

EYE MOVEMENTS IN THE ROCK CRAB *PACHYGRAPSUS MARMORATUS* WALKING ALONG STRAIGHT AND CURVED PATHS

BY H. PAUL*, H.-O. NALBACH† AND D. VARJÚ‡

*Lehrstuhl für Biokybernetik, Universität Tübingen, Auf der Morgenstelle 28,
D-7400 Tübingen, Federal Republic of Germany*

Accepted 29 May 1990

Summary

1. Freely walking rock crabs (*Pachygrapsus marmoratus* Fabricius) were videotaped from above in a quasi-natural environment. The angular position of the long axis of the body and of both eyes in the horizontal plane were studied.

2. Compensatory eye movements are elicited along both straight and curved paths only during body rotation around the yaw axis. Hence, eye movements reduce the rotational component of the visual image flow during locomotion.

3. Fast saccades, which reset the eyes after a slow compensatory excursion relative to the body, are simultaneously initiated on both sides. They occur either after or before a body turn starts. Therefore, they are partially of central origin.

4. Crabs with one or both eyes blinded are still capable of performing compensatory eye-stalk movements. Thus, nonvisual cues, such as leg proprioceptive afferences or statocyst signals, are also effective in freely walking crabs. However, reducing the number of legs does not substantially impair the movements of the eyes in either seeing or blinded animals.

5. Fixing the seeing eyes to the carapace characteristically alters the pattern of locomotion. Body rotations are jerky in a stationary environment. The tendency to follow a rotating panorama by means of body turns is much higher than in intact animals.

Introduction

It has been known for decades that stalk-eyed crustaceans stabilize their eyes in space while rotating around the yaw axis. After a period of stabilization, during which their eye stalks rotate relative to the body, a saccadic reset brings the eyes back near to their previous position (von Buddenbrock *et al.* 1954; Dijkgraaf,

* Present address: Department of Zoology, University of Glasgow, Glasgow, G12 8QQ, Scotland, UK.

† Present address: Max-Planck-Institut für biologische Kybernetik, Spemannstrasse 38, D-7400 Tübingen, FRG.

‡ To whom reprint requests should be sent.

Key words: eye movements, body turns, visual flow field, multisensory interaction.

1956a,b). Since freely moving animals perform similar eye movements in the dark, it is concluded that visual control is also supplemented by nonvisual cues, which have been shown to come from leg proprioceptors and from the canal organ of the statocysts. There was a dispute between von Buddenbrock *et al.* and Dijkgraaf about the relative role of reafference and central efference in eliciting compensatory eye movements, the latter arguing that sensory input is needed only to stabilize the eyes against imposed body rotation (von Buddenbrock and Moller-Racke, 1952, 1953; von Buddenbrock *et al.* 1954; Dijkgraaf, 1953a,b, 1956a,b).

More recently a tremendous amount of information has been collected in behavioural experiments in which the properties of the different sensory systems have been investigated separately. To study the role of retinal slip speed of the statocysts and of leg proprioceptors, the animals were tethered and the panorama, the crab itself or the legs were rotated (for reviews see Sandeman, 1977, 1983; Neil, 1982). In spite of all this work, it is still not entirely clear what the biological functions of the compensatory eye movements are, and to what extent leg proprioceptors, statocysts and central efferences support the visual input under natural conditions. Therefore, we took up the old questions of von Buddenbrock and Dijkgraaf, and reinvestigated the eye movements in freely walking crabs by means of improved techniques. We aimed to reveal the contribution of the different senses to the compensatory eye movements of freely walking animals. Furthermore, we were interested in discovering whether the eye movements eliminate the rotatory component of the visual flow (Nalbach and Nalbach, 1987), or whether they only reduce the average image velocity across the eye (Varjú and Sandeman, 1982). The answer to this question would help us to understand why crabs need compensatory eye movements. A comparable study of eye movements during locomotion in the land crab *Cardisoma guanhumi* appears in a following paper (Barnes, 1990).

Materials and methods

Experiments were conducted with 15 crabs of the species *Pachygrapsus marmoratus* with carapace widths ranging from 3.0 to 4.4 cm, supplied by the Laboratoire Arago in Banyuls-sur-Mer. The animals were kept in groups of at most six and observed for several months in a basin 40 cm in height and 180 cm in diameter. The bottom (heavy concrete plates) was covered with a 1 cm deep layer of sea water, which communicated with a 120 l reservoir underneath. Since rock crabs tiptoe during walk, their bodies were not immersed in the water. The entire water volume was circulated, filtered and aerated. The salinity was checked three times a week and, if necessary, reset to 3.5 ‰.

Natural daylight was supplemented by indirect illumination from ceiling light sources. The crabs were filmed from above with a video camera mounted on the arm of a lightweight crane, which allowed the camera to be moved horizontally by hand 115 cm over the bottom. The experimenter was hidden behind a screen and observed the animals on a video monitor. A grid of 10 cm × 10 cm numbered

squares painted on the bottom allowed the animal's position within the basin to be reconstructed, even if the camera had been moved.

A rostro-caudally painted marker on the carapace served to identify the long axis of the body. The eyes carried white plastic strips of 2.5 cm length and 2.5 mg weight, glued to the peninsula of non-corneal exoskeleton on the back of the eyecups. They moved freely above the carapace and enhanced the resolution of the eye excursion. In a group of experiments we fixed the eyes by glueing the strips to the carapace. In another group the eyes were blinded with a coat of saline-resistant paint.

The inner wall of the basin was homogeneously white. The panorama seen by the animals contained, in the majority of experiments, only the devices for filtering and aerating the water, and 3–4 piles of small rocks which served for shelter. In a few experiments a drum of 100 cm in both height and diameter was placed in the basin with its bottom edge just over the water surface. Its inner surface was covered with regularly spaced black and white vertical stripes of 8 cm width. The drum could be rotated by hand.

The video records were analysed frame by frame. The coordinates of both ends of the marker on the back of the animal and of the strips on both eyes were read every 200 ms by means of a digitizing pad. To study the synchrony of the saccades in the two eyes, the sampling interval was reduced to the lowest possible value of 20 ms.

The time course of the angular position of the body and the eyes was smoothed by a 1–2–1 binomial filter. From these data the angular velocity and acceleration were computed. The time course of the translation velocity was not smoothed to avoid occlusion of short stops. This means that a reading error of, for example, 1 mm in consecutive frames at 200 ms intervals resulted in an apparent velocity of 0.5 cm s^{-1} in resting animals.

Explanation of symbols used (angles in degrees, distances in cm, time in s)

In the space coordinate system

x, y	coordinates of the centre of the body
Dt	sampling time interval
$v = (x^2 + y^2)^{1/2} / Dt$	translation velocity
Θ	angular position of the translation vector
Φ_B, Φ_L, Φ_R	angular position of the longitudinal axis of the body, and of the left and the right eye, respectively
$w = D\Phi_B / Dt$	angular velocity of the longitudinal axis of the body
$a = dw / Dt$	angular acceleration of the longitudinal axis of the body

In the coordinate system fixed to the animal (values relative to the longitudinal axis of the body)

α_L, α_R	angular position of the left and the right eye, respectively
$D\alpha = \alpha_L - \alpha_R$	deviation of the angular position of both eyes
$\Theta_T = \Theta - \Phi_B$	angular position of the translation vector

Results

Intact animals

At rest the crabs maintain a stereotyped eye position, with the properly mounted pointers on the eyes roughly parallel to the longitudinal axis of the body. During eye movements the pointers thus indicate angular deviations from this resting position. The sample record in Fig. 1A illustrates that during body rotation around the yaw axis eye position is retained in space for a while, i.e. the eyes *counterrotate* relative to the body (Fig. 1B). From time to time the eyes flick in the direction of body rotation. Both Fig. 1A, and more pronouncedly Fig. 1B, demonstrate that the eyes move in synchrony most of the time. Deviations are caused by previous unequal saccades, which are not corrected for during the compensatory phase. Unequal eye flicks occur without any obvious relationship to objects or conspecifics. During translation without rotation (20th to 26th seconds of the record) no substantial eye movements occur.

Owing to the ability of crabs to move in any direction relative to the longitudinal axis of the body, there is no fixed relationship between body rotation and walking direction. During the period discussed here the animal maintains the translation vector at 90° (Fig. 1C), while the walking direction relative to the longitudinal axis of the body changes from straight forward (0° , Fig. 1D) to the left side of the animal (90°). Consequently, the source of the body rotation is the change of the walking direction relative to the body axis (Fig. 1D), without alteration of the walking speed (Fig. 1E).

These findings indicate that rock crabs move their eyes to compensate primarily for body rotation. We therefore evaluated selected periods with straight and curved paths, with and without body rotation. Usually no eye movements can be observed without body rotation, no matter how the crab walks (Fig. 2A–D), but there are occasional exceptions (see below). However, body rotation is compensated for along both straight and curved paths (Fig. 2E–H).

Crabs with eyes free to move in an oscillating or rotating striped drum respond with both eyes and also with body rotation. However, the tendency to follow the panorama with the body is rather weak (dashed line in Fig. 8E, see also below). In a stationary striped drum the longitudinal axis of the body oscillates when the animal walks sideways (see Fig. 8F). Since the eyes compensate for these oscillations, this observation suggests that the orientation of the eye is under steady visual control during walking.

The fast flicks turn the eyes into the direction of body rotation. During continuous and fairly uniform body rotation, the amplitude of these saccades, and hence the duration of stable eye position, may continuously increase (Fig. 2F). When a body turn in one direction is immediately followed by a turn in the opposite direction, the saccade can fail to occur (Fig. 2H).

Since during a saccade one eye moves from the midsagittal axis to the side, the other one from the side to the midline, one might expect differences with respect to the moment of onset and time course of the movement. Indeed, the velocity of the eye moving away from the midline is almost constant and amounts to about

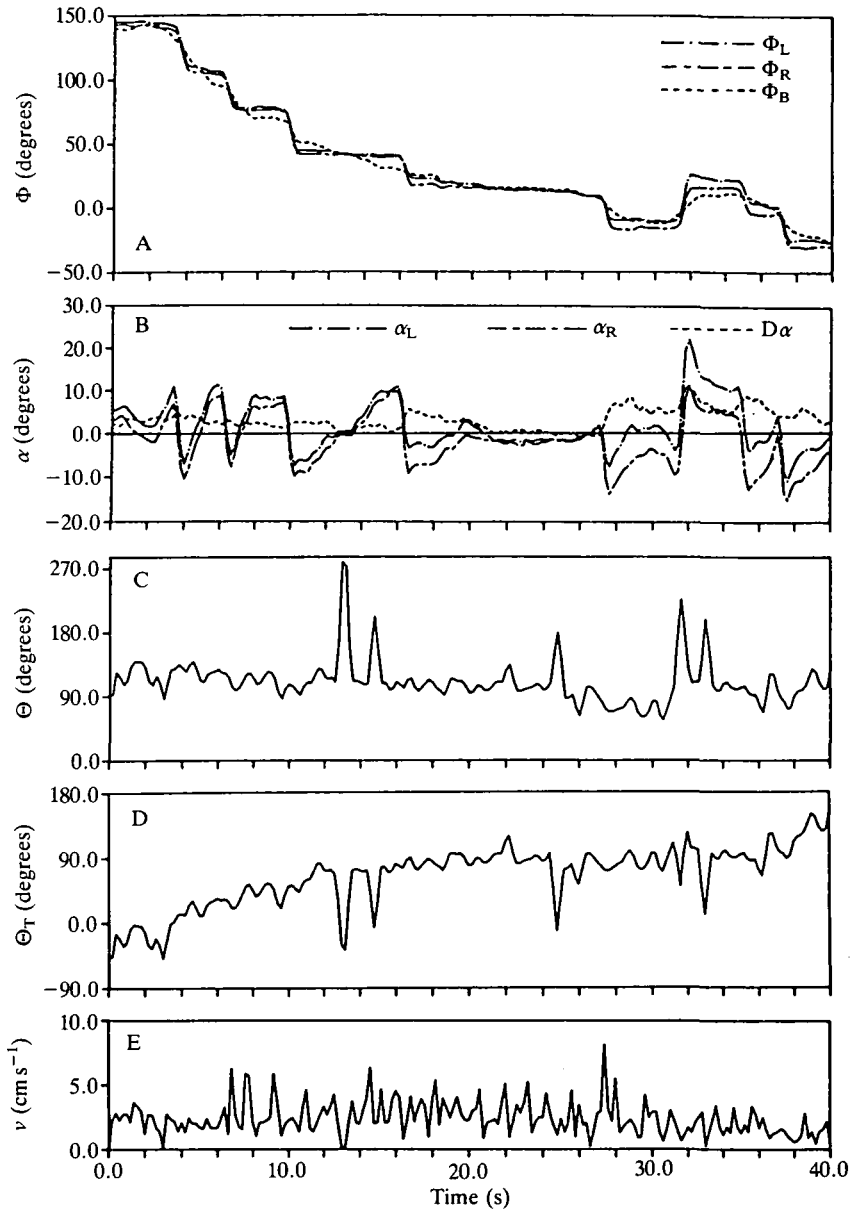


Fig. 1. Eye and body movements of an intact crab. In A–D upward deflections of the traces indicate left turns. (A) Angular position of the body (Φ_B), of the left (Φ_L) and of the right eye (Φ_R). (B) Angles between the body axis and the eyes (α_L, α_R) and their difference ($D\alpha$). Upward deviations of $D\alpha$ mean convergence. (C) The direction of the translation vector in the space coordinate system and (D) relative to the longitudinal axis of the body. In D, 0° indicates forward, $+90^\circ$ sideways walk to the left. (E) Translation velocity.

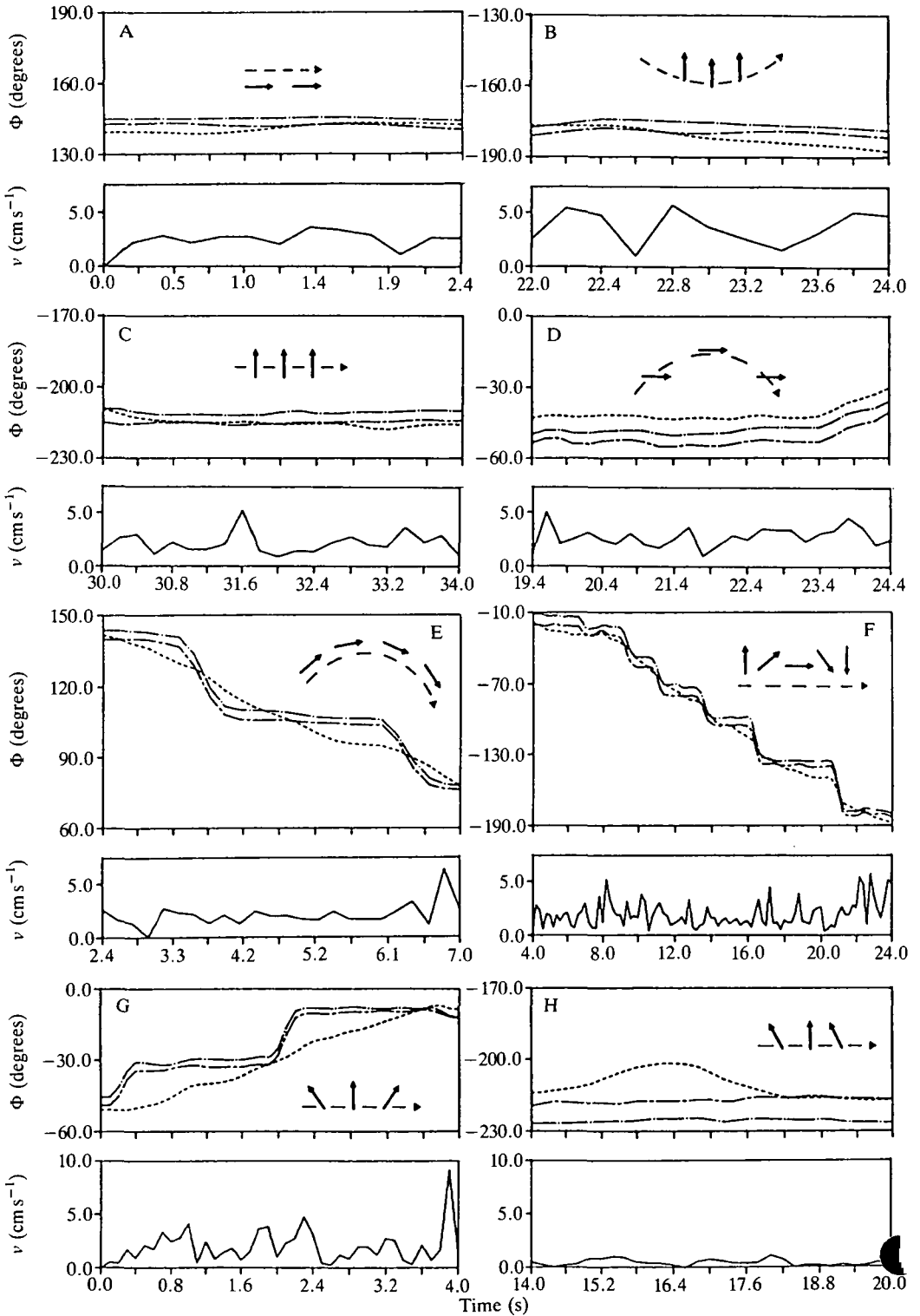


Fig. 2

Fig. 2. Intact crabs walking along straight and curved paths without (A–D) and with (E–H) body rotation. Angular position of body and eyes in the upper diagrams, translation velocity in the lower diagrams. Insets: solid arrows indicate body axis, dashed lines the walking path. Only body rotation in the yaw axis results in compensatory eye movements. Conventions as in Fig. 1.

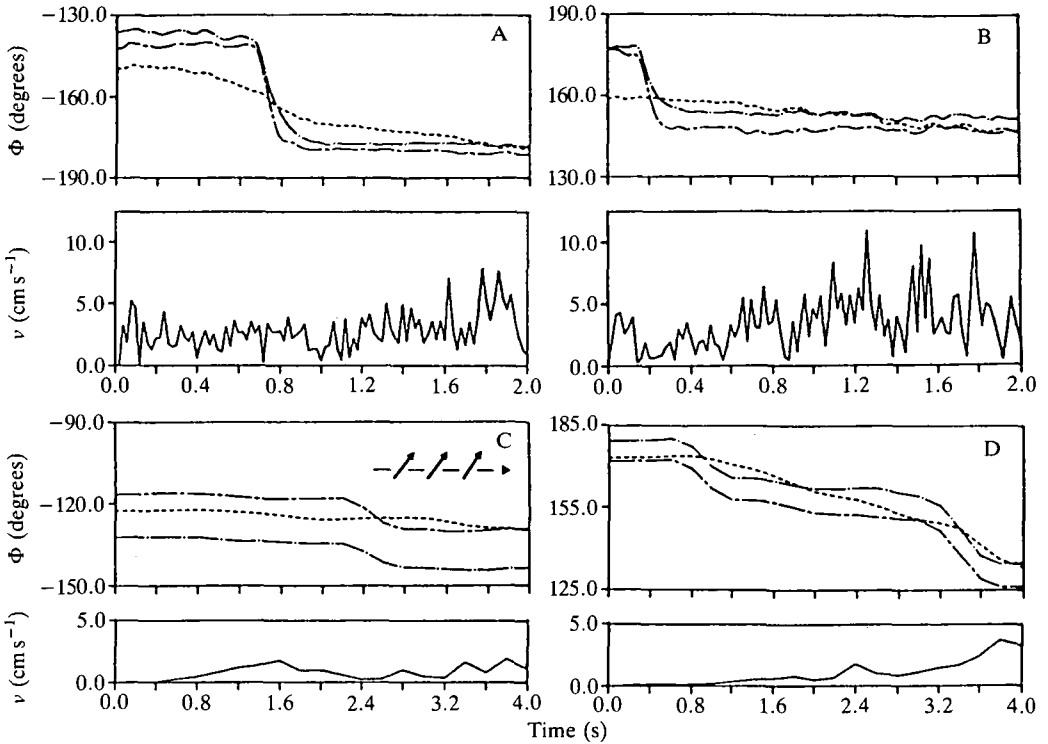


Fig. 3. Saccades of both eyes begin simultaneously, the eye moving towards the midline slowing down halfway through its saccade (A,B). Saccades may begin after (A) or before (B,D) the start of the body rotation, or even without body rotation (C). Temporal resolution 20 ms in A,B; 200 ms in C,D. Conventions as in Figs 1 and 2.

250°s^{-1} , whilst the other eye slows down about halfway through its saccade, and its average velocity amounts to only about 120°s^{-1} (Fig. 3A,B). Within the accuracy of the highest possible temporal resolution (20 ms), both eyes start simultaneously. Saccades can precede body rotation (Fig. 3B), even when the animal begins to turn after a rest (first saccade in Fig. 3D), but they can also be initiated after the start of body rotation (Fig. 3A) or without body rotation (Fig. 3C). This happened when the crab slowed down for a brief stop.

Crabs with one eye blinded

It has been shown in several experiments with tethered crabs in a rotating

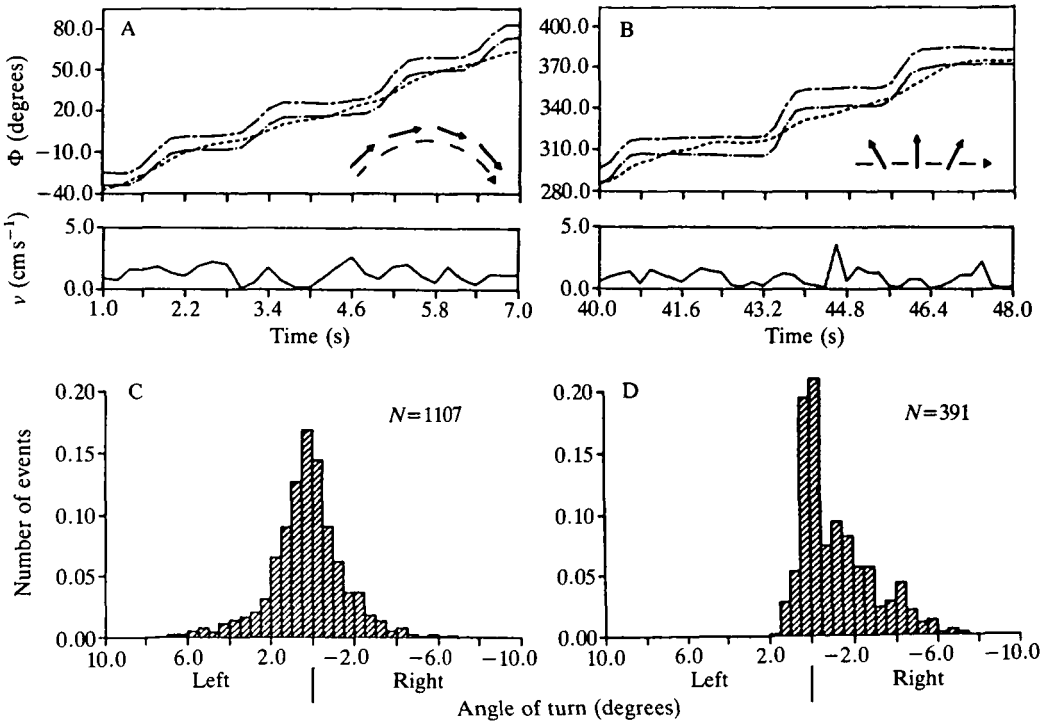


Fig. 4. Right eye blinded. Translation along curved (A) and straight (B) paths with body rotation. Frequency of left and right turns in an intact crab (C) and in a crab with the right eye blinded (D). Bin width 0.5° . N , number of frames evaluated. Conventions as in Fig. 1 and 2.

striped drum that the blinded eye is driven by the seeing one (Horridge and Sandeman, 1964; Barnes and Horridge, 1969; Nalbach, 1989), especially when the illumination of the panorama is low enough (Nalbach *et al.* 1985). That the seeing eye drives the blinded one in freely walking animals is also shown by the sample records in Fig. 4A,B. In addition, we find that monocular crabs turn more often towards the blinded side (Fig. 4C,D). Since the coated eye receives less light than the seeing one, this asymmetry is probably caused by negative phototaxis, which has been observed in *Pachygrapsus* (Drzewina, 1908).

Blinded crabs

Blinding both eyes should reveal to what extent nonvisual cues alone enable the animal to stabilize the eyes in space. The blinded animal often walks along objects, contacting them with the raised hindmost pair of legs, apparently seeking for tactile cues. When it turns at the same time, we observe periods of eye stabilization and fast flicks, as in intact animals, but the eye stabilization is far from complete: the eyes drift relative to the surroundings between saccades (Fig. 5A). Without contact with objects, both the longitudinal axis of the body (Fig. 5B, dashed curve) and the walking speed (Fig. 5B, lower diagram) oscillate. These oscillations of the

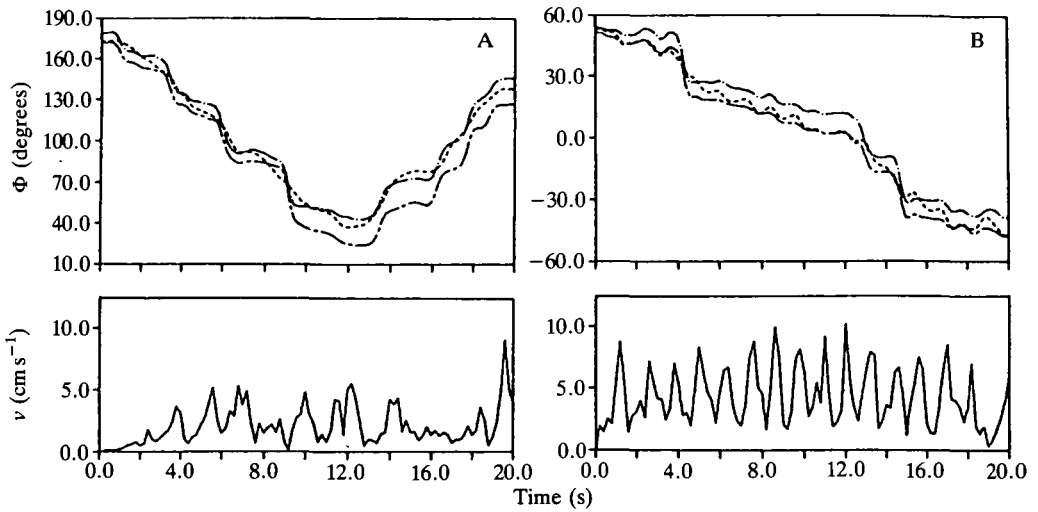


Fig. 5. Blinded crab with (A) and without (B) contact with objects. Conventions as in Figs 1 and 2.

body axis are only imperfectly compensated for by eye movements. These results indicate that the good stabilization of the eyes in intact crabs is largely mediated by the visual input. However, they also show that either mechanosensory afferences or efferent signals of central origin or both are involved in stabilizing the eyes in freely moving crabs.

Crabs with four legs

Since in tethered animals leg proprioceptive signals are very effective in eliciting eye movements relative to the body (Varjú and Sandeman, 1982), reducing the number of legs might modify the compensatory eye movements. We tested this with two animals, one of which (A) lost the first two pairs of pereiopods and the left chela months before the experiments. Therefore, it was possibly accustomed to being crippled. In the other crab (B) the same losses were induced by autotomy 1 day before the recording session. The results presented in Fig. 5 were obtained with this animal before autotomy. The locomotor ability of these crippled animals was markedly reduced, since they could support the frontal part of the body only by the right chela. As a consequence, the angular position of the body axis oscillated during walking (dashed curves in Fig. 6). With respect to eye stabilization, the seeing crab A performed just as well as an intact animal (Fig. 6A,B). The performance of the blinded animal B was not impaired by the autotomy (compare Figs 5 and 6C,D).

The possible role of statocysts

The results presented in the previous section reveal that the loss of 50% of the legs has no noticeable influence on the compensatory eye movements even in

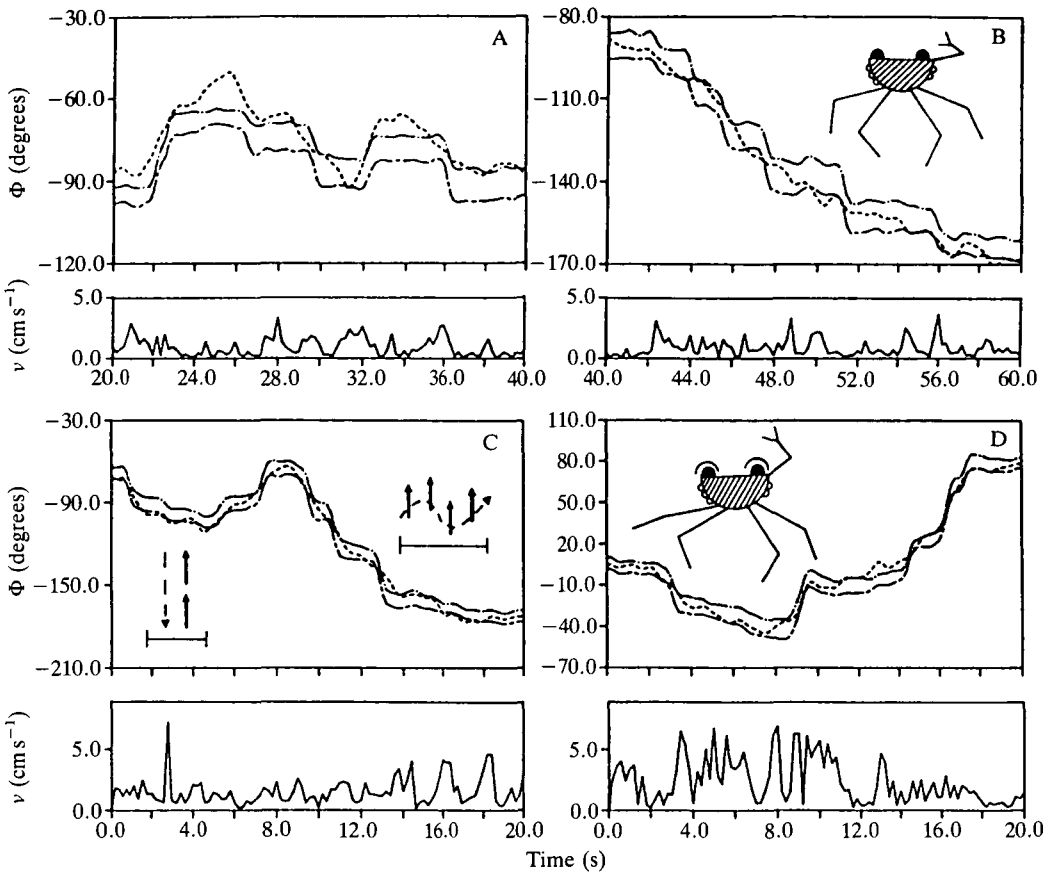


Fig. 6. Crabs with four legs. (A,B) Animal A, seeing. (C,D) Animal B, blinded. Conventions as in Figs 1 and 2.

blinded animals. One could argue that the canal organ of the statocysts alone provides sufficient information. We could not test this within the scope of this study by surgically removing the canal organ. It is, however, known from experiments with the crab *Scylla serrata*, that angular acceleration of the body has to be greater than 12°s^{-2} in order to excite the canal organ (Silvey and Sandeman, 1976). A comparable value, 9°s^{-2} , resulting in a gain of 0.5, has been obtained in *Mictyris longicarpus* (Nalbach, 1990). We therefore calculated the distribution of the angular acceleration of the body of four intact animals (Fig. 7A, lumped data), as well as of the crippled and blinded animal (Fig. 7B). Since in these freely walking animals acceleration often exceeds threshold, *Pachygrapsus* should be able to stabilize the eyes by means of the statocyst. In fact, we have evidence that *Pachygrapsus* also responds with compensatory eye movements to the angular acceleration of the body around the yaw axis, and thus possesses an efficient canal organ (Nalbach and Paul, 1990).

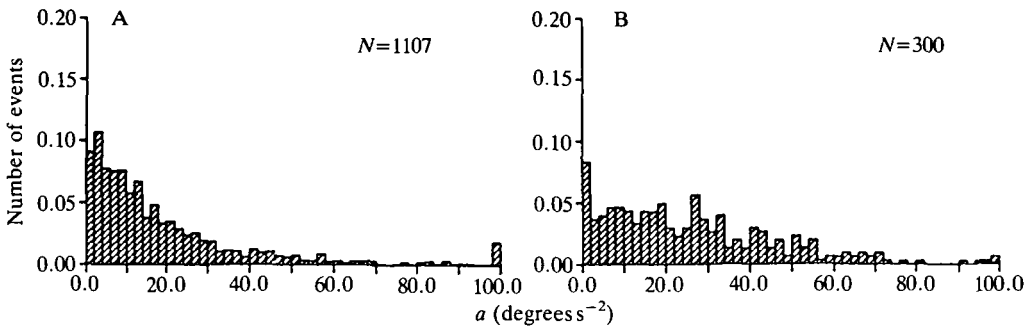


Fig. 7. The distribution of angular acceleration a of the body obtained with an intact crab (A) and with a crippled and blinded animal (B). Bin width 2°s^{-2} . N , number of frames evaluated.

Crabs with immobilized eyes

We have seen that blinding impairs the pattern of locomotion with respect to both body rotation and walking speed (Fig. 5A). If eye stabilisation is indeed predominantly under visual control, then preventing the seeing eye from performing compensatory movements might severely influence the animal's behaviour, since we have seen that in unimpaired animals in a rotating drum eye and body movements interact (Fig. 8E). We therefore immobilized both eyes, as described in the Materials and methods section. The animals still walked in any direction relative to the longitudinal axis of the body. However, they stopped more often than intact crabs, and performed body rotations in a steplike fashion (Fig. 8A). These steps sometimes resembled a subcritically damped oscillation. When the crab was in contact with an object, the steps were larger and somewhat smoother (Fig. 8B).

In a rotating striped drum, both walking (Fig. 8C) and standing animals (Fig. 8D) tried to follow the pattern by means of body rotation. They turned the body against the legs over a large angle, then relocated the legs, and finally rotated the body once more. There was, however, a considerable slip speed between animal and panorama.

Discussion

The role of efferences and afferences in controlling eye movements

Saccades

Our results provide good evidence that motor commands of central origin are responsible for the resetting of the eyes. First, there is the *a priori* evidence obtained from *Carcinus* that there is no proprioceptive information on the eye position (Horridge and Sandeman, 1964; Nalbach, 1989), and that the end point of the slow compensatory excursion is not determined by anatomical constraints (Sandeman *et al.* 1975). Second, our experiments have shown (i) that, as Dijkgraaf

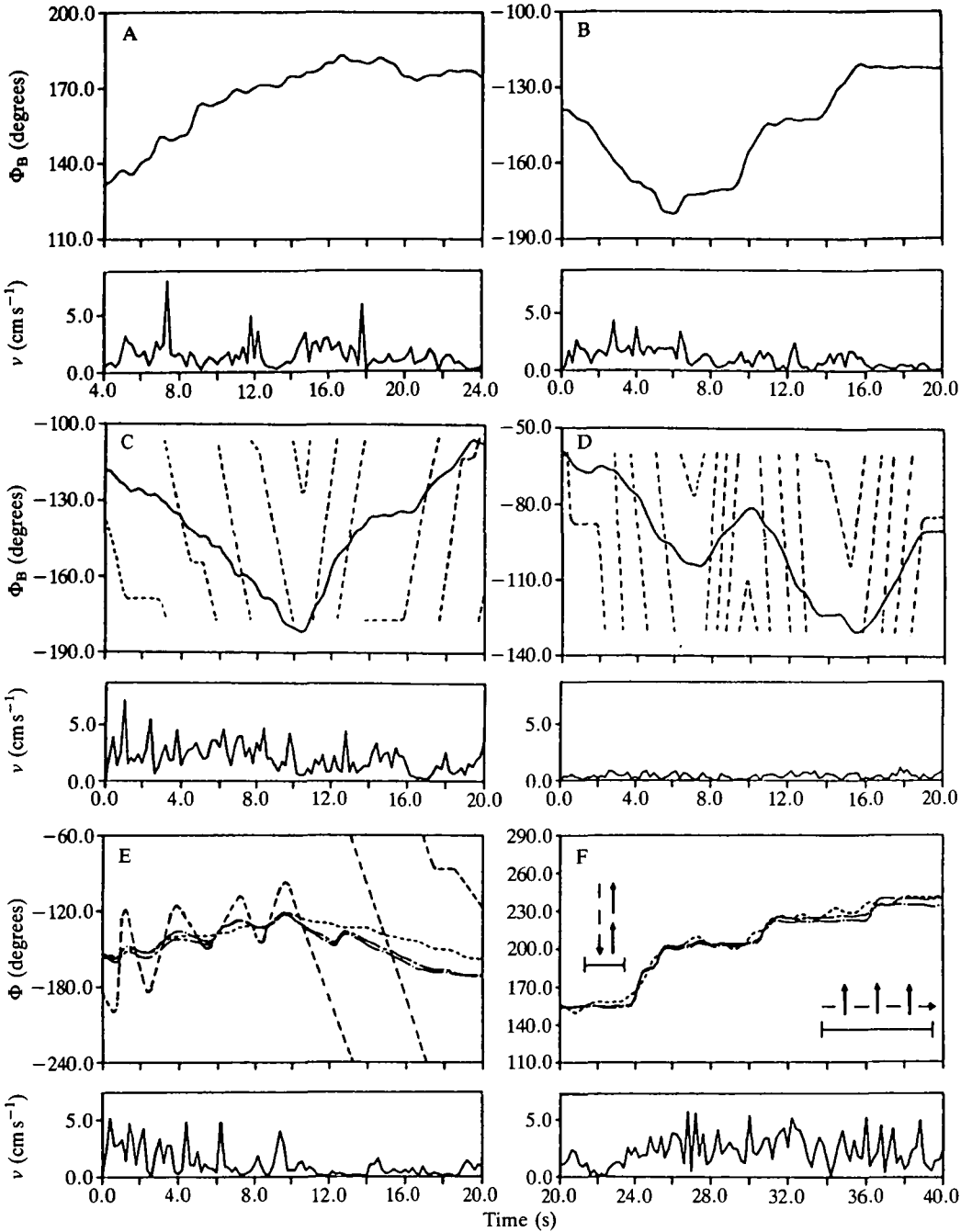


Fig. 8. Crab with eyes fixed walking freely in the basin without (A) and with (B) body contact with objects, in the rotating striped drum during a walk (C) and during turning on the spot (D). Unimpaired animal in an oscillating (left side E) or rotating (right side E) drum. F shows the same animal in a stationary striped drum walking forwards (left side) and sideways (right side). The broken lines in C, D and E indicate the angular position of a stripe. Conventions as in Figs 1 and 2.

(1956a) demonstrated in *Palinurus* and Sandeman (1978) demonstrated in *Leptograpsus*, there are anticipatory saccades preceding a body turn (Fig. 3B,D), (ii) that saccades can be observed without apparent body rotation (Fig. 3C), and (iii) that in freely moving animals saccades are initiated simultaneously on both sides (Fig. 3A,B). The latter result contrasts with experiments carried out in *Carcinus* held within a striped drum, where the eye flicking away from the midline starts 26–86 ms earlier than the other one (Horridge and Burrows, 1968; Barnes and Horridge, 1969). The velocity of saccades is about 2–3 times slower in tethered *Carcinus* (up to 45°s^{-1} towards, up to 110°s^{-1} away from, the midline, W. J. P. Barnes, personal communication) than in freely walking *Pachygrapsus*, where we found 120°s^{-1} and 250°s^{-1} , respectively. At present we cannot decide whether this finding is a species difference or is due to differences between tethered and freely walking animals. If the latter holds, then sensory information, e.g. from leg proprioceptors, might supplement central commands. The question remains open, since the positions of both eyes have not been recorded simultaneously during leg or statocyst stimulation. The asymmetry in speed between inward and outward movements of the eyes during the saccades seems to be caused by differences between abductor and adductor muscles, which also manifests itself during the pursuit phase of eye movements in *Carcinus* (Sandeman *et al.* 1975).

In addition, our experiments reveal that the size of saccades varies over a large range. It can monotonically increase during a prolonged uniform body rotation (Fig. 2F) or vary randomly without any apparent relationship to external events. A survey of our data (Fig. 9A–C) shows that the size of saccades can lie anywhere between 5 and 50° , regardless of whether the animal is intact, blinded or otherwise operated upon. We would not expect such a large variation were the onset of saccades to be determined by anatomical constraints or external stimuli. Therefore, we have to assume that saccades are triggered by central commands in accordance with the immediate need of the animals.

Compensatory slow movements

It is generally assumed that these movements are entirely under sensory control, with the visual input apparently dominating. It is, however, possible that in freely walking animals the motor commands to the legs are paralleled by equal and opposite motor commands to the eyes. Our results can easily be explained without such an assumption, but they do not exclude it.

Nonvisual cues

The responses of blinded animals (Figs 5, 6) are to a certain extent unexpected, since sinusoidal leg movements imposed on blinded and tethered animals of the closely related species *Leptograpsus variegatus* elicit eye rotation equivalent, on average, to that of the legs within a large range of frequencies (Varjú and Sandeman, 1982). It is somewhat surprising that in the freely walking blinded *Pachygrapsus* the eyes drift during the compensatory phase relative to the surroundings much more than in seeing animals, as indicated by Figs 5 and 6. This

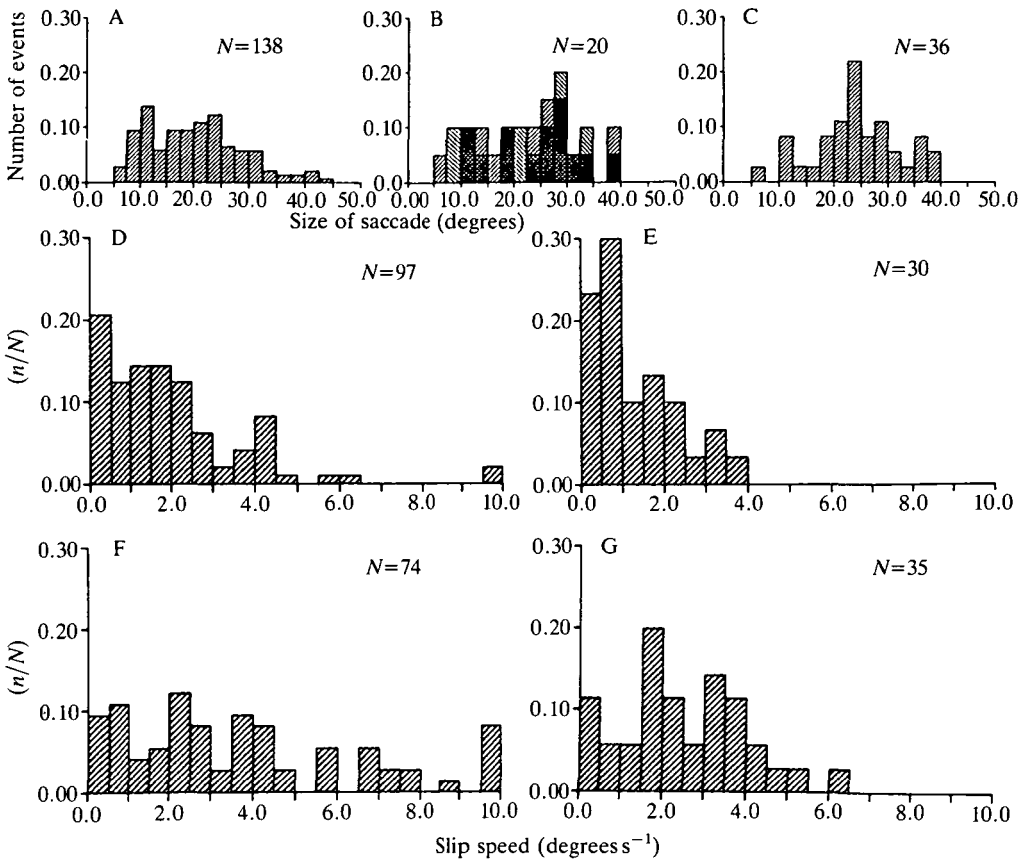


Fig. 9. Distribution of the size of saccades in intact (A), monocularly blinded (B) and crippled and binocularly blinded (C) animals. Note that in B the responses of both seeing (▨) and blinded (▩) eyes are almost identical. Bin width, 2.5° . The distribution of the slip speed relative to the surroundings in intact (D), crippled (E), binocularly blinded (F), and crippled and bilaterally blinded (G) animals. Bin width, 0.5°s^{-1} . n , frequency of occurrence; N , total number of observations.

is demonstrated in a quantitative manner in Fig. 9D–G, where the histograms show the distribution of drift velocity obtained with intact, binocularly blinded, crippled and blinded as well as crippled crabs. As long as the crab can see, drift velocity seldom exceeds 4.5°s^{-1} , and lies most frequently between 0 and 1°s^{-1} , the average value being $1.9 \pm 1.82^\circ\text{s}^{-1}$. In the blinded animal it is almost evenly distributed between 0 and 6°s^{-1} , with an average of $3.25 \pm 2.76^\circ\text{s}^{-1}$. So, in freely walking animals the leg proprioceptors cannot mediate perfect compensatory eye movements, even though they might be aided by statocysts signals (Fig. 7, Dijkgraaf, 1956b).

The imperfect stabilization of the eyes by means of proprioceptive leg signals might have an obvious explanation apart from the possibility that imposed leg movements are not equivalent to those produced by a freely walking animal. In the

experiments of Varjú and Sandeman (1982), the gain of the leg–eye reflex amounted to 1 only when the distance between the body and the substratum was very short, which corresponds to crouching. Since crabs walk with their bodies held high above the substratum, the gain might be considerably reduced.

It is also not clear why reducing the number of legs has no influence upon the performance of the animals. Possibly, the hind legs are not involved in signalling rotation at all, since in blinded animals they are lifted and used to obtain tactile information. When, in tethered animals, leg movements are imposed on only one side of the animal, the gain of the leg–eye reflex is halved. Since, in this situation, the legs on one side signal ‘rotation’ and on the other side ‘no rotation’, this experiment is quite different from reducing the number of legs of freely walking animals.

The biological significance of compensatory eye movements

In the Introduction we proposed two reasons why stalk-eyed animals need to stabilize their eyes. First, they might need to eliminate the rotational component of the visual flow field, for example, in order to utilize the purely translational component for depth perception by means of motion parallax (Nalbach and Nalbach, 1987). Second, they might need to reduce the average image velocity across the eye, for example, in order to improve detection of moving predators in front of a structured background (Varjú and Sandeman, 1982). Our results, and those of a following study (Barnes, 1990), reveal that, around the yaw axis, compensatory eye movements are elicited only during body rotation. They are absent otherwise, even if the animal moves along a curved path (Fig. 2) and one eye is blinded (Fig. 4). It therefore appears likely that the animals try to avoid a rotatory component in the visual flow for longer periods. Taking the results in Fig. 2F as an example, we can infer that, owing to compensatory movements, the eyes are stable over 80 % of the time that the body rotates continuously. During the remaining time, the eyes move very quickly and visual information is probably not available.

One must not overlook the fact that rotation causes, as a rule, much higher average retinal slips than does translation. During rotation, the retinal slip is independent of the distance and angular position of objects relative to the animal. During translation, objects seen at 90° relative to the translation vector have the highest retinal slip, the value depending on their distance from the animal. To give an example, an object at 38 cm lateral distance causes, in an animal walking with a velocity of 2 cm s^{-1} , the same retinal slip as a rotation at a velocity of 3° s^{-1} . Now, 2 cm s^{-1} was about the average walking speed of the animals, and 3° s^{-1} the average drift tolerated during the period of compensation (Fig. 9D). Thus, when the lateral distances of the nearest objects are greater than 38 cm, translation does not cause retinal slips larger than the average within the compensatory periods during rotation. Therefore, the purpose of compensatory eye-stalk movements could also be the reduction of average retinal slip.

In any case, it appears to be particularly important to reduce the time during

which the rotatory component of the visual flow – and, in turn, the average retinal slip – is high. This is shown by the behaviour of animals with eyes fixed to the carapace (Fig. 8A,B). They avoid continuous rotation, and, if they rotate, then they do this quickly and for a short time. The trace of the angular position of the body closely resembles that of the freely moving eyes. However, the angular velocity of body rotation never reaches values as high as that of the eyes, due to differences in mass and inertia. By fixing the eyes to the carapace we converted the crab functionally into an insect. We could not, of course, reduce body size and mass to that of an insect. Indeed, this large body size and high inertia might be one of the reasons why stalk-eyed crustaceans need stalked eyes.

We thank W. J. P. Barnes for valuable discussions and for correcting the manuscript. Financial support came from the DFG (SFB 307).

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