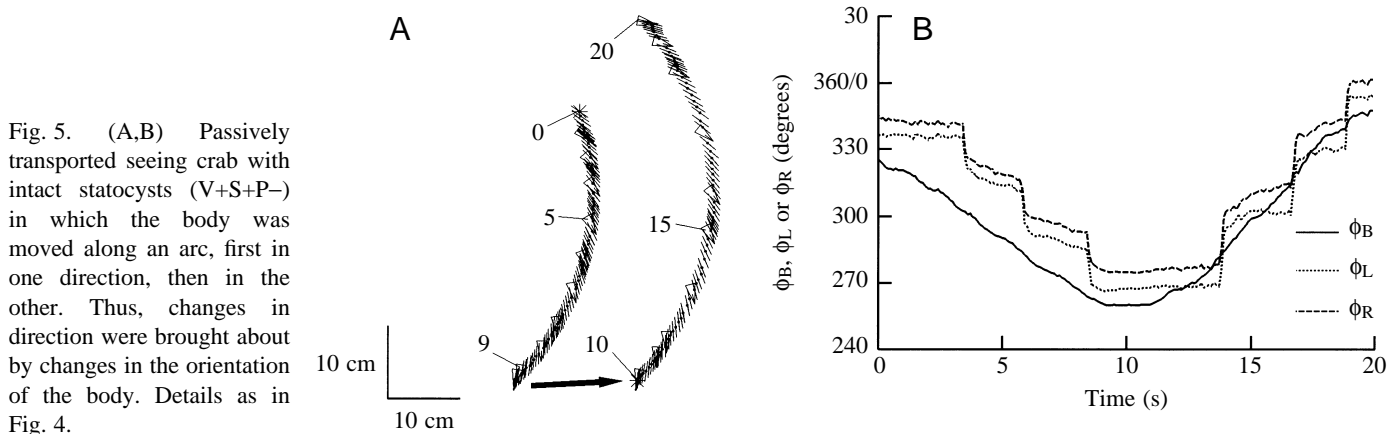
Fig. 5 differs from Fig. 4 in that the passively transported crab (V+S+P-) was moved along an arc first in one direction then the other, so that the movements involved both rotation and translation of the body axis. Here the plot of ϕ_B , ϕ_L and ϕ_R against time looks quite different. The orientation of the long axis of the body changes almost sinusoidally, while eye position in space changes in a stepwise manner, periods of compensation being separated by short-duration saccadic resetting movements (fast phases of nystagmus). Here again, note that compensation for body turning is not perfect, since the eyes only partially compensated for body turns (i.e. the lines representing ϕ_L and ϕ_R are often sloping rather than horizontal between the fast phases of nystagmus).

The third example (Fig. 6) shows results obtained with a freely walking intact crab (V+S+P+). From 1.5 to 5 s, the crab changed its direction without altering its body orientation. As in Fig. 4, no eye movements were induced during this period of pure translation. For the remainder of the recording (5–20 s), the crab walked in approximately the same direction while making a number of changes to the orientation of the long axis of its body. Thus, the body axis (ϕ_B) alters irregularly with time. The eyes, however, are well stabilised in space, the only movements with respect to external coordinates being saccades.

These results reinforce the conclusions of our previous work (Barnes, 1990; Paul *et al.* 1990; Barnes and Nalbach, 1993) that crabs compensate for rotation but not for translation. There is also some indication that compensation is less efficient when crabs are deprived of part of their normal sensory input. This question is addressed quantitatively below.

Quantitative comparisons of different experimental groups

The above experiments covered the lower parts of the speed range of which crabs are capable, where translational velocities of freely walking animals were generally less than 10 cm s⁻¹. Thus, sequences of forward and diagonal walking were more common than sideways walking, the preferred means of fast locomotion. Data were obtained for all eight combinations of our experimental situations. Since the angular velocity of



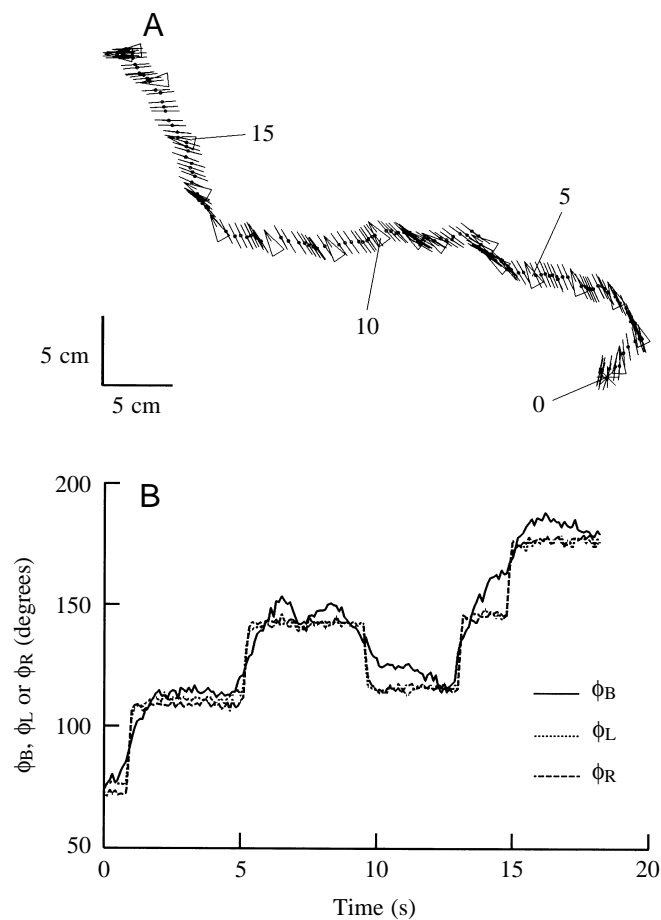


Fig. 6. (A,B) Free walking of intact crab (V+S+P+). Details as in Fig. 4.

freely walking crabs seldom exceeded 50°s^{-1} , all data sets were restricted to $-50 < m_B < +50$. There remained, however, some differences between the groups of passively transported crabs (P- groups) and the free-walking ones (P+ groups). In particular, the passively transported animals usually had a higher mean translational velocity, a higher mean angular velocity and a lower mean angular acceleration (Table 1). These and other differences between the groups must be borne in mind when comparing them.

One of the simplest ways of comparing the different experimental groups is to examine the distribution of $\Delta\phi_E$, the change in the angular position of both the eyes in space for all segments of the data. With perfect compensation, $\Delta\phi_E$ should always be zero. This was never the case even in the V+S+P+ situation with all three senses operational (Fig. 7). However, its value obtained with intact crabs hardly ever exceeded $\pm 5^{\circ}$, with a width at half height of $\pm 2.0^{\circ}$. This is not very different from 1.4° , the angular separation of ommatidia in the horizontal plane near the equator in *Cardisoma* (W. J. P. Barnes and A. Chesi, in preparation), so that compensation is reasonable in the context of the eye's acuity. The three groups where two senses are present (Fig. 7B,C,E) and the groups with vision only (Fig. 7F) and leg proprioceptor input only (Fig. 7D) are all very

Table 1. Comparisons of translational velocity, angular velocity and angular acceleration for all eight combinations of V+/V-, S+/S- and P+/P-

	Translational velocity, v (cm s^{-1})	Angular velocity, ω (degrees s^{-1})	Angular acceleration, a (degrees s^{-2})
V+S+P+	4.21 ± 3.06	11.10 ± 3.80	100.32 ± 17.41
V+S-P+	4.25 ± 2.25	10.96 ± 2.80	92.80 ± 12.95
V-S+P+	6.98 ± 3.99	12.21 ± 4.96	106.01 ± 22.54
V-S-P+	3.54 ± 1.78	9.63 ± 2.22	84.92 ± 10.08
V+S+P-	10.17 ± 1.79	11.77 ± 2.23	41.42 ± 10.13
V+S-P-	12.56 ± 1.71	19.46 ± 2.11	58.04 ± 9.57
V-S+P-	12.17 ± 2.68	15.06 ± 3.20	76.33 ± 14.70
V-S-P-	13.09 ± 4.16	31.19 ± 5.10	73.45 ± 23.17

Values are means \pm S.D. for all experimental sequences illustrated in Figs 7-10.

Sequences are included here and in Figs 7-10 when they fell within any of the following limits: $v < 50 \text{ cm s}^{-1}$; $\omega < 50^{\circ} \text{ s}^{-1}$; $a < 250^{\circ} \text{ s}^{-2}$; $-50 < m_B$ or m_L or $m_R < +50$; or $-2 < \text{gain} < 5$.

V+/V-, seeing/blind; S+/S-, with/without statocysts; P+/P-, freely walking/passively transported; m_B , m_L , m_R , angular velocity of the body, left eye and right eye, respectively.

All differences between freely walking (P+) groups and equivalent passively transported (P-) groups (e.g. between V+S-P+ and V+S-P-) are statistically significant (z-test: $P < 0.01$) except the V+S+P+/V+S+P- comparison for angular velocity, where the difference is not statistically significant.

similar but have a $\Delta\phi_E$ of at least $\pm 20^{\circ}$, while the V-S+P- group (Fig. 7G) is little different from the control group V-S-P- (Fig. 7H) that lacks all three senses. We can therefore tentatively conclude that the absence of any of the three sensory inputs involved in eye compensation causes a significant decline in performance while, at least over the range of angular accelerations we used, the canal organs of the statocysts are hardly effective at all on their own. In view of their frequency response, it is probable that the statocysts are more important at faster accelerations not achievable in this study.

Since both the visual system (Horridge, 1966b) and also the leg proprioceptor system (in view of the Bode plots illustrated in Fig. 3C,D) are velocity-based, we have also plotted the data so as to examine the ability of the eyes to compensate for different velocities of turns. In Fig. 8, m_E , which represents the mean angular velocity of both eyes in space over each segment of record analysed, is plotted against m_B , the mean angular velocity of the long axis of the body over the same time period. In each plot, the horizontal line through zero indicates perfect compensation for turns, while the diagonal dotted line indicates no compensation. Lines of best fit are drawn for all data, the P values (from a t -test) indicating whether they are significantly different from a slope of 1 (no compensation). The results reinforce the conclusions drawn above. Intact freely walking crabs compensate best (have regression lines with the shallowest slope), followed by the three groups in which two senses are available. Again, the statocyst-only group (V-S+P-)

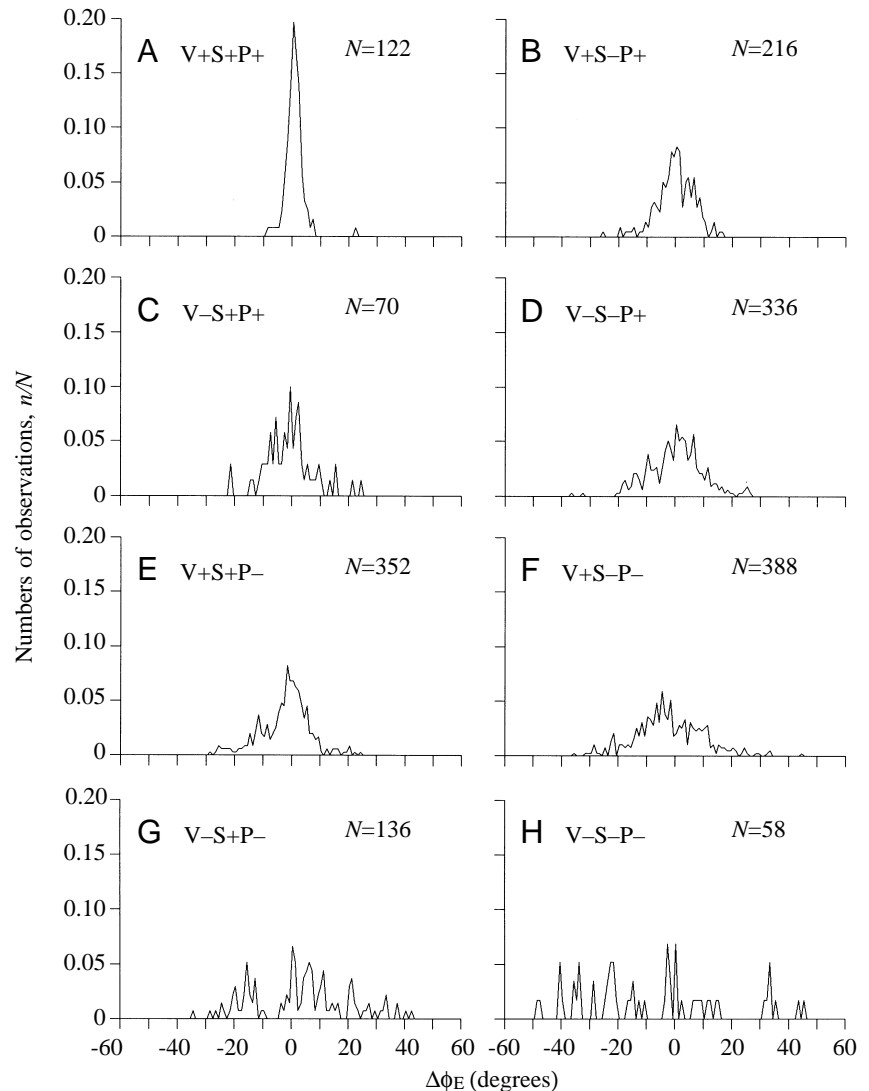


Fig. 7. (A–H) Distribution of the changes in the angular orientation of both eyes in space ($\Delta\phi_E$) during compensatory eye movements (i.e. leaving out fast phases of nystagmus) for all eight combinations of V+/V–, S+/S– and P+/P–. Bin width, 1° ; n/N , number of observations as a decimal fraction of the total (N).

performs very badly. This is not to say that the statocysts have no role, however, for each of the S+ groups on the left-hand side of Fig. 8 has a significantly lower slope than its equivalent on the right-hand side (compare A with B, C with D, E with F, and G with H in Fig. 8). A similar kind of comparison (of A with C, B with D, E with G, and F with H in Fig. 8) indicates the importance of the visual system, for all groups with vision have lower slopes than their equivalents without. Indeed, the same is true of the leg proprioceptors (compare A with E, B with F, C with G, and D with H in Fig. 8). Whereas both leg proprioceptors and statocysts appear to have their effects over the whole velocity range covered by our analysis, the same is not true for the visual system, for the V+S–P– group only compensates for velocities of up to 25°s^{-1} . Indeed, outside the range $-25 < m_B < +25$, the regression lines clearly differ (Fig. 8F).

A final measure of compensation is given by the gain of responses under the different conditions (Fig. 9). We have chosen to plot this against mean angular acceleration a to determine whether, as might be expected, the canal system of the statocyst compensates well for higher angular

accelerations. Since the visual system incorporates a negative feedback loop, we would not expect gains of greater than 1 in any of the V+ groups. The other senses are responding without feedback, however, so gains of any V– group should not be so limited. Gains exceeding 1 are, indeed, most numerous in a group where vision was absent (V–S–P+, Fig. 9D), but they are not uncommon in all V+ groups (Fig. 9A,B,E,F). They mostly occurred at low velocities (data not shown), so did not result in substantial overcompensations in terms of the angular distance moved by the eyes. Fig. 9 also illustrates that the canal organs of the statocysts do generate eye movements in the V–S+P– situation (Fig. 9G), since the gain values were more widely scattered than in the V–S–P– situation (Fig. 9H). Negative values were, however, not uncommon; but this is not surprising since the crabs, during their movements, have angular decelerations which result in eye movements in the opposite direction to those in response to angular accelerations (post-rotatory after-nystagmus; see Fig. 6A of Barnes, 1990).

Gains are compared directly for the different groups in Fig. 10. Groups whose 95 % confidence intervals do not overlap

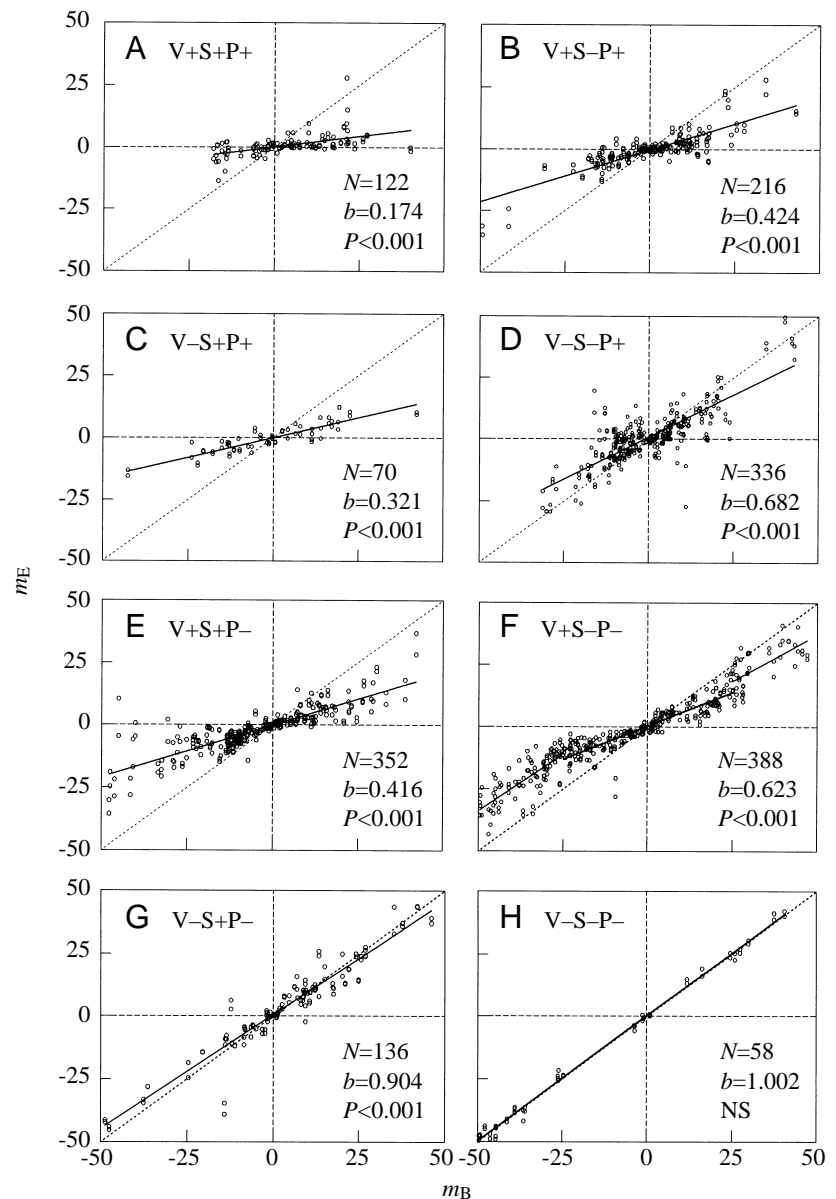


Fig. 8. (A–H) Dependency of the regression coefficient of the angular velocity of the eyes (m_E) on that of the body (m_B) for all eight combinations of V+/V–, S+/S– and P+/P–; i.e. a representation of the mean angular velocity of each eye in space over each segment of record analysed against the mean angular velocity of the long axis of the body over the same time period. The horizontal dashed line through zero represents perfect compensation for turns, while the diagonal dotted line represents no compensation. N , number of observations; b , slope of the regression line (solid line on graphs); P , statistical significance of regression line from a slope of 1 (t -test). NS, not significant. All differences between the slopes of V+ and equivalent V– groups (e.g. between V+S+P+ and V–S+P+), between the slopes of S+ and equivalent S– groups (e.g. V+S+P+ and V+S–P+), and between the slopes of P+ and equivalent P– groups (e.g. V+S+P+ and V+S+P–) are statistically significant (t -test: $P < 0.001$).

are statistically different (Sokal and Rohlf, 1981). Thus, intact animals (V+S+P+) have a significantly higher gain than all but groups V+S–P+ and V–S+P+, while all groups except V–S+P– have significantly higher gain than the control group V–S–P–.

These different ways of analysing the data bring out the different roles of the visual system, statocysts and leg proprioceptors, but above all they clearly demonstrate the need for all three systems to act together to produce accurate compensation for body turns (changes in the angular orientation of the longitudinal axis of the body) in freely walking crabs.

Discussion

Compensatory eye reflexes in *Cardisoma guanhumi*

Comparison of visual, statocyst and proprioceptive reflexes

Although Barnes (1990) measured the gain of the optokinetic responses of *Cardisoma guanhumi* in response to

movements of a striped pattern at a wide range of different velocities, no information on the frequency responses of these three reflexes in *C. guanhumi* has been available until now. These data, presented as Bode plots (Fig. 3), show that the visual system and the leg proprioceptive system respond best below 0.1 Hz, while the statocyst system only achieves a high gain above this frequency. Actually, both visual and leg proprioceptive systems perform rather better than this, since high-frequency responses to both these stimuli (for the visual system, see Barnes, 1990; for the leg proprioceptor system, see Varjú and Sandeman, 1982) were not apparent in the frequency analysis because of adaptation. Nevertheless, it is clear that the statocyst responses increase the frequency range of compensation, as observed in other crabs (for reviews, see Nalbach, 1990a; Barnes and Nalbach, 1993). Moreover, since the visual system operates through a negative feedback loop, it has the potential to provide more accurate compensation,

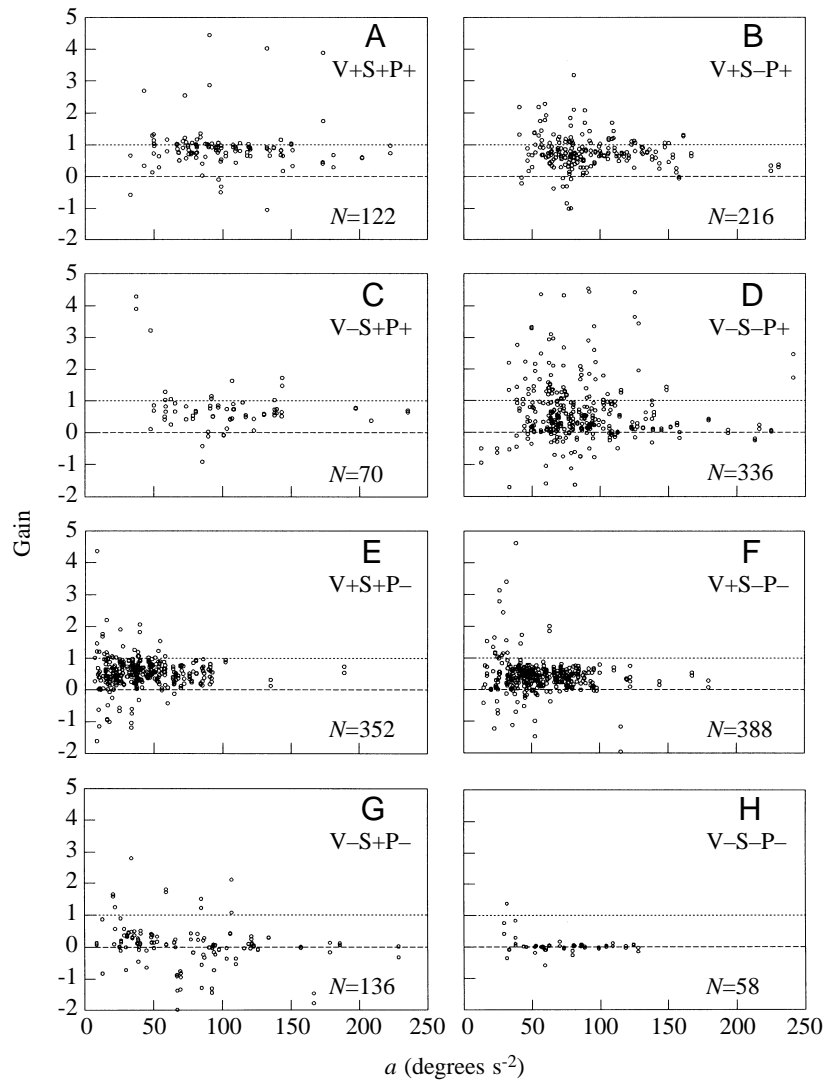


Fig. 9. (A–H) Dependency of the gain of the eyes on the angular acceleration of the body (a) for all eight combinations of V+/V–, S+/S– and P+/P–. N , number of observations.

because it can correct for external disturbances. Indeed, Neil (1982, 1985) suggested that the other systems bring the eyes into the range where fine control can be achieved by vision; i.e. the role of the legs and the statocysts is to reduce retinal image speed and thus to bring it into the working range of the optokinetic system (Nalbach, 1990a).

At the lower frequency range at which they function, visual and proprioceptive systems are approximately in phase with the stimulus, while the statocyst system shows a phase lead. This is as expected since the canal organs of the statocysts respond to angular acceleration but not to constant velocity or, for that matter, to linear acceleration (Fraser and Sandeman, 1975). However, partly because of the transmission delays inherent in any neural system, this phase lead declines at higher frequencies, so that when the statocyst system has a high gain its responses occur approximately in phase with the turns of the crab.

Relationship to habitat and eye design

As Zeil *et al.* (1986, 1989) have shown, the eyes of semi-terrestrial crabs come in two basic designs. So-called ‘flat-

world’ crabs, which live on beaches and mud flats, have their eyestalks close together and, like rabbits (Dubois and Collewyn, 1979) for example, have a pronounced acute zone for vertical resolution around the equator. ‘Complex environment’ species, in contrast, have their eyestalks far apart and lack this distinct acute zone for vertical resolution. This difference may be illustrated graphically by plotting R_v/R_h against E/c , where R_v is vertical resolution, R_h is horizontal resolution, E is eyestalk separation and c is carapace width. *Cardisoma guanhumi*, with R_v/R_h equal to 2.57 and E/c equal to 0.57 (W. J. P. Barnes and A. Chesi, in preparation), belongs to the ‘flat-world’ category. This is somewhat surprising since they live in mangrove swamps rather than on beaches or mud flats. Although such ‘flat-world’ crabs stabilise their eyes mainly by visual cues (for studies in the pitch and roll planes, see Nalbach *et al.* 1989; Nalbach, 1990a; for studies in the yaw plane, see Nalbach, 1990a), *C. guanhumi* additionally has well-developed proprioceptive and statocyst reflexes. In this respect, it is thus much more like rock crabs such as *Leptograpsus variegatus*. Certainly leg proprioceptor-generated eye movements have a much higher gain than in the shore crab

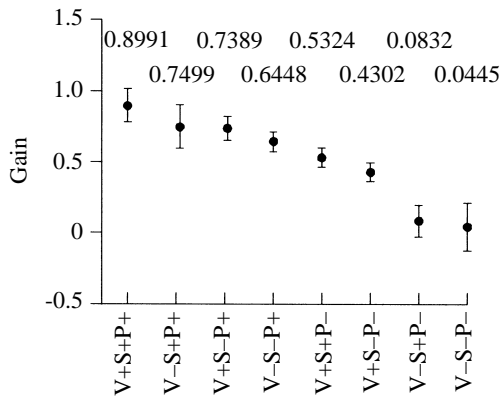


Fig. 10. Comparison of the distributions of the gain (mean \pm 95 % confidence interval) for all eight combinations of V+/V-, S+/S- and P+/P-. Mean values are given above the graph. Groups whose 95 % confidence intervals do not overlap are statistically different.

Carcinus maenas, a relatively more aquatic species (W. J. P. Barnes, H. Paul, C. Gordon and U. Herr, in preparation).

Sensory basis of compensation for body rotation

More direct information on the contributions of the different senses to compensation for body rotation is provided by the sensory deprivation experiments which, unlike previous work (e.g. Barnes, 1990; Paul *et al.* 1990), systematically examine all possible combinations of seeing/blind, with/without statocysts and with/without movement information from leg proprioceptors. Whether we are examining the angular position of the eyes in space (Fig. 7), the velocity of the eyes in relation to the velocity of body turns (Fig. 8) or gain (Figs 9, 10), the best compensation is seen when all three senses are present. Indeed, the absence of any one sense leads to a significant decline in performance. It cannot be excluded that some differences between the P+ and P- groups are due to our inability to mimic the angular velocity and angular acceleration of freely moving crabs when moving them on the trolley (Table 1). However, Fig. 8 (where the horizontal axis is angular velocity) and Fig. 9 (where the horizontal axis is angular acceleration) indicate that the only time when such an effect could have distorted the data was in the V+S-P- group, and this distortion has been avoided in Fig. 8F by calculating different regression lines for different sections of the data.

The most quantitative comparisons between the different combinations of senses can be made either by comparing the slopes of the regression lines in Fig. 8 or the gains in Fig. 10. They show clearly that the contributions of the three senses are additive since, with only one exception, responses where two senses are operating show better compensation than those where there is only one active sense, and having all three senses improves compensation still further. The canal organs of the statocysts perform worse on their own than either of the other two senses, but they do play an important role since animals with statocysts (S+ groups) perform considerably better than those without (S- groups). Given that *C. guanhumi*

has such large eyes and well-developed visually elicited behaviours, it is perhaps surprising that leg proprioceptive inputs are clearly as important as vision in compensating for body turns. Support for this conclusion comes from recent experiments by Layne (1998), who showed that the eye movements of crabs walking on a ball in response to the movement of stripes round the animal could be halted or even reversed by leg proprioceptive input of opposite sign.

How leg proprioceptors generate eye movements during turns in walking animals is by no means clear since, during walking, half the legs are being moved in one direction, while the rest are being moved in the other. In a further paper (W. J. P. Barnes, H. Paul, C. Gordon and U. Herr, in preparation), we will show that, if leg proprioceptive inputs contributed to eye movements only during locomotor power strokes, then this would produce leg proprioceptive inputs of appropriate sign and strength, as predicted by Varjú and Sandeman (1982). This gating is partly the result of changes in reflex gain, for the gain is higher when the legs are loaded, lowered or touching the ground, as occurs during the locomotor power stroke. But even when these differences are summed, they do not appear to be sufficient on their own. It is thus probable that there is also a central mechanism for gating the reflex according to the walking rhythm, comparable with the gating of inputs from the eyes, ocelli and wind-sensitive hairs that occurs in the control of flight orientation in locusts (Rowell and Reichert, 1985).

A final point that must be considered here is a possible contribution from centrally generated eye movements to the stabilisation of the eyes of walking animals. Clearly, the saccadic resetting movements of the eyes (fast phases of nystagmus) fall into this category, but there is no evidence from our data to support such a conclusion for the slow compensatory phases of the eye movements. But neither can they be absolutely excluded. Certainly, the absence of eye movements in the V-S-P- condition is no evidence against compensatory eye movements generated by the central nervous system, since in the absence of active turns they would not have been predicted.

Multimodal control of sensory guidance

As discussed above, multisensory control of eye movements increases the range of velocities to which crabs can respond and brings the control system into the range where visual feedback can provide accurate compensation for body turns. Indeed, the presence of all three senses can even act directly on the gain of the visual system, increasing it by a factor of up to five, so that its closed-loop gain approaches unity (Nalbach and Nalbach, 1987). In such ways, multisensory control produces good compensation for body turns which, as our sensory deprivation experiments have shown, declines significantly when even one sense is absent. In addition, it provides effective compensation under a variety of conditions, such as featureless environments and low light intensities, where visual mechanisms acting alone might have been insufficient. Since *C. guanhumi* is largely active at night (W. J. P. Barnes, personal observation), such multimodal control

might have particular significance for the detection of predators by this species.

In other animals too, multisensory convergence seems to be a common feature of sensory guidance mechanisms. In insects, visual stabilisation is provided by head movements, since the eyes are part of the head capsule and cannot be moved separately from the head. In dipteran flies, which have been extensively studied by Hengstenberg and others (for a review, see Hengstenberg, 1991), head stabilisation during flight is dependent on both visual (compound eyes and ocelli) and mechanosensory (halteres, wing campaniform sensilla and neck proprioceptors) inputs, while gravity, sensed by leg proprioceptors, only plays a role in walking flies. But this example is one of many. The use of compound eyes, ocelli and wind-sensitive hairs in the control of flight direction in locusts (Rowell *et al.* 1985) has been referred to already. Additionally, light cues, a magnetic compass and mechanosensory inputs resulting from wave action are all used by turtle hatchlings to find the open sea (Lohmann and Lohmann, 1996), chemical and vibratory stimuli both play a role in mate location in male spiders of the genus *Cupiennius* (Barth, 1993) and olfactory stimuli, tactile stimuli and near-field sound are all important in the process by which honeybees perceive the information of the dance language (Dreller and Kirchner, 1993). It could be argued that the taxes and kineses of Fraenkel and Gunn (1940) illustrate many of the exceptions to this generalisation. But it is probable that, as these responses occurred under simplified laboratory conditions, they represent components of sensory guidance mechanisms rather than complete ones. Indeed, it is probably fair to say that, in the same way that reflexes form components of many mechanisms of motor control, kineses and taxes represent the building blocks from which whole sensory guidance mechanisms are constructed.

Why compensate for body turns?

Our work has shown that crabs go to extraordinary lengths, involving three different sensory systems, to simplify the chaotically complex visual input that they receive so that the images that reach the eye can be more readily interpreted. This input comprises both stationary and moving objects of differing sizes and in different parts of the visual field, all influenced by the crab's own movements which involve rotation as well as translation.

The simplest conclusion is that, to make use of their excellent vision (by invertebrate standards), crabs need precisely controlled compensatory eye movements to reduce retinal image speed (Paul *et al.* 1990). This is because moving objects (including predators and mates) are much harder to detect against a moving background. But it is also reasonable to suppose that, since the optic flow field provides information about an animal's movements (change in direction, velocity, distance travelled) as well as giving the animal a three-dimensional view of the world by motion parallax, some of this information is used by crabs and is made accessible by eye movements that compensate for the rotatory but not the translatory components of optic flow.

The functional role of this flow-field analysis remains an enigma. Present data indicate that, since freely walking crabs do respond to moving stripes with body turns, the direction of movement is influenced by the rotatory component of the visual flow field (Paul *et al.* 1990). Thus, a role in course control can be envisaged. Also, Nalbach's (1990b) study of soldier crab (*Mictyris longicarpus*) escape responses showed that turns away from the predator were based on evaluation of angular displacement on external (world-centred) coordinates, such world-centred coordinates being provided by the eye movements that compensated for body turns. In contrast, Land and Layne (1995) could not see any obvious role for eye movements in their study of fiddler crab (*Uca pugilator*) tracking control systems in both courtship and defence. Thus, we have a phenomenon, a sophisticated system incorporating multisensory control, to compensate for the rotatory component of optic flow without a full understanding of how the information made available is used. Such a mechanism makes good functional sense, but more field and laboratory experiments are clearly required before we can put flow-field analysis by crabs into its true behavioural perspective

Appendix: explanation of symbols used in the space coordinate system

a	angular acceleration of body axis (in degrees s ⁻²) $\frac{1}{n} \sum_{t_1}^{t_2} d\omega/dt,$ where n is the number of data points between limits t_1 and t_2
gain	amplitude of response divided by amplitude of stimulus $[(\Delta\phi_B - \Delta\phi_L \text{ or } R)/(\Delta\phi_B)]$
m_B	regression coefficient of body (= slope of regression line). Its value is the angular velocity of the body axis (in degrees s ⁻¹) and its sign is the direction of the movement (+ anticlockwise; - clockwise)
m_L, m_R, m_E	regression coefficients of left, right and both eyes. Their values are the angular velocities of the eye(s) (in degrees s ⁻¹) and their sign is the direction of the movement (as for m_B)
v	translational velocity (cm s ⁻¹)
ϕ_B	angular position of the long axis of the body in external coordinates
ϕ_L, ϕ_R, ϕ_E	angular position of left, right and both eyes in external coordinates
t	time
t_1 and t_2	start and end points of each segment of body (and eye) movement
ω	angular velocity, $d\phi_B/dt$, calculated between each frame analysed (degrees s ⁻¹)

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