SENSORY BASIS AND FUNCTIONAL ROLE OF EYE MOVEMENTS ELICITED DURING LOCOMOTION IN THE LAND CRAB *CARDISOMA GUANHUMI*

By W. JON P. BARNES

Department of Zoology, University of Glasgow, Glasgow G12 8QQ, Scotland, UK

Summary

Eye movements in the horizontal plane and the rotatory component of body movement have been continuously recorded in land crabs, *Cardisoma guanhumi* Latreille, walking freely in an arena.

The results show that the eyes compensate for locomotor turns by moving in the opposite direction to the body, thus reducing the image motion of surrounding objects on the retina. Gains often approach unity, so that stabilization of the rotatory component of self-generated image motion is good. Of the three compensatory eye reflexes that could contribute to these responses, optokinetic responses play a major role, since the gain of the responses of freely walking blinded crabs was about half that of crabs that could see. Since blinded crabs held above a ball moved their eyes whenever they rotated the ball about a vertical axis (i.e. turned), a significant role for leg proprioceptor-driven eye movements is also presumed. It is unclear whether vestibular nystagmus, driven by the statocysts, also has a role to play.

In contrast to the high-gain compensatory responses that accompany turns, the translatory component of locomotion elicits compensatory eye movements only under the most favourable circumstances, when the crab walks along a runway facing a set of stripes. Even then, the responses are of very low gain (0.02–0.09). Amongst several possible factors, this is partly because lateral ommatidia, which drive the optokinetic responses, will face the poles of the flow field during sideways walking, and partly because stationary contrasts (as occur at the poles of the flow field) reduce the gain of optokinetic responses.

It is argued that, by compensating for turns but not translatory locomotor movements, crabs effectively separate the rotatory from the translatory components of the visual flow field around them. Since only the former can be used in course control, while only the latter provides information on ground speed and the three-dimensional layout of the environment, such a separation makes good functional sense.

Introduction

Crabs, like most other higher crustaceans, have movable eyes on stalks. Although they do not use their eyes to fixate and track objects of interest, as do mantis shrimps (Cronin *et al.* 1988), they do show a variety of other eye movements, many of which have been intensively studied (see reviews by Sandeman, 1977; Neil, 1982). These include protective eye retractions, tremor, slow drift in the absence of stationary contrasts in the visual field, fast saccadic eye movements that re-centre the eye in its socket, eye scanning and compensatory reflexes. Such compensatory reflexes belong to a class of equilibrium responses that do not in themselves correct for deviations from equilibrium, since it is the eyes rather than the body that moves, but instead compensate for such deviations. In crabs, compensatory eye reflexes occur in response to movements of the visual field (e.g. rotation of a striped drum around the animal), rotation of the crab and imposed leg movements, the relative strengths of these reflexes differing in crabs from different environments (Nalbach *et al.* 1989). Visual responses occur to vertical as well as horizontal stimulus movements (Barnes and Horridge, 1969*b*) and also on reillumination following a change in drum position during a period of darkness – the phenomenon of optokinetic memory (Horridge, 1966*a*). Detailed comparisons of memory responses and responses to step-like displacements of a striped pattern (Fleischer, 1980) show that the memory response is best described as a long-time-constant movement detection system, which lies in parallel with the system responsible for detecting faster movements. Recently, Nalbach (1989) has confirmed this finding and gone on to show that *Carcinus* has three movement detection systems of different time constant lying in parallel with each other.

Since stabilization of the image of the world on the retina is a prerequisite for good vision, it has always been assumed that the main function of these eye movements was to compensate for the movements of the animal, whether voluntary or involuntary. Such compensation is not as simple as might at first be assumed, for the combination of self movement and the real movement of objects in the environment means that freely moving animals receive a highly complex visual input called the 'visual flow field'. As has been most elegantly described by Buchner (1984), such a visual flow field can be decomposed into three components, which result from the animal's rotatory and translatory movements and also from the movements of non-stationary objects. Useful information about the animal's own performance and the position of objects around it can be gained from these different components. For instance, since rotation results in image rotation in the opposite direction to the movement, the rotatory component of the visual flow field can assist in course control. Deviations from an intended path would lead to image motion that is proportional to the deviation. Second, information on locomotor velocity and the three-dimensional layout of the environment are available from the translatory component of the flow field. As Fig. 1A shows, movement in a straight line causes image motion in the opposite direction, movement being greater the nearer the objects are to the animal. The apparent motion of very close objects, which move past it at the speed it is travelling,
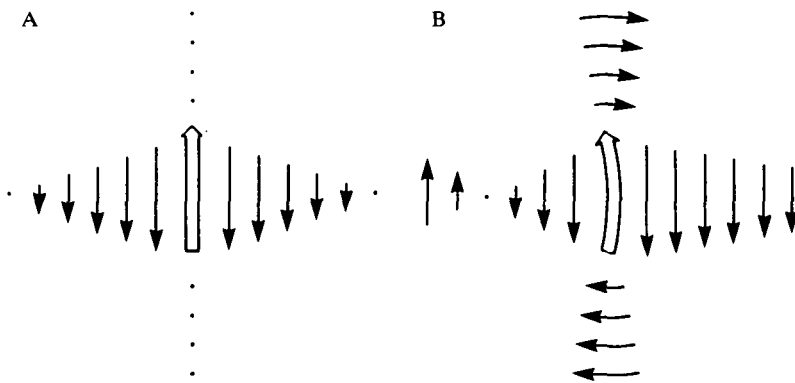
Fig. 1. Visual flow fields in and at right angles to the direction of motion during pure translatory locomotion (A) and a combination of translation and rotation (B). During pure translation, the flow field is symmetrical, the relative movements of objects depending both on their distance and their angle to the subject, being maximal at right angles to the direction of locomotion and zero along the line of motion. When translation is combined with rotation, their effects are additive. Thus, the motion seen on the outside of the curve in B is increased, while that on the inside of the curve depends upon distance. Nearby, the translation effect dominates, but further away the rotatory component of the flow field is larger and the direction of the perceived motion is reversed.

provides information on its own velocity, while the relative motion of different objects provides information on their respective distances from it (the phenomenon of motion parallax). To gain all this useful information, it is, however, necessary to separate the different components of the flow field from each other, since movement along a curved path (Fig. 1B) results in a complex flow field that defies easy analysis.

As Zeil *et al.* (1986) have shown, the eyes of semi-terrestrial crabs come in two basically different designs. 'Flat world' species such as *Uca* and *Ocypode* that inhabit beaches or mud flats have long, vertically oriented eye stalks that lie close to each other and are raised high above the carapace, whereas 'complex environment' species such as *Pachygrapsus* and *Cardisoma* that inhabit rocky shores or mangrove swamps have short, widely separated eye stalks. Since the vertical resolving power of the eyes of flat-world species reaches a high maximum at the eye equator which looks at the horizon, they are admirably adapted for estimating distance monocularly since the distance of an object from the eye can be estimated from the height of the eye above the ground and the angle between the object and the horizon. In contrast, the wide separation of the eyes of complex-environment species, also seen in some larval crustaceans, is suggestive of binocular depth perception. Certainly, such crabs do not have such a pronounced maximum in the vertical resolving power of their eyes.

This study, carried out on the semi-terrestrial, sideways-walking, complex-environment species *Cardisoma guanhumi*, utilises techniques that allow the recording of both horizontal eye movements and body rotation in crabs free to

walk around in a large arena (Barnes, 1982). It demonstrates that freely moving crabs separate the rotatory from the translatory component of the visual flow field by showing compensatory eye movements to only the former, and investigates the mechanisms that enable them to do this. A comparable study, using different techniques, of the eye movements of freely moving rock crabs (Paul *et al.* 1990) appears alongside this account. Both studies substantially update earlier qualitative observations by von Buddenbrock *et al.* (1954) and Dijkgraaf (1956*a*,*b*). Preliminary accounts of some of these experiments have appeared elsewhere (Barnes, 1985, 1989).

Materials and methods

Land crabs (*Cardisoma guanhumi*), averaging about 6 cm carapace width, were purchased in Trinidad in local markets by visiting research workers and transported to Britain by air. They were maintained in large shallow tanks containing coarse sand and gravel from the sea shore and dishes of fresh water so that the animals could submerge themselves. They were fed on raw carrots and green vegetables twice a week.

For the experiments, horizontal eye movements were monitored by a capacitative position-sensing device (Forman and Brumbley, 1980). A 25 mm long 150 μm diameter steel wand carrying a 40 kHz low-voltage signal was attached to the peninsula of non-corneal exoskeleton on the back of the crab's eye and bent back so that its tip moved between two sensors attached to the dorsal surface of the crab's carapace (Fig. 2A).

Body turns in the yaw plane were recorded by a crossed polaroid device

A

Eye-position-sensing device

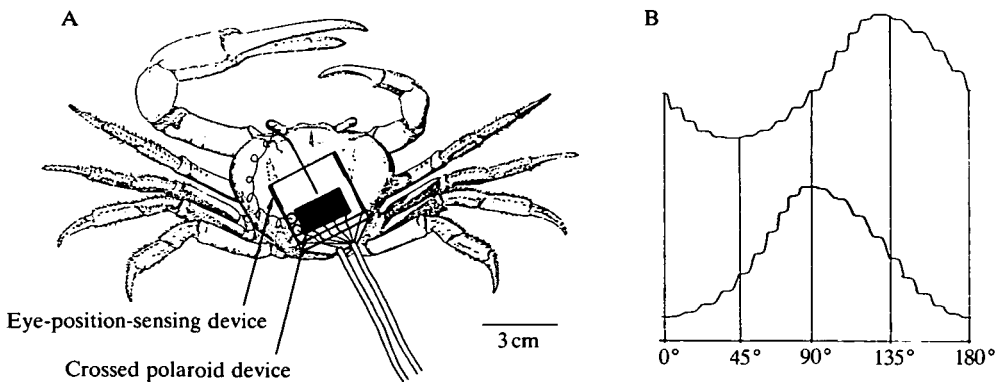Crossed polaroid device

3 cm

B

0°   45°   90°   135°   180°

Fig. 2. (A) Assembly for recording eye movements and the rotatory component of body movement mounted on the back of a crab. (B) Output of crossed polaroid device used to measure rotatory component of crab's movement within the arena. To produce the output shown, the device was removed from the crab and mounted on a turntable which was turned through 180° in 9° steps. Although the output of each photocell changed from positive-going to negative-going or the reverse every 90°, changes in the direction of the crab's movement could be unambiguously recognised because these were the only occasions when the output of both photocells changed at the same time.

(Barnes, 1982). One piece of polaroid was mounted in front of a slide projector that evenly illuminated the arena with polarized light, while two further pieces were mounted on top of light-dependent resistors attached above the eye-movement detecting system on the crab's carapace (Fig. 2A). The latter pieces were orientated at 45° to each other so that points of minimum sensitivity of one device corresponded with points of maximum sensitivity of the other (Fig. 2B). Although tilting of the crab about either pitch or roll axis and any slight unevenness in the illumination of the arena reduced the accuracy with which turns could be measured with this device, careful checks showed that an accuracy of ±10% was possible so long as data from crabs attempting to climb the sides of the arena were excluded.

Long leads supplying and recording the signals allowed the animal complete freedom of movement within a 0.8 m diameter arena. This arena had transparent sides and was itself located within a stationary 1.6 m diameter drum of black and white vertical stripes whose upper and lower borders subtended from about 40° above to about 10° below the eye equator of a crab located at the centre of the arena. The stripes subtended 11.25° at the crab's eye (i.e. stripe repeat distance was 22.5°).

For a few experiments, where it was important to avoid possible inaccuracies of calibration of the above devices for measuring eye movement and body turns, 12 frame s^{-1} ciné films were made from above of crabs moving freely within the arena. Narrow black and white stripes were attached to the wand on the crab's eye and to the carapace to mark the crab's transverse axis. They were clearly visible on the ciné film, allowing eye and body position to be accurately measured (±1°) from drawings of selected projected ciné frames.

To test ideas about the possible mechanisms that crabs might use to separate rotation from translation, eye movements were recorded from crabs held within an optokinetic drum consisting of two sets of three stripes, with and without additional stationary contrasts (see Fig. 10A).

Results

Eye movements in freely moving crabs

Many years ago, von Buddenbrock *et al.* (1954) and Dijkgraaf (1956*a,b*) filmed free-walking lobsters (*Palinurus*) and crabs (*Carcinus* and *Maja*) and described how they compensated for body turns by moving their eyes in the opposite direction to the body, thus tending to reduce the image motion of surrounding objects on the retina. These observations are confirmed in this study by simultaneous recordings of the eye and body movements of *Cardisoma* walking freely within the arena. Body turns about the yaw axis are invariably compensated for by movements of the eyes. In the example shown in Fig. 3A, the crab began by walking forwards, a movement that is accompanied by small-amplitude oscillations of the body. Each of these small oscillations was accompanied by an eye movement in the opposite direction, so that when the body swivelled to the right,
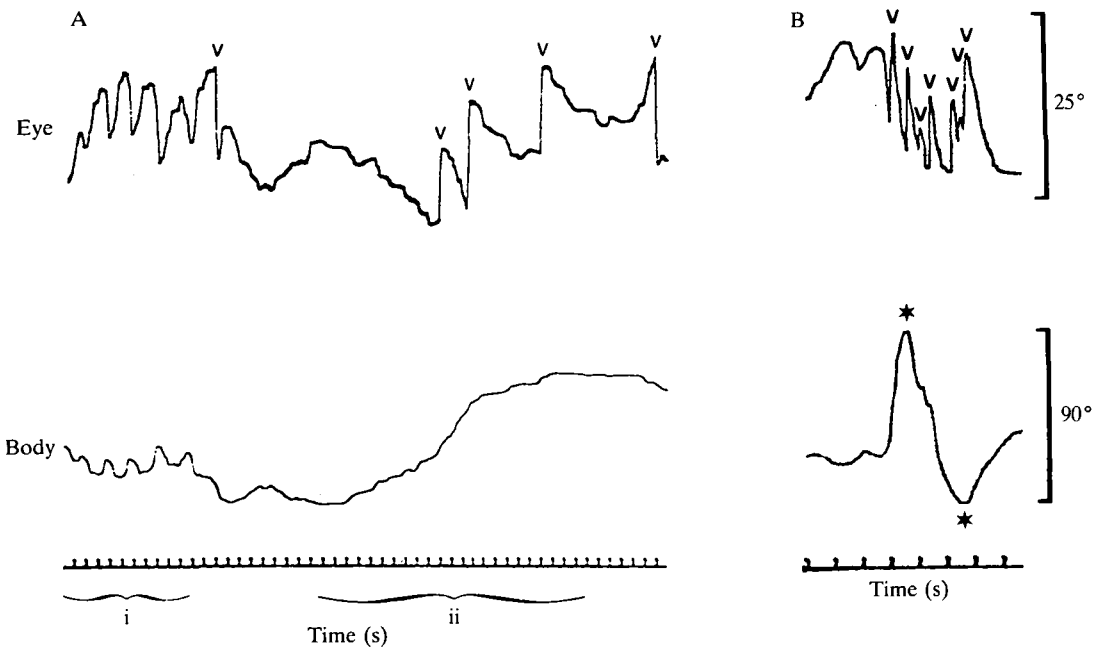
Fig. 3. Movement of right eye and body of a crab walking freely within the arena. In A, the crab began by walking forwards (i) and then turned through 75° to the right (ii). In B, a 190° right turn was completed in 5 s. Eye movements to the left are indicated by a downward movement of the trace. ★, second crossed polaroid (not shown) indicates that these are continuous turns, not reversals of direction. v, fast phases of nystagmus.

the eyes moved to the left and *vice versa*. Subsequently, a 75° right turn was accompanied by compensatory eye movements to the left with interposed fast phases of nystagmus (saccades) in the same direction as the turn. Close examination of such records shows how well, qualitatively, the crab is compensating for the rotatory component of its visual flow field. Changes in the velocity of body turns are replicated by the eyes, whose movements, if one excludes the fast phases of nystagmus, are the inverse of the body rotations recorded by the crossed polaroid device. Even though the gain of optokinetic responses to fast movements of a striped drum is low (Horridge and Sandeman, 1964), fast active turns evoke compensatory eye movements. For instance, in the record shown in Fig. 3B, a 190° turn of the body completed in 5 s was accompanied by a compensatory eye movement that was almost as fast as the saccadic re-centring movements of the eye.

The fast phases of nystagmus are saccadic eye movements that reset the eyes in their sockets. Their time of occurrence during active turning in *Cardisoma* is much more variable than during optokinetic nystagmus in *Carcinus* (Barnes and Horridge, 1969a) or passive turning of the lobster *Palinurus* about its vertical axis (Dijkgraaf, 1956a), when the fast phases almost invariably occur when the eye is approaching the end of its traverse. Nevertheless, these data do not provide

confirmation for the observation of Dijkgraaf (1956b) that, during such active turns, the fast phases usually occur when the eyes are near the middle of their traverse, so that both eyes end up spending most of their time facing in the direction of the turn. The 75° right turn of Fig. 3A does, to a degree, illustrate the point that Dijkgraaf is making, but such occurrences, while not uncommon, are in the minority. Nor have I seen, *contra* Bethe (1897), Dijkgraaf (1956a) and Paul *et al.* (1990), fast phases in the same direction as a turn preceding such turns.

For precise quantitative measurements of eye and body movements, ciné films of walking crabs were analysed frame by frame as already described. From plots of eye *versus* body angle, it can be seen that the system gain (amplitude of eye excursion excluding fast phases divided by amplitude of turn) often reaches unity (mean of 0.80 in Fig. 4A), so that stabilization of the rotatory component of self-generated image motion is good. During low-amplitude turns (less than 20°), compensation is equally good for fast and slow turns, but for larger turns the line of best fit for a plot of gain *versus* velocity of turn has a significant negative slope ($P<0.001$, t-test; data not shown); i.e. there is poorer compensation for large fast turns.

Although crabs are usually thought of as sideways-walking animals and, indeed, most species do walk sideways when walking fast (Clarac and Barnes, 1985), they are capable of walking in any direction. Thus, changes in direction can be brought about by changes in the direction of walking as well as by rotation of the crab about its yaw axis. An example of such a change in the direction of locomotion, brought about in this instance by a change from forwards to sideways locomotion, is shown in Fig. 5. It is not accompanied by any eye movements, thus supporting the claim that the eye movements seen during yaw movements of the body axis are compensating for the rotatory component of visual flow.

Effects of sensory deprivation on eye movements

That *Cardisoma* exhibits the same compensatory eye movements as other crabs is shown in Fig. 6. Optokinetic nystagmus is produced by holding a crab within a drum of rotating black and white vertical stripes. The eyes follow the movement of the stripes, flicking back at intervals to their starting position (Fig. 6E,F). The responses occur at high gain over a wide range of velocities (Fig. 6G). It would be surprising if such a reflex did not contribute to the eye movements of freely turning animals, in spite of a claim to the contrary by Dijkgraaf (1956a). Therefore, as a first step in investigating the sensory basis of the compensatory eye movements seen in freely moving crabs, crabs were blinded by pushing an opaque plastic cap over the eyecups. Under such conditions, the eyes still compensate for turns, though eye movements are much less smooth than when the eyes can see (Fig. 7A). Since the eyecups of *Carcinus* lack proprioceptors (Horridge and Sandeman, 1964), it is probable that compensatory eye movements seen in blinded crabs are open-loop. The lack of fine control is thus not surprising. Quantitative examination of the eye responses of blinded free-walking crabs shows that, in the absence of vision, the gain of the compensatory responses is reduced to a mean of
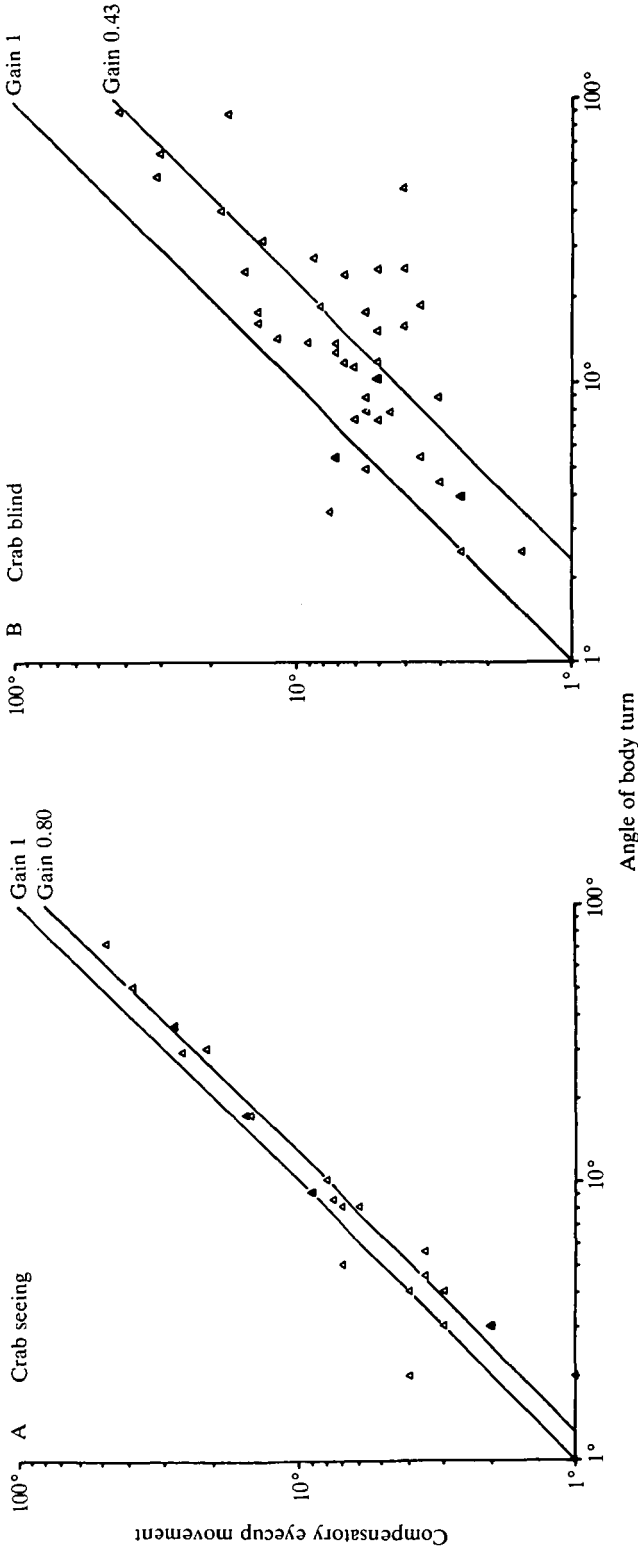
Fig. 4. Plots of amplitude of compensatory eye movement (fast phases of nystagmus excluded) against amplitude of turn for two crabs (A and B) walking freely within the arena. In A, both eyes were free to see and move. In B, the crab was blinded by covering both eyes with opaque plastic caps. Lines on the graphs represent gains (angle of eye response divided by angle of turn) of 1.0 and 0.8 (A) and 1.0 and 0.43 (B). The lower values in each case represent the mean response of the crab. Comparable data were obtained with three other pairs of animals.
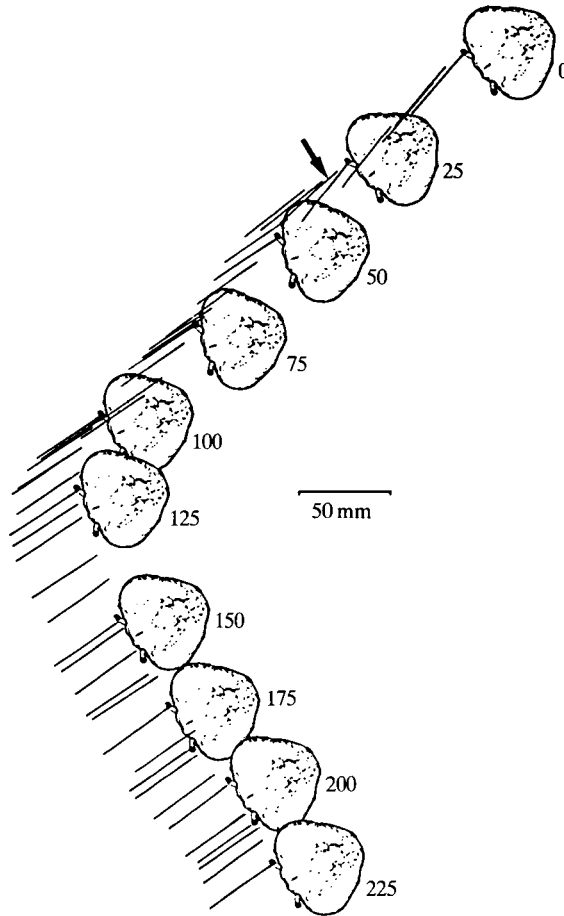
Fig. 5. Positions of eye and body in space drawn from a 12 frame s^{-1} ciné film of the crab walking in the arena. The position of the body is drawn every 25 frames, the position of the wand attached to the eye every five frames. Note saccade at frame 30 (arrow). Except for this saccade, the position of the eye in space remains constant within ±1°. The change from forwards to sideways locomotion is not accompanied by any eye movement.

between 0.4 and 0.5, and their variability is increased (Fig. 4B). This clearly indicates a role for vision in these responses, but also shows that they are not driven exclusively by visual inputs.

In a few preliminary experiments, blinded crabs have been held by the carapace either above a plastic football supported in a bucket of water or on a polystyrene ball supported on an air cushion with ball motion about all axes monitored by the method of Dahmen (1980). Under such conditions, neither optokinetic nystagmus nor vestibular nystagmus can contribute to the eye responses. However, as leg rotation about the body produces eye movements in blinded crabs in the same direction as the legs are moved (Fig. 6C,D), a role for eye movements driven by
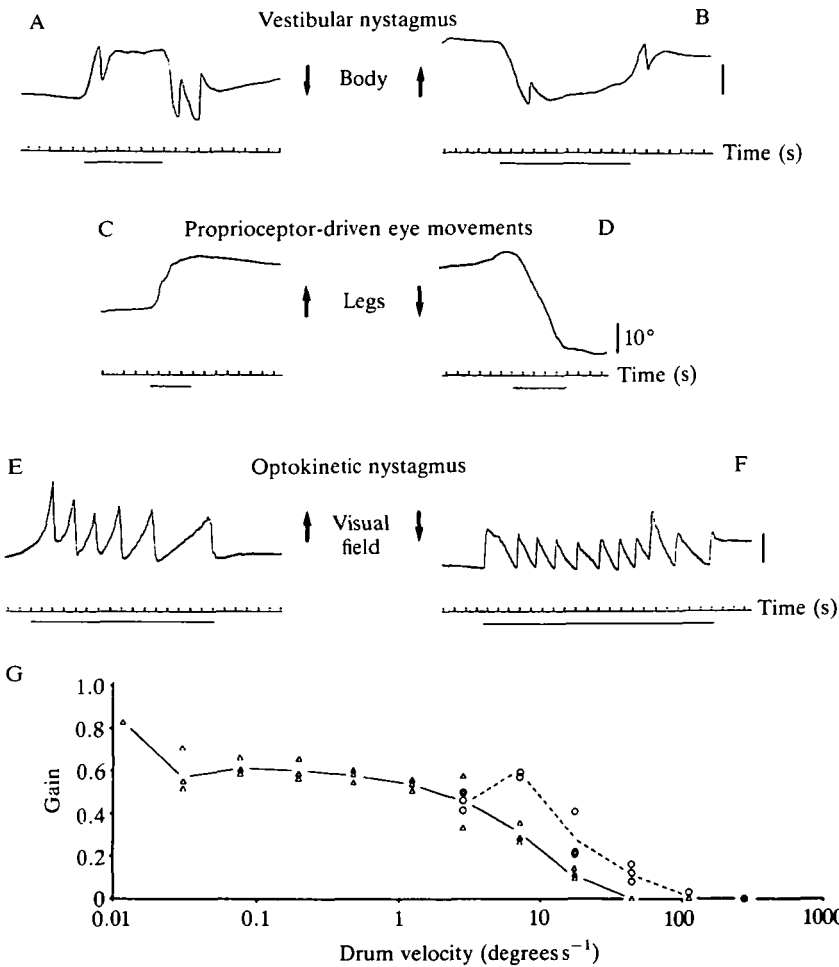
Fig. 6. Compensatory eye reflexes in *Cardisoma*. (A,B) Vestibular nystagmus pro-
duced by rotation of a blinded crab about its vertical axis, the responses occurring at
the start and end of the movement. (C,D) Leg proprioceptor-driven eye movements
generated by rotation of a platform held under the legs of a blinded animal.
(E,F) Optokinetic nystagmus elicited by rotation of a black and white striped drum
around the animal. Compensatory eye movements to the right (indicated by an
upwards movement of the traces) are produced by acceleration to the left, leg
movements to the right and drum movement to the right, as seen in A, C and E;
compensatory eye movements to the left are produced by acceleration to the right, leg
movements to the left and drum movement to the left, as shown in B, D and F. The
horizontal bars indicate the period of stimulation. (G) Gain (eye velocity divided by
drum velocity) of optokinetic response in *Cardisoma* measured from experiments in
which a striped drum was rotated continuously around the animal at a range of
velocities. At high drum speeds, the response shows considerable adaptation, waning
from an initial value (open circles and dashed line) to a lower one (open triangles and
continuous line) within 30 s. Comparable data were obtained with two other animals.
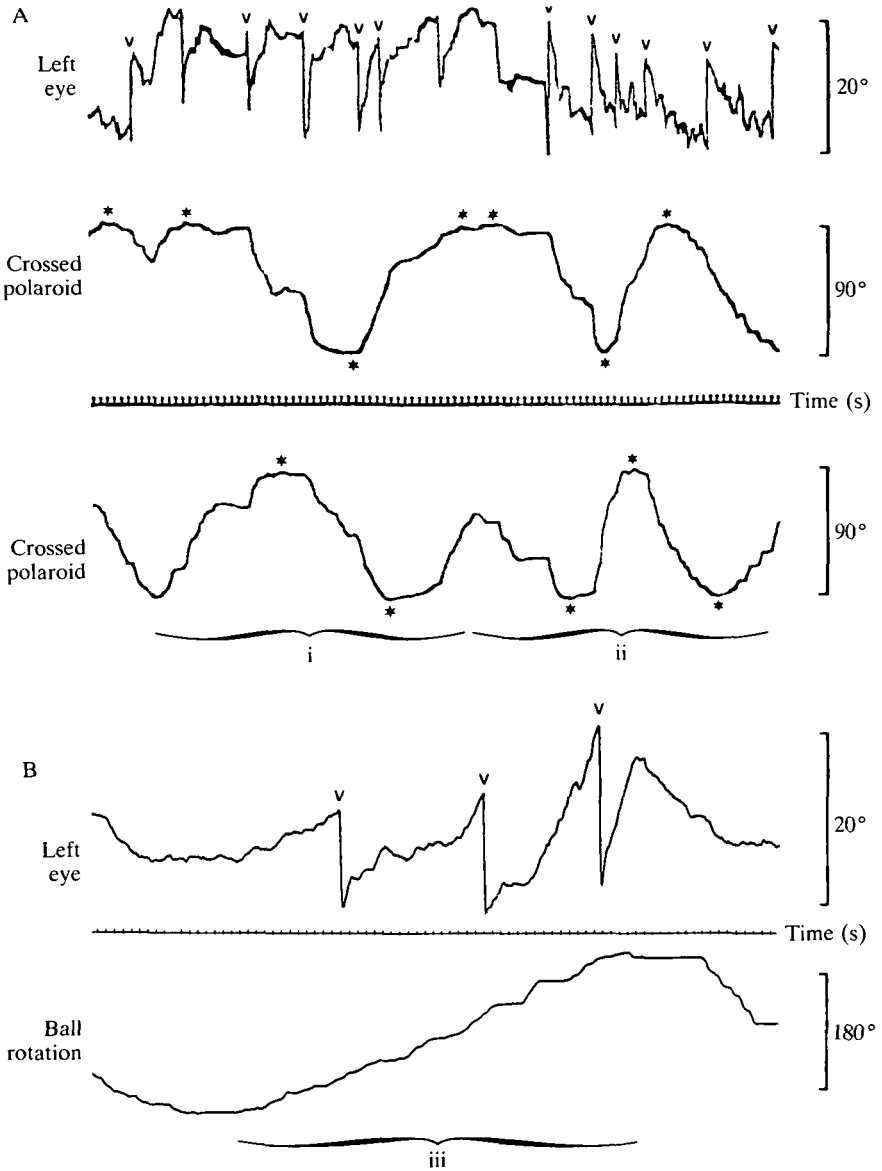
Fig. 7. (A) Compensatory eye movements in a blinded crab. The crab walks around the edge of the arena, first in an anticlockwise direction, the curved path involving 220° of rotation to the left (i), then in a clockwise direction, the path involving 265° of rotation to the right (ii). (B) Eye movement elicited by leg proprioceptors in a blinded and rigidly fixed crab turning a polystyrene ball under its legs. Compensatory eye movements to the right (as shown in iii) are generated whenever the crab rotates the ball about a vertical axis in a clockwise direction (i.e. turns left). Eye movements to the left are indicated by a downward movement of the trace in both A and B, and anticlockwise ball rotation by a downward movement of the trace in B. ★, comparison of the outputs of the two crossed polaroid devices indicates that these are continuous turns, not changes of direction. (v) fast phases of nystagmus.

leg proprioceptors (Dijkgraaf, 1955; Varjú and Sandeman, 1982) is not excluded by this procedure. From these experiments, it seems clear that when the crabs are rotating the ball about a horizontal axis (i.e. they are walking in a straight line, in most cases sideways), no compensatory eye movements occur. However, whenever the crab revolves the ball about a vertical axis (i.e. turns), the eyes show compensatory responses, moving in the direction in which the ball was being turned (Fig. 7B). It is thus probable that proprioceptive input from the legs during the stance phase of locomotion (see Discussion) also contributes to the eye movements of freely moving crabs.

Eye movements during translatory movements

The above experiments clearly indicate that crabs compensate well for the rotatory component of self-generated image motion. Experiments were therefore designed to investigate whether translatory locomotion also generates compensatory eye movements. As described in the Introduction, movement in a straight line produces much more complex effects at the retina than does rotation. No displacement of the image occurs along the line of direction of walking (the poles of the flow field), while maximum displacement occurs at right angles to this, being greater the nearer the objects are to the eye (Fig. 1A).

In these experiments, crabs walked sideways down a runway facing a set of stripes, the experimental arrangement being such that image displacement of objects across the front of the eye during such a walk would have been in the range 85–150°. Such locomotory movements did not invariably induce clear compensatory eye movements, even though turns executed during or immediately after such walks did induce such movement. For instance, compensatory movements to small body oscillations are clearly seen in all traces, as they are to turns in Fig. 8A,C. In contrast, although small superimposed eye movements compensating for the apparent movement of the stripes past the front of the eye are seen in Fig. 8A,B, they do not appear to be present during the walk illustrated in Fig. 8C.

To examine this quantitatively, the net angular deviation of the eye (difference between eye positions at the start and end of a walk down the runway taking account of any interposed fast phases of nystagmus) was plotted against the net angular change in body angle (difference between body positions at start and end of walk) for leftward and rightward walks along the runway. If there is a component of eye movement induced by the translatory movement of the crab, this will cause the lines of best fit to be shifted upwards and downwards, respectively, in Fig. 9A,B, since walking left should cause the eyes to move to the right and *vice versa*. As can be seen, this occurs to a small, but statistically significant, degree ($P=0.025$, covariance analysis), though the mean gain of this component of eye movement, calculated as net angular deviation of the eye divided by angular displacement of stripes past the front of the eye, is very low (0.02–0.09) compared to that occurring in response to the rotatory component of locomotor movement.

Since the gain of the eye movements compensating for translatory locomotion of
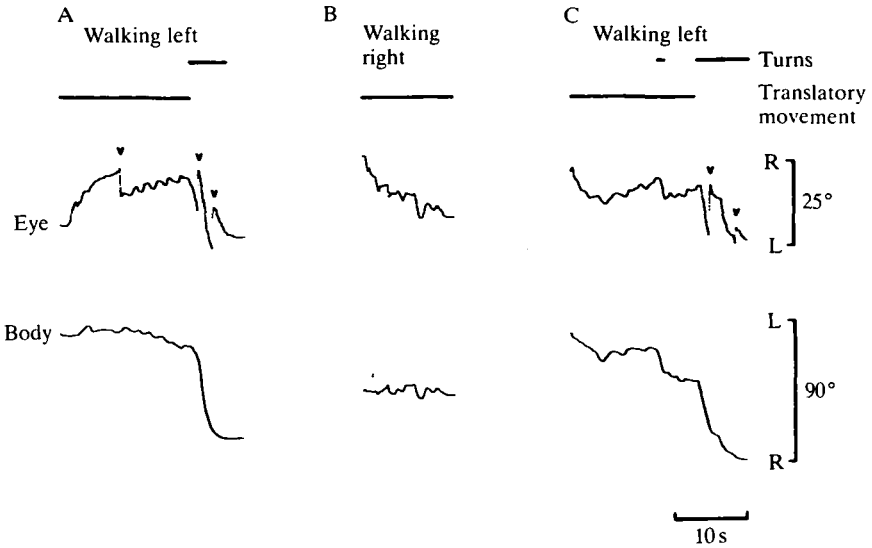
Fig. 8. Eye movements during translatory locomotor movements, the crab walking sideways down a runway facing a set of stripes. In A and B, but not C, there is a small net movement of the eye in the direction of the apparent motion of the stripes past the front of the eye. At the end of these sideways walks in A and C (and also during the walk in C) the crab turns to the right, these turns being accompanied by strong compensatory eye movements in the opposite direction. L, left; R, right; v, fast phases of nystagmus.
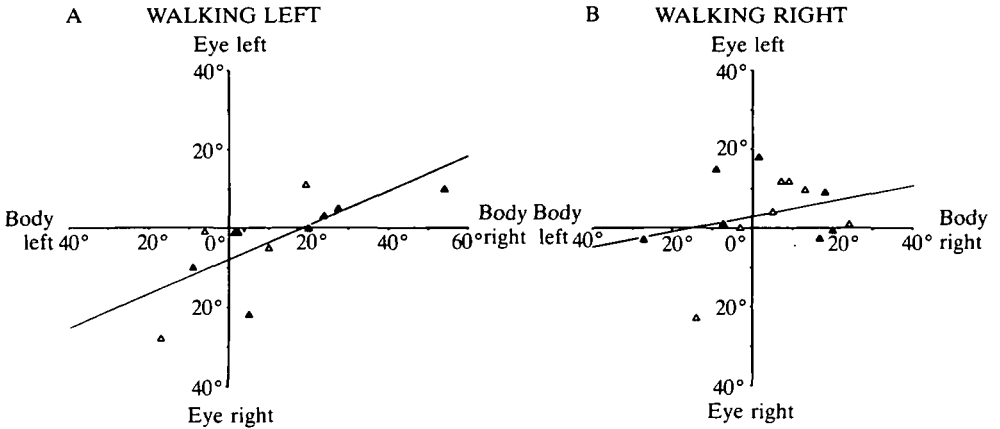

Fig. 9. Plots of net change in eye angle against net change in body angle between the starts and ends of sideways walks down a runway, the crab walking to the left in A, to the right in B. Solid triangles, the side of the runway faced by crab is covered with vertical stripes, the other side being plain. Open triangles, both sides of the runway are covered in stripes. Although lines of best fit drawn from all the data do not have statistically different slopes, they do show a significant vertical displacement from each other ($P=0.025$, covariance analysis), indicating that eye movements have a small translatory component under these experimental conditions.

the crab are so low, they can play no real role in stabilizing the retinal image. Instead, one is drawn to the conclusion that the control system governing the eye movements during free walking is designed to separate the rotatory from the translatory components of the visual flow field, but that the apparent movement of the stripes past the front of the eye is such a powerful visual stimulus that a small response to translation occurs. Certainly, in experiments where crabs were fixed to a trolley and towed sideways down the runway past the stripes, no eye movements were recorded.

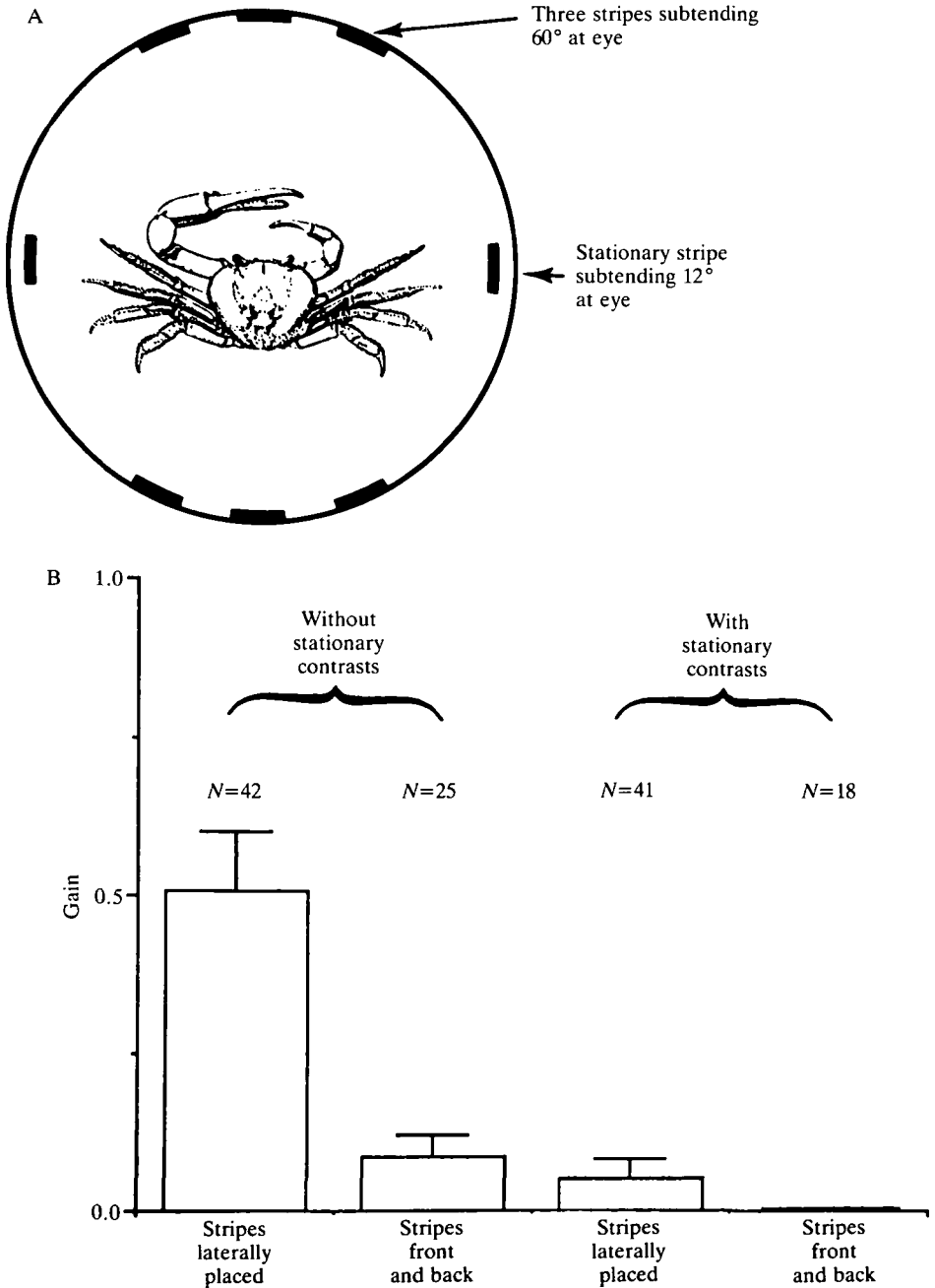*Why do translatory locomotor movements not evoke high-gain compensatory eye movements?*

In theory, there could be a number of reasons why high-gain eye responses do not occur during translatory locomotor movements. (1) The optokinetic responses might be so weak that, in the absence of congruent input from leg proprioceptors and statocysts, resulting eye movements are of low gain. (2) The input for optokinetic responses might be summed over the whole eye, in which case image motion in one direction over anteriorly facing ommatidia would be largely cancelled out by image motion in the opposite direction seen by posteriorly facing ommatidia. (3) Optokinetic responses might be driven largely by laterally facing ommatidia which, since they point in the direction of the poles of the visual flow field during sideways locomotion, would only be stimulated by turning movements of the crab. (4) The presence of stationary contrasts at the poles of the flow field might largely inhibit eye responses that would otherwise occur during translatory locomotor movements. The last three of these possibilities are briefly investigated here.

That summation of inputs from different ommatidia is involved in the generation of high-gain optokinetic responses in *Carcinus* is clearly shown by the comparatively weak responses elicited by movement of a pinlight (Horridge, 1966b) or single stripe (Barnes, 1968). To investigate whether such summation plays a role in the prevention of responses to translatory body movements in *Cardisoma*, the eye movements generated by translatory locomotor movements were recorded both when the crab walked sideways down a runway with patterns of stripes front and back, and also when the striped pattern was present only at the front with the back wall of the runway lacking contrasts. As can be seen from Fig. 9A,B, translatory movements of the crab down the runway with stationary contrasts on only one side failed to induce higher-gain eye responses to

Fig. 10. (A) Optokinetic drum used to study effectiveness of different parts of the eye in initiating optokinetic responses and the degree to which stationary contrasts in the visual field inhibited such responses. (B) Histograms showing means and standard deviations of the gains of the eye responses to sinusoidal oscillation of the optokinetic drum illustrated in A at an amplitude of 2.1° peak-to-peak and frequency of 0.1 Hz. As indicated on the histograms, the crab was tested under four experimental conditions, the two sets of stripes being placed either at the front and back of the crab or laterally, both with and without stationary contrasts in the visual field. N, number of observations.

translation, even though the image motion seen by anteriorly facing ommatidia could not have been cancelled out by the input from posteriorly facing ommatidia, since the latter faced a field lacking stationary contrasts (compare solid and open triangles on graphs).

The results illustrated in Fig. 10B do, however, show that optokinetic responses

A

Three stripes subtending
60° at eye

Stationary stripe
subtending 12°
at eye

B

Without
stationary
contrasts

With
stationary
contrasts

$N=42$

$N=25$

$N=41$

$N=18$

Gain

1.0

0.5

0.0

Stripes
laterally
placed

Stripes
front
and back

Stripes
laterally
placed

Stripes
front
and back

are driven largely by laterally facing ommatidia (confirming data of Sandeman, 1978, and Nalbach and Nalbach, 1987, in other crab species) and that optokinetic responses are largely inhibited by the presence of stationary contrasts in the visual field. The experiment involved recording the optokinetic responses to low-amplitude sinusoidal oscillations of a drum consisting of two sets of three stripes each subtending 60° at the eye (Fig. 10A). Responses to four stimulus conditions were compared. These were as follows: (1) stripes laterally placed with no stationary contrasts in the visual field; (2) stripes positioned at the front and back of the crab with no stationary contrasts; (3) moving stripes laterally placed with a stationary stripe positioned at the front and back of the crab; and (4) oscillating pattern at the front and back and stationary contrasts laterally placed. This is the condition illustrated in Fig. 10A, and most nearly corresponds to the situation faced by a sideways-walking crab.

In the absence of stationary contrasts, good responses were obtained when the stripes were laterally placed (mean gain 0.50±0.09 in the experiment illustrated in Fig. 10B), but much weaker ones when the moving pattern was seen by anteriorly and posteriorly facing ommatidia (gain 0.09±0.04 in this example). Since laterally facing ommatidia face the poles of the flow field during sideways walking, they would be stimulated by turning movements of the crab but not by translation. A critical experiment would, of course, be to see what happened during forwards walking down the runway, since the laterally facing ommatidia would then be exposed to apparent movement of the visual field, but *Cardisoma* cannot be persuaded to do this.

With the addition of stationary contrasts, the above responses were reduced, in the experiment illustrated (Fig. 10B), to 0.05±0.03 and zero when the moving pattern was laterally placed and anteriorly/posteriorly placed, respectively. In other repetitions of this experiment, the condition of oscillating stripes front and back and lateral stationary stripes (which, as stated above, most nearly corresponds to the situation faced by a sideways-walking crab) sometimes gave rise to weak optokinetic responses, but they were always of low gain compared to the responses induced by other stimulus conditions.

Discussion

Sensory basis of eye movements in freely moving crabs

All three known types of compensatory eye movement could play a part in generating the eye movements of freely moving crabs. During optokinetic nystagmus, the eyes move in the same direction as the movement of the striped pattern, which is equivalent to the eyes of freely turning crabs moving in the same direction as the apparent movement of the environment. During vestibular nystagmus, generated by the stimulation of thread hairs within the horizontal canals of the statocysts (Dijkgraaf, 1956a; Sandeman and Okajima, 1972), the eyes of a blinded crab rotated about its vertical axis would similarly move in the opposite direction to the turn during the acceleration phase of the motion. Third,

horizontal eye movements generated by leg proprioceptive input occur in the same direction as the legs are moved about the body. Hence, the input from legs engaged in the stance phase of locomotion could contribute to the eye movements seen during active turns, since the horizontal component of their movement relative to the body is in the opposite direction to the turn.

These experiments clearly show that vision plays a primary role in the eye movements seen in freely moving crabs, since the crab's ability to compensate for active turns falls to about a half when the eyes are covered. But the experiments provide no evidence that equivalent inputs from the statocysts influence eye movements in actively turning crabs. Indeed, no eye movements in free-moving blinded crabs were observed in this study that could have corresponded to the post-rotatory after-nystagmus that occurs upon cessation of rotation of a blinded crab about its vertical axis (Fig. 6A,B). It does, however, seem certain that input from leg proprioceptors is involved, since blinded crabs held above a ball exhibited eye movements whenever they rotated the ball about its vertical axis. Since, during active turns, legs in swing and stance phase are moving in opposite directions with respect to the body, it is by no means clear how the legs produce these eye movements. Possibly, as suggested by Varjú and Sandeman (1982), there is a gating mechanism whereby the eyes receive inputs from the legs only when they are in contact with the ground.

A further possibility is that at least a component of these eye movements might be centrally generated. This is highly probable for all fast, saccadic eye movements. Indeed, there is good evidence from previous work that fast phases of nystagmus are centrally generated in both eyes by a mechanism that seems to be triggered when the motor output frequency to muscle 21, which moves the eye in the horizontal plane towards the midline, reaches a high frequency (Horridge and Burrows, 1968; Sandeman *et al.* 1975*a*). There is no reason to suppose that compensatory eye movements have a central component, but our experiments do not preclude this possibility.

Functional role of compensatory eye movements in crabs

Predicting the main findings of this investigation and that of Paul *et al.* (1990), Varjú and Sandeman (1982) and Nalbach and Nalbach (1987) have proposed alternative theories about the functional role of compensatory eye movements in crabs. The former suggest that the eye movements might serve to reduce the average image velocity across the eye, while the latter propose that they are used to eliminate the rotatory component of the visual flow field. Although Paul *et al.* (1990) find, as I have done, that crabs only compensate for the rotatory component of the visual flow field produced by their own active movements, they hesitate to distinguish between the above theories. Their reason is that, in their experimental situation, translatory movements of the crab would have generated image motion on the retina no larger than the crab tolerates anyway with its rather imperfect compensation for body rotations. My data do allow such a distinction. Whereas crabs compensated for the rotatory component of visual flow with a gain of about

0.8 (mean values of 0.68–0.83 in different experiments), crabs walking sideways down the runway facing a set of contrasting stripes produced compensatory eye movements with a gain of only 0.02–0.09. Clearly, crabs are separating the rotatory from the translatory components of the visual flow field by compensating for the former but not the latter, in accordance with the prediction of Nalbach and Nalbach (1987). Since a gain of 1.0 represents perfect compensation in the horizontal plane, crabs seldom compensate completely for their turns. Close examination of records such as those of Figs 3 and 5, however, suggests that, most of the time, the crabs compensate rather well, periods of significant slip only tending to occur just before or after a fast phase of nystagmus when optokinetic interneurones are depressed (Sandeman *et al.* 1975*b*).

Separation of rotatory and translatory components of the visual flow field

The mechanisms crabs use to separate the rotatory from the translatory components of the visual flow field clearly require further investigation. Four possible mechanisms have already been mentioned. The first was that optokinetic responses might be too weak to be effective unless there was congruent input from leg proprioceptors and statocysts. This seems unlikely. Optokinetic responses are not weak in the absence of congruent input from other receptors (Fig. 6G), though it remains true that, whereas rotatory movements of the crab stimulate all three sensory systems, only the eyes provide the animal with an input that could lead to compensatory responses during translatory movements. There is similarly no evidence in favour of the second mechanism, i.e. that the input for optokinetic responses is summed over the whole eye. Although there is ample evidence that increasing the number of contrasts increases the amplitude of optokinetic responses up to a certain level, where the response saturates (Kunze, 1963, 1964), there is no evidence that, during sideways locomotion, the input from the apparent movement of stripes past the front of the eye is cancelled out by apparent movements in the opposite direction seen by backward-facing ommatidia (Fig. 9A,B). The third and fourth mechanisms do, however, appear to be important. Optokinetic responses are largely driven by laterally facing ommatidia, as previously found by Sandeman (1978) and Nalbach and Nalbach (1987) in other crab species, and inhibited by stationary contrasts in the visual field (Fig. 10B). Since *Cardisoma* usually walk sideways, such ommatidia would face the poles of the flow field and, hence, would be stimulated only by rotatory movements. Disappointingly, laterally facing ommatidia also generate the optokinetic response of the forward-walking soldier crab *Mictyrus* (Nalbach and Nalbach, 1987).

Although crabs like *Cardisoma* which live in complex environments respond equally well to optokinetic stimulation above and below the eye equator, flat-world crabs like *Mictyrus* and *Ocypode* only respond to moving contrasts when they are seen by ommatidia in the upper half of the eye (Nalbach and Nalbach, 1987). Since, in a flat environment, the upper half of the eye mainly views distant objects, it will not be subject to any significant image motion during translatory locomotion because the objects are so far away. Thus, the separation of the

rotatory from the translatory components of the flow field is simply achieved by taking advantage of the geometry of the situation (Nalbach and Nalbach, 1987).

Possible uses of flow-field analysis

The advantages of separating the translatory from the rotatory components of the visual flow field are many and varied, but have yet to be investigated in crabs. Probably the most important factor is the detection of the three-dimensional layout of the environment. As Horridge (1987) has argued for insects, it is probable that crabs 'see' objects entirely by their motion relative to each other and to the eye. Indeed, there is no evidence that the brain of an insect (or a crab for that matter) builds up an image of the world around it (Horridge, 1986). Thus, if motion is of paramount importance, it makes sense to isolate the translatory component of the flow field so that the relative positions of objects can be readily resolved by means of motion parallax (Longuet-Higgins and Prazdny, 1980). Second, there is preliminary evidence from the work of Davis and Ayers (1972) that the motion of a striped pattern past a lobster or crayfish (and various other animals) can both induce and control the speed of locomotion. Finally, it is possible that, although the rotatory component of the visual flow field has been abolished by compensatory eye movements, deviations from an intended course could still be detected by using, for instance, efference copy signals from the commands to the eye muscles.

References

BARNES, W. J. P. (1968). The optokinetic responses of the crab, *Carcinus maenas*. PhD thesis. University of St Andrews.

BARNES, W. J. P. (1982). Recording of eye and body movements in freely moving crabs. *J. Physiol, Lond.* **329**, 19P–20P.

BARNES, W. J. P. (1985). The control of equilibrium. Introduction. In *Feedback and Motor Control in Invertebrates and Vertebrates* (ed. W. J. P. Barnes and M. H. Gladden), pp. 253–258. London: Croom Helm.

BARNES, W. J. P. (1989). Freely walking crabs show compensatory eye movements in response to body turns but not translatory locomotor movements. In *Neural Mechanisms of Behavior* (ed. J. Erber, R. Menzel, H. J. Pflüger and J. Todt), p. 172. Stuttgart, New York: Thieme Verlag.

BARNES, W. J. P. AND HORRIDGE, G. A. (1969a). Interaction of the movements of the two eyecups in the crab *Carcinus*. *J. exp. Biol.* **50**, 651–671.

BARNES, W. J. P. AND HORRIDGE, G. A. (1969b). Two-dimensional records of the eyecup movements of the crab *Carcinus*. *J. exp. Biol.* **50**, 673–682.

BETHE, A. (1897). Das Nervensystem von *Carcinus maenas*. Ein anatomische–physiologisher Versuch. 1. Theil. −1. Mittheilung. *Arch. mikrosk. Anat. EntwGesch.* **50**, 460–546.

BUCHNER, E. (1984). Behavioural analysis of spatial vision in insects. In *Photoreception and Vision in Invertebrates* (ed. M. A. Ali), pp. 561–621. New York: Plenum Press.

CLARAC, F. AND BARNES, W. J. P. (1985). Peripheral influences on the coordination of the legs during walking in decapod crustaceans. In *Coordination of Motor Behaviour* (ed. B. M. H. Bush and F. Clarac), pp. 249–269. Cambridge: Cambridge University Press.

CRONIN, T. W., NAIR, J. N., DOYLE, R. D. AND CALDWELL, R. L. (1988). Ocular tracking of rapidly moving visual targets by stomatopod Crustacea. *J. exp. Biol.* **138**, 155–179.

DAHMEN, H. J. (1980). A simple apparatus to investigate the orientation of walking insects. *Experientia* **36**, 685–687.

DAVIS, W. J. AND AYERS, J. L. (1972). Locomotion: control by positive-feedback optokinetic responses. *Science* **177**, 183–185.

DIJKGRAAF, S. (1955). Rotationssinn nach dem Bogengangsprinzip bei Crustaceen. *Experientia* **11**, 407–409.

DIJKGRAAF, S. (1956a). Kompensatorische Augenstieldrehungen und ihre Auslösung bei der Languste (*Palinurus vulgaris*). *Z. vergl. Physiol.* **38**, 491–520.

DIJKGRAAF, S. (1956b). Über die kompensatorische Augenstielbewegungen bei Brachyuren. *Pubbl. Staz. Zool. Napoli* **28**, 341–358.

FLEISCHER, A. G. (1980). Analysis of the biphasic optokinetic response in the crab *Carcinus maenas*. *Biol. Cybernetics* **37**, 145–158.

FORMAN, R. AND BRUMBLEY, D. (1980). An improved capacitative position transducer for biological systems. *J. exp. Biol.* **88**, 399–402.

HORRIDGE, G. A. (1966a). Optokinetic memory in the crab, *Carcinus. J. exp. Biol.* **44**, 233–245.

HORRIDGE, G. A. (1966b). Optokinetic responses of the crab *Carcinus* to a single moving light. *J. exp. Biol.* **44**, 263–274.

HORRIDGE, G. A. (1986). A theory of insect vision: velocity parallax. *Proc. R. Soc.* B **229**, 13–27.

HORRIDGE, G. A. (1987). The evolution of visual processing and the construction of seeing systems. *Proc. R. Soc.* B **230**, 279–292.

HORRIDGE, G. A. AND BURROWS, M. (1968). The onset of the fast phase in the optokinetic response of the crab, *Carcinus. J. exp. Biol.* **49**, 299–313.

HORRIDGE, G. A. AND SANDEMAN, D. C. (1964). Nervous control of optokinetic responses in the crab *Carcinus. Proc. R. Soc.* B **161**, 216–246.

KUNZE, P. (1963). Der Einfluss der Grösse bewegter Felder auf den optokinetischen Augensteilnystagmus der Winkerkrabbe. *Ergebn. Biol.* **26**, 55–62.

KUNZE, P. (1964). Eye-stalk reactions of the ghost crab *Ocypode*. In *Neural Theory and Modeling* (ed. R. F. Reiss), pp. 293–305. Stanford: Stanford University Press.

LONGUET-HIGGINS, H. C. AND PRAZDNY, K. (1980). The interpretation of a moving retinal image. *Proc. R. Soc.* B **208**, 385–397.

NALBACH, H.-O. (1989). Three temporal frequency channels constitute the dynamics of the optokinetic system of the crab, *Carcinus maenas* (L.). *Biol. Cybernetics* **61**, 59–70.

NALBACH, H.-O. AND NALBACH, G. (1987). Distribution of optokinetic sensitivity over the eye of crabs: its relation to habitat and possible role in flow-field analysis. *J. comp. Physiol.* A **160**, 127–135.

NALBACH, H.-O., ZEIL, J. AND FORZIN, L. (1989). Multisensory control of eye-stalk orientation in space: crabs from different habitats rely on different senses. *J. comp. Physiol.* A **165**, 643–649.

NEIL, D. M. (1982). Compensatory eye movements. In *The Biology of Crustacea*, vol. 4 (ed. D. C. Sandeman and H. L. Atwood), pp. 133–163. New York, London: Academic Press.

PAUL, H., NALBACH, H.-O. AND VARJÚ, D. (1990). Eye movements in the rock crab, *Pachygrapsus marmoratus* walking along straight and curved paths. *J. exp. Biol.* **154**, 81–97.

SANDEMAN, D. C. (1977). Compensatory eye movements in crabs. In *Identified Neurons and Behavior in Arthropods* (ed. G. Hoyle), pp. 131–147. New York: Plenum Press.

SANDEMAN, D. C. (1978). Regionalization in the eye of the crab *Leptograpsus variegatus*: eye movements evoked by a target moving in different parts of the visual field. *J. comp. Physiol.* **123**, 299–306.

SANDEMAN, D. C., ERBER, J. AND KIEN, J. (1975a). Optokinetic eye movements in the crab, *Carcinus maenas* I. Eye torque. *J. comp. Physiol.* **101**, 243–258.

SANDEMAN, D. C., KIEN, J. AND ERBER, J. (1975b). Optokinetic eye movements in the crab,

Carcinus maenas. II. Responses of optokinetic interneurones. *J. comp. Physiol.* **101**, 259–274.

SANDEMAN, D. C. AND OKAJIMA, A. (1972). Statocyst-induced eye movements in the crab, *Scylla serrata*. I. The sensory input from the statocyst. *J. exp. Biol.* **57**, 187–204.

VARJÚ, D. AND SANDEMAN, D. C. (1982). Eye movements of the crab, *Leptograpsus variegatus* elicited by imposed leg movements. *J. exp. Biol.* **98**, 151–173.

VON BUDDENBROCK, W., MOLLER-RACKE, I. AND SCHALLER, F. (1954). Neue Experimente über die Augenstielbewegungen von *Carcinus maenas*. *Experientia* **10**, 333–334.

ZEIL, J., NALBACH, G. AND NALBACH, H.-O. (1986). Eyes, eye stalks and the visual world of semi-terrestrial crabs. *J. comp. Physiol.* A **159**, 801–811.