J Comp Physiol A (1989) 165:577–587

Journal of Comparative Physiology A Sensory, Neural, and Behavioral Physiology

Visual control of eye-stalk orientation in crabs: vertical optokinetics, visual fixation of the horizon, and eye design

Hans-Ortwin Nalbach[1], Gerbera Nalbach[1], and Luise Forzin

Lehrstuhl für Biokybernetik, Universität Tübingen, Auf der Morgenstelle 28, D-7400 Tübingen.
Federal Republic of Germany and [1] Max-Planck-Institut für biologische Kybernetik, Spemannstrasse 38,
D-7400 Tübingen, Federal Republic of Germany

Accepted May 16, 1989

Summary. 1. Pitch and roll eye movements of three species of crabs (*Heloecius cordiformis*, *Mictyris longicarpus*, *Pachygrapsus marmoratus*) were recorded in response to visual stimuli.

2. The 'flat world' species (*Heloecius*, *Mictyris*) with a zone of high vertical acuity around the equator of the eye (Zeil et al. 1986) turn the eye stalks towards a horizontal contrast line presented close to their specialized zone and pursue it for some degrees when it rotates away (Figs. 5a, b, 6a, b, 8, 10a). We interpret this as fixation of the horizon and discuss its relevance for the proposed mechanisms for 'vision in a flat world' (Zeil et al. 1986; Nalbach and Nalbach 1987).

3. Both types of crabs, the 'flat world' and the 'complex world' species, stabilize their eyes against dynamic perturbations not only via mechanosensory systems (Fig. 7, Nalbach et al. 1989) but also via an optokinetic system (Figs. 1, 2). In roll even nystagmic saccades can be elicited which, however, occur more unreliably and are about four times slower than in yaw. They are missing completely in pitch.

4. Regional distribution of optokinetic sensitivity over the eye in pitch and roll (Figs. 3, 4) is discussed as adaptation to image flow occurring under natural conditions.

5. The results obtained with the rock crab, *Pachygrapsus* (Fig. 4), suggest that movement detectors looking into opposite directions in the visual field might interact specifically to extract global rotational image flow.

Introduction

Animals which possess an area of acute vision usually make movements to bring the image of a structure of interest into this specialized area. Well-known examples are fixation movements in primates (Yarbus 1967) and praying mantids (Rossel 1980), or a male bibionid fly chasing a female keeping it in the field of view of its specialized dorsal eye (Zeil 1983). Zeil et al. (1986) described a zone of high vertical visual acuity all along the equator of the eye of crabs which live in flat environments. This structure has its counterpart among vertebrates in the visual streak of rabbits, cheetahs, or plains kangaroos which also live in predominantly flat environments (Hughes 1977). It was hypothesized that these acute zones might be of advantage in obtaining size and depth information monocularly simply by retinal elevation of the image of objects on the ground. The ventral gradient of vertical visual acuity is in good agreement with such a proposition (Zeil et al. 1986). It was further shown that the 'flat world' crabs are only sensitive to optokinetic stimulation when the moving structures are presented above the horizon (Nalbach and Nalbach 1987). This was interpreted as a means for separating the components in the visual flow field which are generated by translation and rotation during locomotion, taking advantage of the geometry of a flat surrounding. Particularly, in crabs with such specialized eyes we might expect well-developed visual control of eye-stalk orientation in pitch and roll which would align the acute zone with the horizon. On an inclined plane, retinal elevation can still provide depth information provided that the eyes are aligned with respect to the plane rather than to the gravitationally defined horizontal. This suggests these species should play down postural information from their statocysts and leg proprioceptors (Neil 1982; Sandeman 1983) in the control of average orientation of the eye stalk. Indeed, we found that in *Heloecius cordiformis*, an ocypodid crab living on mud flats along the fringes of mangroves, stabilization of eye stalks around pitch and roll axes is dominated by visual input although they still make use of their statocysts to compensate for dynamic perturbations (Nalbach et al. 1989). Crab species from more structured habitats rather rely on leg proprioceptors, as in the marble rock crab *Pachygrapsus marmoratus*, or on the statocysts, as in the green shore crab *Carcinus maenas*.

In the present study we compare eye pitch and roll elicited in *Mictyris*, *Heloecius*, and *Pachygrapsus* to see whether the underlying visual mechanisms differ between these representatives of 'flat' and 'complex world' species.

Material and methods

The set up was essentially the same as in the previous study (Nalbach et al. 1989). In short, a drum (diameter 28 cm, length 37 cm) with horizontal axis and carrying various patterns (to be described during presentation of the experiments) was oscillated (amplitude ±10°, frequency 0.1 Hz) or continuously turned (about 6°/s) around the crab, which either faced the wall of the drum (pitch) or its closed end (roll). The crabs were held in space by a rod glued to their carapace while their legs rested on a Plexiglas hemisphere (diameter 10 cm) which allowed the dactyli to slide over the smooth surface during walking movements. The angular positions of the eye stalks and the stimulus pattern were filmed with a video camera and analyzed frame by frame. In the experiments with *Mictyris* the crabs walked on an air-cushioned Styrofoam ball (Dahmen 1980; Nalbach and Nalbach 1987). Their eye movements were monitored by means of a capacitive position recording device (Sandeman 1968).

Results

Influence of pattern structure

In principle, visual eye stabilization relative to a structured surround can be accomplished by perception of relative movement resulting in an optokinetic reaction, or by perception of the relative position of features resulting in a fixation response, or by both mechanisms together. A distinction between both mechanisms can be made with moving patterns of different amounts of contours: A position-sensitive mechanism can be expected to work most efficiently when only a few well-defined structures are presented. One even expects the eyes to counterrotate against the sense of pattern rotation when the object *enters* the sensitive zone (Reichardt and Poggio 1976). On the other hand, visual position information is obscured by multiple presentations of the same object, which hence effectively excludes visual fixation (Varjú 1975). In such a situation, however, many ommatidia are stimulated by coherent image motion, the optimal stimulus for an optokinetic control circuit (Horridge and Sandeman 1964).

In order to discriminate between a position- (fixation), and a movement-sensitive (optokinetic) visual control system, we turned patterns at constant velocity with different numbers of stripes either around the transverse (pitch) or the longitudinal (roll) axis of the crabs. During the first 40°–90° of pattern displacement, the crabs turn their eyes with the direction of pattern motion (Fig. 1, *Heloecius*; Fig. 2, *Pachygrapsus*). During pitch, the eyes remain displaced in a final position despite the ongoing pattern rotation. This is quite similar to visually induced eye-stalk roll in mysid shrimps (Neil 1975) and to head roll in flies (Hengstenberg 1984). During roll, more or less regular oscillations of the eyes are superimposed onto this average displacement.

When we analyzed these relatively regular oscillations in response to the striped patterns with improved time resolution (intervals 100 ms instead of 500 ms as before) for *Pachygrapsus*, they turned out to be nystagmic eye movements with a slow pursuit phase and a rapid reset phase. Hitherto they have only been described during yaw (Horridge and Sandeman 1964; Kunze 1964). The saccadic velocity of the eye moving towards the midline of the animal is slower (about 34°/s) than that of the eye that makes its saccade away from the midline (about 55°/s). In yaw, the eye stalk of a freely walking *Pachygrapsus* makes a saccade to the side with an average velocity of about 250°/s and only with about 120°/s towards the midline (H. Paul, H.-O. Nalbach, D. Varjú, unpublished). A similar asymmetry was also observed in the pursuit phase of the horizontal optokinetic nystagmus and was attributed to asymmetries in the eye muscles (Sandeman et al. 1975). After the movement of the pattern has stopped, the eyes usually remain in their displaced position.

During both pitch and roll, the crabs respond more vigorously to a multiple stripe pattern than to one or two stripes only. From this we conclude that visual stabilization of eye-stalk orientation is predominantly under control of an optokinetic system. The increase in average eye-stalk displacement or appearance of nystagmi is most prominent in *Pachygrapsus*, while in *Heloecius* even with only one stripe strong responses can be elicited. Furthermore, the data obtained with *Heloecius* provide a hint that an additional fixation mechanism

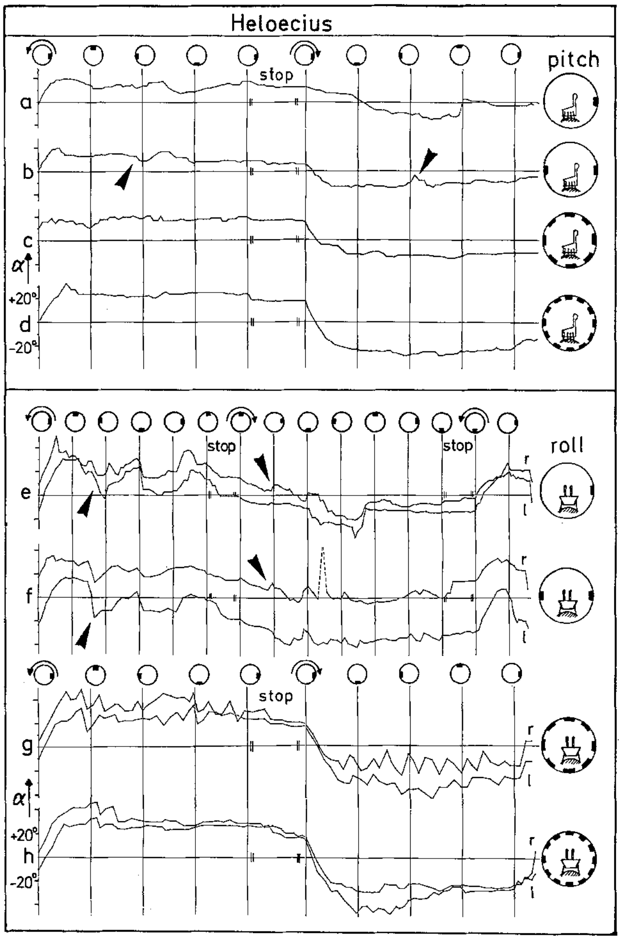

Fig. 1a–h. Time course of eye-stalk deflection α relative to the body in *Heloecius* in a continuously turning drum (about 6°/s) during pitch and roll with different patterns. Vertical width of the black stripe in **a**, **b**, **e**, **f** was 5°; basic spatial wavelength λ of the equidistant black and white striped pattern in **c** and **g** was 30°, in **d** and **h** 10°. *l*, left eye; *r*, right eye. Every 90° the position of a mark on the drum is shown. Pauses of movement lasted about 60 s. Upward deflection around pitch and roll (of the right eye) means raising the line of sight, downward deflection means lowering the line of sight. The starting position of the eye stalk is chosen arbitrarily. Dashed line in **f** denotes a short eye withdrawal. Data sampled at intervals of 500 ms. *Arrows* denote possible fixation movements when the stripe is close to the eye equator and the eye moves against the direction of the drum

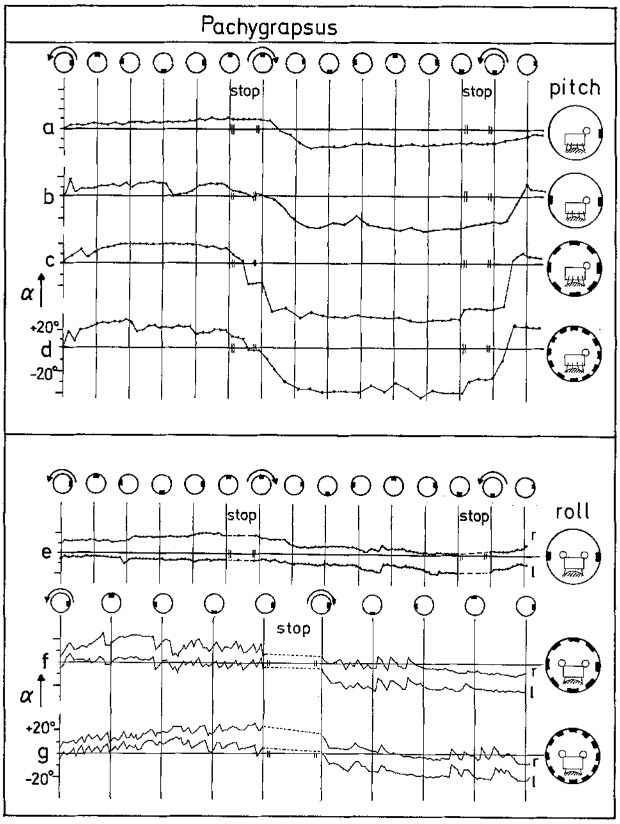

Fig. 2a–g. Time course of eye-stalk deflection α relative to the body in *Pachygrapsus* in a continuously turning drum (about 6°/s) during pitch and roll with different patterns. No clear responses were recorded during roll with one stripe only. For further description see Fig. 1

might exist. When the two-stripe pattern was turned around the transverse axis of the crab and the stripes enter a narrow region around the equator of the eye, in two instances the crab moved its stalks against the direction of pattern movement, thereby pitching its gaze onto the stripe (see events marked by arrows in Fig. 1b). Similar events might also be present in the recordings of eye roll (tentatively marked by arrows in Fig. 1e, f), where they are, however, hidden by the irregular pattern of eye movements. Possible fixation movements were observed only rarely, however, and thus position control seems to play no major role under these experimental conditions.

Distribution of visual sensitivity for vertical motion

Further insight into the properties of the optokinetic system sensitive to vertical image motion may be gained from the distribution of its sensitivity over the eye. Since position control can be expected to play only a minor role in eye movements elicited by moving stripes, we studied the reactions to a single black stripe, sinusoidally oscillating (amplitude 10°, frequency 0.1 Hz) at different mean positions around the transverse (pitch) or longitudinal (roll) axis of the crabs.

As might be expected from its eye design (Zeil et al. 1986), in *Heloecius* such a stimulus elicits the largest eye pitch and roll when presented close to the horizon of the crab (Fig. 3a, b). Response amplitudes are about the same when the stripe oscillates ipsi- ($\vartheta = 0°$) or contralaterally ($\vartheta = 180°$) to the recorded eye during roll, or when the stripe is frontal ($\vartheta = 0°$) or behind ($\vartheta = 180°$) the crab during pitch. A stripe presented above the eye equator evokes distinctly larger eye movements than one below. Similarly, with yaw stimulation *Heloecius* responds to a moving pattern mainly when it is presented above the eye equator (Nalbach and Nalbach 1987).

With two stripes separated by 180° the response amplitude peaks when both stripes oscillate around the equator (Fig. 3c, d). The responses are slightly larger than calculated from the responses evoked with a single stripe, assuming linear superposition (dashed lines in Fig. 3c, d).

In *Pachygrapsus*, as in *Heloecius*, the largest responses are also evoked when the stripe(s) oscillates around the equator (Fig. 4). In detail, however, there are differences. In the single-stripe experiment during roll, the eye facing the stripe in its equatorial position has about twice the amplitude than the contralateral eye (Fig. 4a). During pitch, when the single stripe is presented behind the animal, *Pachygrapsus* does not respond at all (Fig. 4b). One is tempted to relate this to a restricted visual field. In *Heloecius* the eyes are raised above the carapace by long vertically erected stalks while in *Pachygrapsus* the stalks are very short. In the two-stripe experiment, however, the responses are much larger than predicted by linear summation of the responses to one stripe (Fig. 4c, d). Therefore, the animal must be able to see the contralateral (during roll) or backward (during pitch) stripe, such that a reinforcement of the response in the two stripe situation becomes possible.

Contribution of a position-dependent component

During these experiments the crabs not only oscillated their eye stalks in response to the sinusoidally oscillating pattern but also changed the mean position of their eye stalks in response to the mean position of the stripes (Fig. 5a–d). In order to interpret this finding we have to appreciate the experimental procedure in detail: The drum was turned stepwise to the new position and sinusoidally oscillated for 60 s after a pause of about 30 s. Figure 5e, f shows the eye position to be expected if the crab fixates the stripe when it appears close to the equatorial acute zone. In this case the eyes should move upwards when the stripe is above the equator and downwards when it is below the equator, independent of the direction into which the drum is rotated from position to position. With our experimental procedure the mean position of

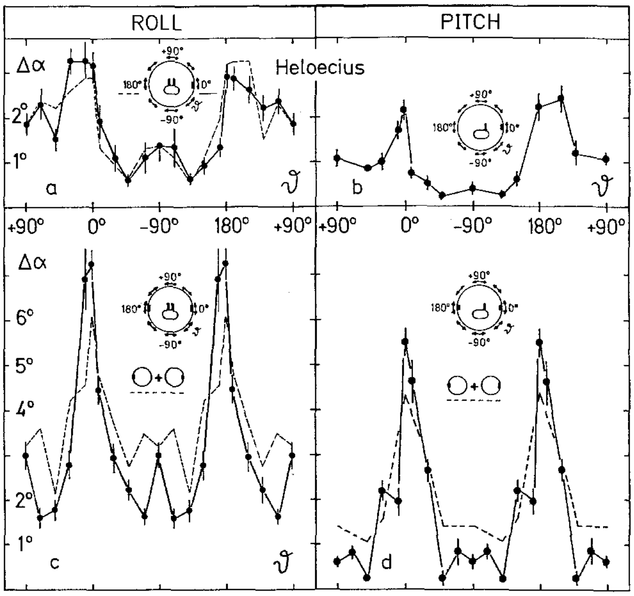

Fig. 3a–d. Regional distribution of sensitivity to vertical motion in *Heloecius*, either roll (**a**, **c**) or pitch (**b**, **d**), indicated by the response amplitude $\Delta\alpha$. For definition of angular position ϑ of the stripe relative to the equator of the eye see insets in **a**, **b**. The drum was sinusoidally oscillated with amplitude ±10°, frequency 0.1 Hz. It carried one stripe 5° high (**a**, **b**) or two, separated by 180° (**c**, **d**). In **a**, the solid line shows data for the right eye (ipsilateral to $\vartheta = 0°$) and the *dashed line* shows the same data drawn as if obtained from the left eye (ipsilateral to $\vartheta = 180°$). In **c**, **d** the dashed lines are calculated by summing the response amplitudes from **a** and **b** according to the positions of the two stripes in **c** and **d**. Means ± standard error from experiments with two animals

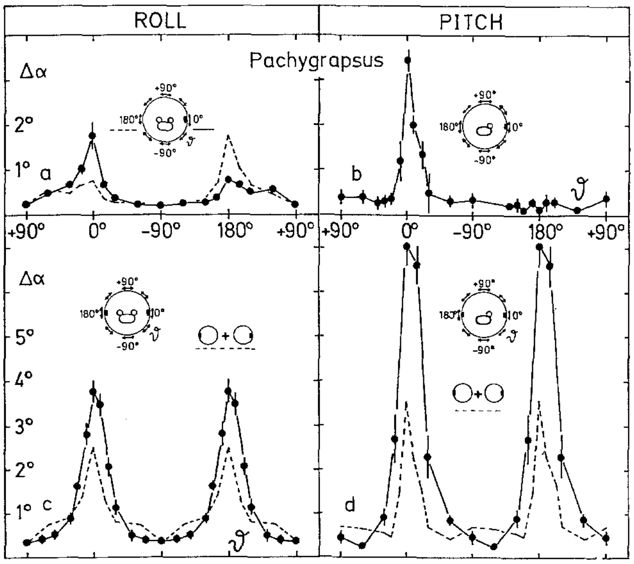

Fig. 4a–d. Regional distribution of sensitivity to vertical motion in *Pachygrapsus*. Average response amplitudes $\Delta\alpha$ ± standard error from experiments with two animals. In these experiments the crabs had no contact to substrate to reduce leg proprioceptive influence (Nalbach et al. 1989). For further description see Fig. 3

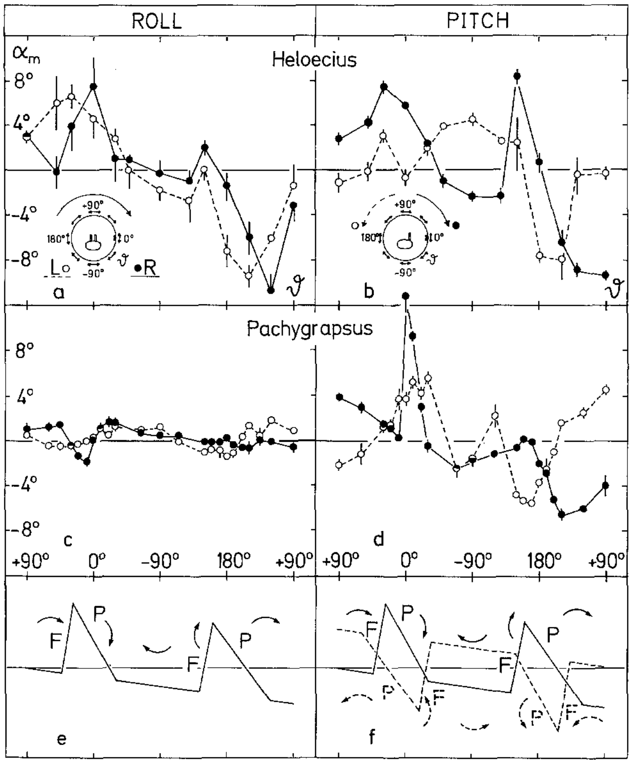

Fig. 5a–f. Mean angular position α_m of the eyes while a single black stripe (5° high) is sinusoidally oscillated (amplitude = ± 10°, frequency 0.1 Hz) at different positions ϑ around the animal. Mean position of the drum was changed in steps of 5°–30° either clockwise or counterclockwise, and after a pause of about 30 s we oscillated the drum for 60 s. For definition of the mean position of the stripe see insets with large arrows indicating direction of sequential change of drum positions. **a**, **c** Roll, clockwise rotation of the drum, mean position of the right (solid line) and left (dashed line) eye. **b**, **d** Pitch, clockwise (solid line) and counterclockwise (dashed line) rotation of the drum. Average values ± standard error from experiments with two *Heloecius* and two *Pachygrapsus*. **e**, **f** Sketched trends of eye deflection during roll (**e**) and pitch (**f**) for the experimental situations in **a–d**. It is assumed that the eye is insensitive to pattern rotation when the stripe is dorsal or ventral to the crab (cf. Figs. 3, 4). *P* indicates that the eye is turned into the same direction as the drum: pursuit movement. *F* indicates that the eye turns against the direction of the drum movement, thus trying to bring the stripe into a specialized zone of the eye: fixation movement. Arrows indicate direction of sequential change of drum position. Note that in the roll situation there is a phase shift between positions of left and right eyes in *Heloecius* (**a**) which is not predicted by the assumption illustrated in **e** and may be caused by the asymmetry of the situation: e.g., for the lateral part of the left eye the stripe enters the equatorial zone of the eye from below while it enters the lateral part of the right eye from above

the eye should reflect such a fixation reaction even if it brings the eye only very slowly into its new position. From the data it thus follows that there indeed exists such a fixation component in *Heloecius* during roll and pitch. In *Pachygrapsus*, however, there is no indication of a fixation mechanism during roll. Nevertheless, during pitch *Pachygrapsus* turns its eyes towards the stripe when it approaches the eye equator from above. Thus, a fixation eye movement against the turning direction is to be seen only when the stripe enters the frontal position ($\vartheta = 0°$) during clockwise rotation of the drum (solid line in Fig. 5d), and when the stripe enters the backward position ($\vartheta = 180°$) during counterclockwise rotation (dashed lines in Fig. 5d).

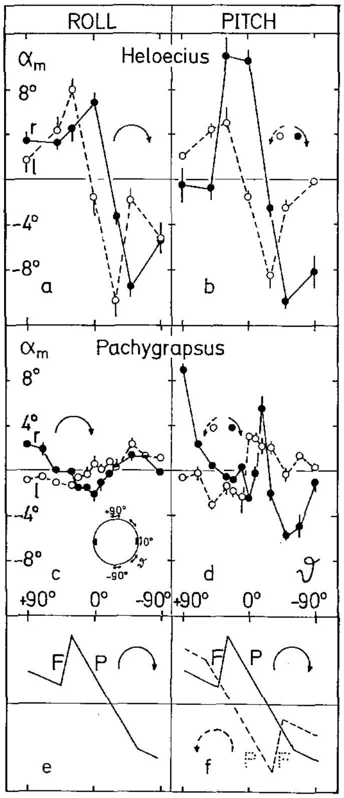

Fig. 6a–f. Mean angular position α_m of the eyes while two black stripes (5° high), separated by 180°, are oscillated (amplitude = ± 10°, frequency 0.1 Hz) at different positions ϑ around the animal. **a**, **c** Roll; **b**, **d** pitch. **e**, **f** Expected trends of the eye stalk deflection. *F* indicates the fixation component, *P* the pursuit component. For further description see Fig. 5

In the two-stripe experiment, the fixation component becomes even more pronounced in *Heloecius* (Fig. 6a, b). It remains weak during pitch in *Pachygrapsus* and even seems to be governed by the directionally sensitive optokinetic mechanism, while during roll the fixation component is missing completely (Fig. 6c, d).

Position-dependent reactions in Mictyris longicarpus

In both species, *Pachygrapsus marmoratus* and *Heloecius cordiformis*, the motion-sensitive component is more prominent than the fixation component. The fixation system is rather slow as the crabs only turn their eyes towards the stripe when it remains in its position for some time. Nevertheless, comparison of the results from the two species leads to the hypothesis that in crabs with a pronounced acute zone the fixation response becomes stronger. *Pachygrapsus* is a rock crab with a poorly developed acute zone along the eye equator, and even *Heloecius*, although living in a predominantely flat terrain, is by no means a specialist. Its acute zone is moderate compared to species which live on shores that are flattened during each high tide (Zeil et al. 1986). Therefore, we extended our experiments to *Mictyris longicarpus*, a crab with a highly prominent acute zone.

When *Mictyris* is oscillated sinusoidally as well as stepwise in a stationary drum that carries a black stripe along its equator, the crab stabilizes its eyes much better in space than when it is oscillated in homogeneous surroundings or in the dark (Fig. 7a). This demonstrates a strong visual contribution in stabilization of the eye stalks besides the statocyst input. It seems, however, to be a fixation response rather than an optokinetic one since with one single stripe oscillated across the equator of the eye a similar or even larger response can be elicited than with a striped pattern (Fig. 7b).

When we turned the single stripe very slowly (3–16°/s) around the longitudinal axis of the crab and recorded eye roll, fixation and pursuit reactions were clearly visible (Fig. 8a). During the fixation movement the crab turns the eye towards the stripe, thereby moving it against the direction of drum motion. The responses were strongest when the stripe was close to the horizon ipsilateral to the recorded eye. There was no response when the stripe was presented to the side contralateral to the recorded eye, due to the restricted visual field of *Mictyris* (Nalbach 1987) and apparent lack of neural coupling of both eyes for roll. The velocity of the fixation movement is less than 3°/s. When the eye catches up with the stripe it follows its displacement for some degrees, and then drifts back to its resting position.

With a black stripe, the fixation movement can be elicited only when it enters the sensitive zone from a dorsal position (Figs. 8a, 9a). With a white stripe, the fixation movement can also eventually be seen when the stripe enters the sensitive zone from a ventral position.

Fixation and pursuit reactions can also be elicited by a contrast edge within the equatorial acute zone of *Mictyris*, using either a broad black stripe in a white drum or a broad white stripe in a black drum (Fig. 8b). Fixation begins when the 'top black' edge is about 28° above the horizon (thin line in Fig. 9a), i.e., when it just enters about the fifth row of ommatidia, counted from the dorsal border of the eye (Nalbach 1987). Pursuit is initiated and continued when the edge of the stripe has entered a narrow zone around the equator. The eye follows the edge for about 15° (range indicated by the heavy bars in Fig. 9a). When the stripes are wider than 10°, the pursuit responses to the two borders of the stripe can clearly be separated (Fig. 9a). Additional experiments on eye pitch (circles in Fig. 9a) reveal the same responses

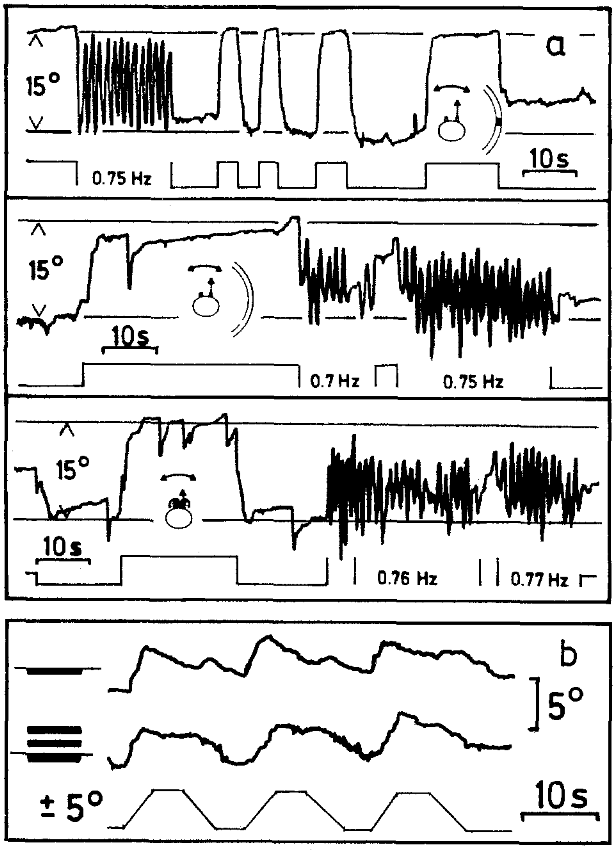

Fig. 7a, b. Sample records of eye stalk stabilization against roll in *Mictyris* under various stimulus conditions. **a** The crab was sinusoidally (frequency indicated) and stepwise oscillated around its longitudinal axis either in a drum with an equatorial black stripe, 10° high, along the wall on the side of the eye which is monitored, or in a homogeneous white drum, or in the dark (see insets). This experiment demonstrates statocyst and also strong visual control of eye-stalk orientation. **b** Either a horizontal black stripe (10° high, ±50° wide) or a pattern consisting of three horizontally extended black stripes (vertical repeating period 40°) is moved up and down across the horizon (see pictograms). Since both reactions are about equal, they are most probably dominated by a fixation rather than by an optokinetic system

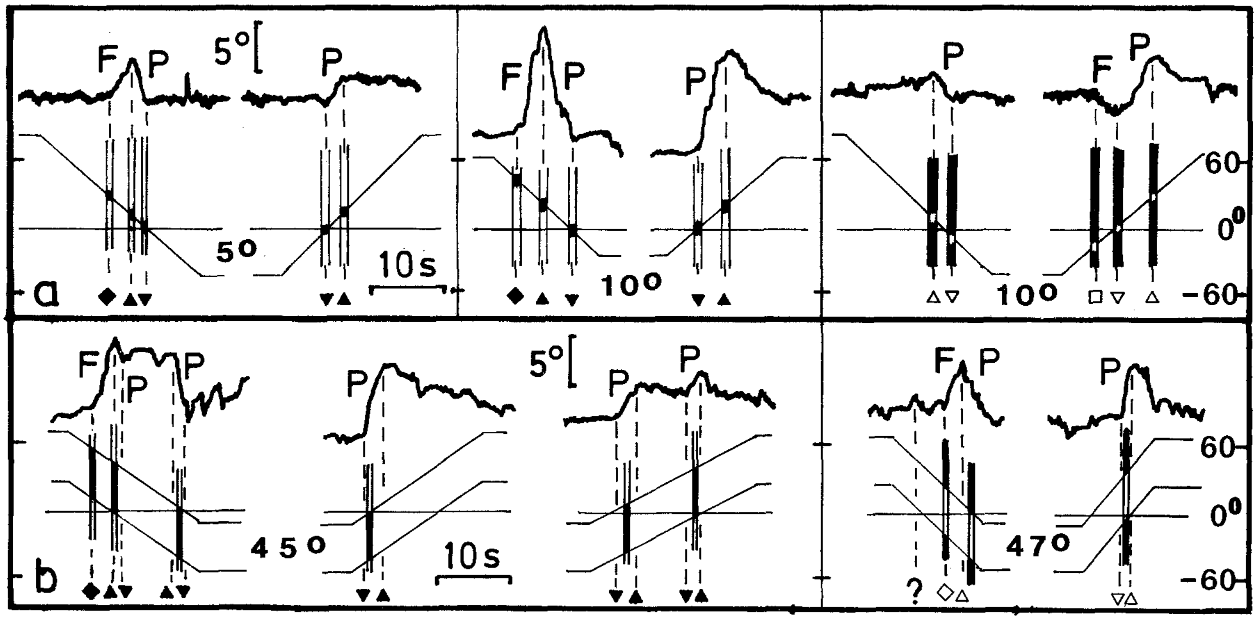

Fig. 8a, b. Roll fixation and pursuit movements of the eye stalks in *Mictyris*. **a** A black stripe, 5° or 10° high, within a white drum, or a white stripe, 10° high, within a black drum which moves up and down across the equator of the eye (see pictograms) elicits a fixation (*F*) and a pursuit (*P*) reaction. As an indication of fixation we take an eye movement against the direction of drum rotation. **b** The same can be seen when the upper or lower edge of a broad black (45° high) or white (47° high) stripe moves across the horizon. Diamonds mark beginning of fixation, triangles mark the upper and lower borders of the pursuit range. Note different scales for eye position and stimulus position (0° denotes horizontal position of the upper edge of the stripe)

as with roll stimulation. Velocity during pursuit is very slow, and even its maximal values are rarely as fast as the stimulus (Fig. 9b).

In order to further analyze the fixation response, we positioned a stationary edge close to the horizon and recorded the tonic deflection of the eye in response to the visual stimulus. When the light side of the edge is above ('top white edge') the eye aligns its equator with the edge within a range of about +5° above to about −15° below the horizon (Fig. 10a). Beyond this narrow range, no stationary response can be observed. Similarly, with a stationary top black edge no response can be elicited with the edge below −10° and above +5°. In the range from the horizon down to −10°, a weak fixation response may exist (Fig. 10b). When the top black edge is positioned, however, at or slightly above the horizon, the eye usually starts to oscillate with an average amplitude of about 5° and a frequency of 0.1–0.2 Hz (Figs. 10b, 11). Therefore, we may call a top white edge "stable" and a top black edge "unstable."

When we repeated the same type of experiment with *Pachygrapsus* and *Heloecius*, we never saw any oscillations or reliable position and black-white transition responses as reported in *Mictyris*. It remains to be shown whether these reactions are special to *Mictyris* or whether they are peculiar to crabs with a pronounced acute zone along the equator.

Discussion

In order to carry the eyes in a favorable orientation relative to the surroundings, one needs positional information. During walking the body oscillates in space, because of the uneven substrate and the stepping movements themselves. To prevent the resulting dynamic perturbations of vision, it is adequate to stabilize the eyes via motion-sensitive mechanisms. Crabs – similar to visually active species of several phyla (discussed in Hengstenberg et al. 1986; Hengstenberg 1988) – are equipped with a multisensory system to control the orientation of their eyes which meets the above requirements (Neil 1982; Sandeman 1983; Nalbach et al. 1989). Leg proprioceptors and the two organs of the statocyst (statolith and canal organ) detect the orientation of the body relative to the substrate and to gravity as well as their respective changes. In the present study we have shown that for control of pitch and roll, in addition, two visual mechanisms can be distinguished: fixation of a contour line close to the equator of the eye, and optokinetic

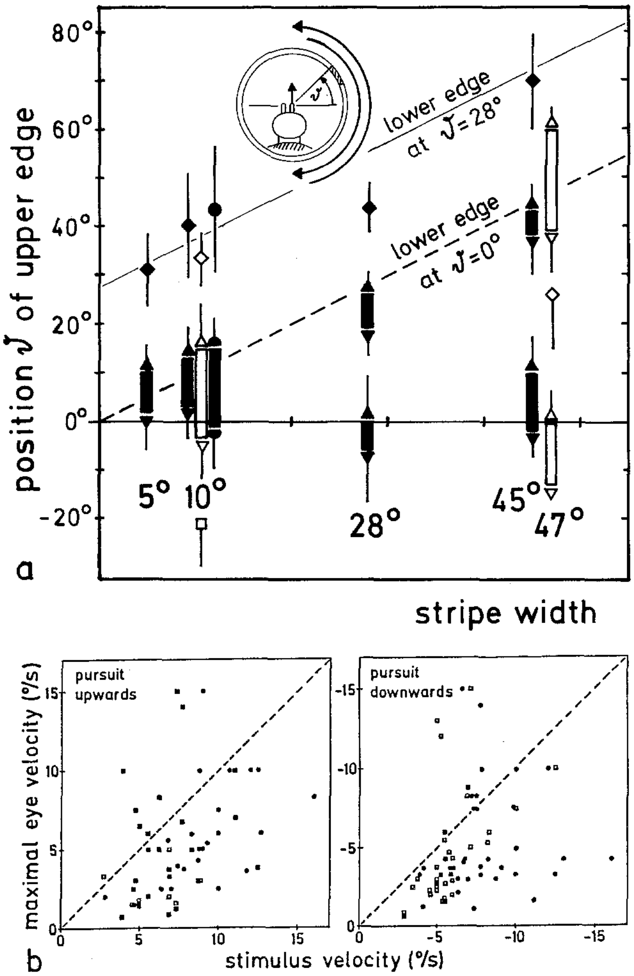

Fig. 9a, b. Fixation and pursuit response of *Mictyris* to stripes of different widths. Filled symbols indicate black stripes, open symbols indicate white stripes. (Half-)circles denote pitch experiments; the other symbols denote roll experiments. **a** Position of the upper edge of the stripe, when the crab either begins with its fixation movement (diamonds) or pursues the edge (triangles which delimit the pursuit range, indicated by large bars). Note that both the upper and lower edge are pursued separately with stripes wider than or equal to 28°. Means with standard error from experiments with one animal. **b** Maximal velocity of eye deflection during pursuit of an edge which either moves upwards or downwards with different stimulus velocities. The dashed line indicates maximal eye velocity equal to the stimulus velocity

eye movements induced by image motion over large parts of the visual field.

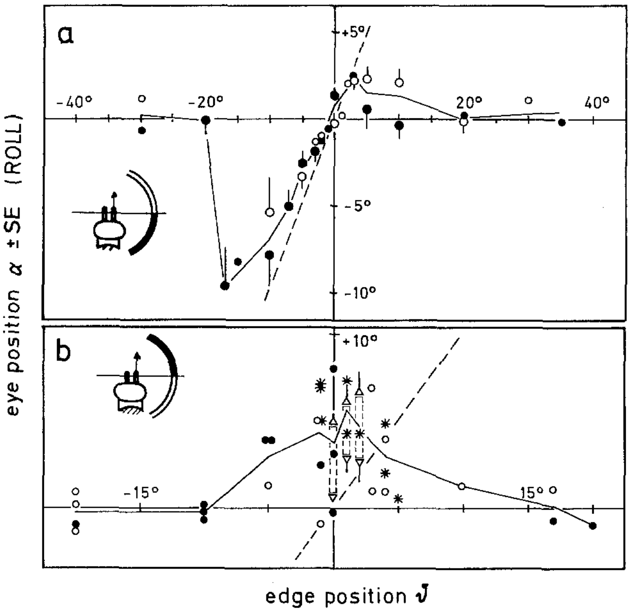

Fig. 10a, b. Responses of *Mictyris* to a stationary edge, either top white (**a**) or top black (**b**). Within a range of +5° to about −15° the crab keeps the top white edge tonically along its equatorial line of sight. The eye usually oscillates (see Fig. 11) when a top black edge is placed 0° to +2° relative to the horizon. In this range, the eye oscillated in 17 cases (triangles delimit upper and lower eye position during oscillation, amplitude indicated by dashed lines; means with standard error); in three cases it moved irregularly (asterisks, average eye position), and in three cases it remained stationary. Stationary eye position after an upward displacement of the edge is indicated by open circles, the position after a downward displacement by filled circles (means with standard error in **a**, single values in **b**). Eye position 0° is defined by the average eye position with the edges beyond $\vartheta = \pm 20°$ or without a stripe. Without the drum surrounding the crab, eyes were deflected 4.5° upward relative to 0°. Note different scales for ϑ in **a** and **b**. Experiments with one animal

Fixation response

In our experiments, the fixation response was most prominent in *Mictyris*, a crab with a pronounced vertical acute zone (Zeil et al. 1986) that lives on flat estuarine beaches (Cameron 1966). The crab only reacts to a contour line which is close either to the true horizon or to a sensitive zone of the eye around its equator (Figs. 9, 10). We cannot distinguish between these two possibilities as the crab was always in its normal upright position relative to gravity. In any case, both interpretations imply mechanosensory or efferent cues apart from visual input which restrict the reaction to only moderate displacements of the eye stalks relative to their preferred orientation. Visual input may even be under direct mechanosensory control as has been shown for the space-constancy neurons in the optic nerve of several decapod crustaceans, including crabs (Wiersma 1970; Wiersma et al. 1977). Usually, these neurons have the whole eye as a potential source of input while mechanosensory input restricts their visual field to the horizon and the area above. It is due to a purely visual component, however, that only a top white edge is accepted as a fixation line (Fig. 10). It may be significant that this arrangement seems to mimic

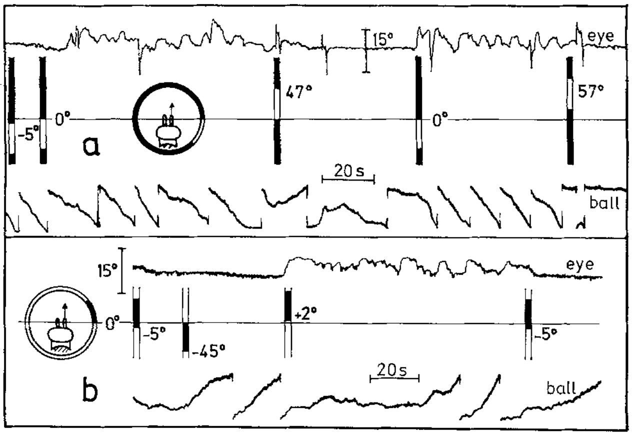

Fig. 11 a, b. Sample record of the roll oscillation reaction in *Mictyris longicarpus*. **a** A white stripe, 47° high, in a black drum. **b** A black stripe, 45° high, in a white drum. In both situations the eye oscillates when the black part is above and the white part is below the horizon, and the border is on the horizon. Pictograms indicate the position of the border and are placed along the time axis where the border was stepped into the new position. Recording of the ball indicates yaw turns of the crab (upwards to the left); after a turn of 90°, the trace is reset. This recording shows that the animals were continuously walking

the natural light distribution across the horizon. The oscillation of the eye in the inverted situation leads to the hypothesis that a mechanism to align the eye with the dorsoventral distribution of light – possibly mediated by sustaining fibers (Glantz et al. 1984) – is in conflict with a mechanism to fixate the horizon. In the natural situation both mechanisms would supplement each other, the horizon line being a direct consequence of the dorsoventral difference in brightness. Still, other hypotheses may account for the observations, and the mechanisms with lead to horizon fixation deserve more detailed study.

In each case, strong visual fixation of the horizon has an important consequence for the orientation of the eye stalk. In a crab that keeps the horizon line within its eye equator, the eye stalks will stand normal to the local surface of the substrate, even if it is slanted. Otherwise, if the statolith organ dominates, the eye stalks will stand parallel to the direction of gravity. Then the angle between eye equator and local surface will vary with the slant. We expect flat world crabs with their pronounced acute zone along the eye equator and an appropriate gradient in vertical visual acuity to rely on the mechanism of visual fixation of the horizon. It would enable them to exploit directly the elevation of objects within their visual field to measure distance and size monocularly (discussed in detail by Zeil et al. 1986). While only field observations can show if crabs indeed make use of such a mechanism the present study strongly suggests that flat world crabs orient their eyes relative to the visual horizon. The reactions are strongest in *Mictyris* (Figs. 9a, 10a), and they are also clearly present in *Heloecius* (Figs. 5a, b, 6a, b), a crab with only a moderate acute zone along the equator (Zeil et al. 1986). Furthermore, in these crabs visual control of eye stalk orientation is strong as compared to the contribution of mechanosensory cues (Fig. 7; Nalbach et al. 1989). By contrast, in the rock crab *Pachygrapsus* mechanosensory input is very important (Nalbach et al. 1989) while visual fixation of the horizon is weak in control of pitch orientation and absent in roll (Figs. 5c, d, 6c, d). This crab, as well as other species which live in visually complex habitats, has no pronounced acute zone or zone of better vertical than horizontal visual acuity (Zeil et al. 1986). Furthermore, in its rocky habitat there is neither a reliable visual horizon nor a constant slant of the substrate. Consequently, from its eye structure as well as from its habitat it cannot make such a simple use of the geometry of its surroundings as can flat world species.

Optokinetic response

While the fixation response in crabs by means of eye-stalk movements is exclusively restricted to the pitch and roll axis, the response to image motion is well known and has been studied in great detail for eye movements around the yaw axis (Neil 1982; Nalbach 1989). The relevant stimulus is the average slip speed of the visual image across the eye. These optokinetic reponses are shown to reduce image flow introduced by – voluntary or involuntary – body turns during self motion (Barnes 1985; H. Paul, H.-O. Nalbach, D. Varjú, unpublished), and in a resting crab they may act as a visual brake which helps the eye to remain in its favored position. When a striped pattern is continuously turned around the dorsoventral axis of the crab, or when the crab itself is turned around this axis, nystagmic eye movements, i.e., a regular sequence of slow, velocity-related eye movements which reduce image motion, and fast, stereotyped reset saccades can be elicited. During roll, however, the crabs only unreliably perform the reset saccades, which also have speed about four times lower than those in yaw (Figs. 1, 2). In pitch, no saccades can be elicited at all. The eyes follow the movement of the drum for some degrees, then come to a halt and remain in their deflected position. The same was observed in the visually induced roll reaction of the eye stalks in mysid shrimps (Neil 1975) and of the head in the blowfly (Hengstenberg 1984). The maximum excursion of the eye stalk or head depends on the velocity with which a striped pattern is turned around the longitudinal axis of the animal. Whether this is also true in crabs remains to be shown. To us it seems that the role of such eye movements is the same as in yaw: to remove the rotational component from the self motion-induced image flow (Nalbach and Nalbach 1987). If this interpretation is correct then the functional part of the response is the movement of the eye, while the stationary end position during continuing pattern rotation is a by-product of a system that is adapted to the narrow range of naturally occurring displacements only.

The response to image motion can mainly be elicited when the eye is stimulated within a narrow region around its equator or slightly above (Figs. 3, 4). Since this is true even in *Pachygrapsus*, which does not possess a pronounced acute zone for vertical resolution (Zeil et al. 1986), this feature seems to be caused by neural processing rather than by the structure of the eye. This hypothesis is supplemented by the finding that two horizontal stripes, separated by 180°, elicit a larger eye movement than can be expected from linear superposition of the responses in the one-stripe experiment (Figs. 3c, d, 4c, d). More complicated interactions between the two sides of the eye (in the pitch and possibly also in the roll situation) and/or the two eyes (in the roll situation) must exist and deserve a more detailed inspection.

The consequence of such an interaction is that the crab more reliably discriminates between translational and rotational image flow: upward-downward movement of one stripe could arise from eye pitch or roll but could, nevertheless, also arise from an upward-downward oscillation (e.g., during walking on a corrugated substrate). If, however, two contrast lines which are separated by 180° move with the same velocity across the eye, the one upwards, the other one downwards, this unambiguously signals rotation.

Even more simply, restricting sensitivity to vertical motion around the equator of the eye could be a means of distinguishing image flow caused by rotatory and translatory self motion when these occur together. In flat world crabs, such an adaptation seems to exist and could enable them to respond exclusively to yaw turns of their body with a compensatory yaw eye movement (Nalbach and Nalbach 1987). Crabs from visually more complex environments lack such a specialization. For roll and pitch, however, both 'types' of crabs have increased sensitivity to vertical image motion close to the equator of the eye. Whatever the geometry of the habitat may be, locomotion on the ground will induce strong image flow in the lower half of the visual field, as angular velocity and possibly also the number of resolvable structures are inversely proportional to the viewing distance. Even worse, translation does not introduce significant image flow in the upper part of the visual field. It is usually covered by the sky which can be untextured and is always far away. Hence, if one simply integrates the output of local motion detectors over the eye, which is usually assumed (e.g. Nalbach 1989), image flows in the upper and lower parts of the visual field induced by translation do not cancel each other out in the sense of optomotor equilibrium (Götz 1975). Consequently, it seems to be a good strategy to respond only weakly to image flow in the upper part and to almost ignore it in the lower part of the visual field to stabilize the eye against pitch and roll (Figs. 3a, b, 4a, b).

For discussion of vertical image motion close to the eye equator we have to distinguish between flat and three-dimensionally structured habitats. In a flat habitat the only horizontally extended contour line is the horizon. Therefore, the only vertical optokinetic stimulus close to the eye equator originates from pitch and roll of the crab, while up-down oscillations during locomotion do not cause image motion as the horizon is at 'infinity.' But they may cause a problem in a rocky environment with plenty of structures at eye height close by. Here, however, image motion on one side is usually counterbalanced by image motion on the opposite side. The comparison should be facilitated by the 'dipole'-like interaction of the movement detectors (see above) which, characteristically, in our experiments is most prominent in the rock crab *Pachygrapsus* (Fig. 4d). A similar interaction was proposed to explain why *Carcinus* does respond much more vigorously to a striped pattern rotating around the yaw axis when the pattern covers more than 180° than can be extrapolated from the responses obtained with more restricted visual fields (Buddenbrock and Friedrich 1933; presently under thourough investigation in waterstriders: H.J. Dahmen, personal communication). Therefore, as for the optokinetic control of eye movements in the yaw plane (Nalbach and Nalbach 1987), we expect crabs from visually complex environments to rely on more elaborate neural mechanisms than flat world crabs to equal them in visual performance.

Acknowledgements. Thanks to Martina Baumann and Ralph Schuster for digitizing the videos, to H.J. Dahmen for valuable discussion and to R. Hengstenberg and D. Varjú for critically reading the manuscript. Supported by an ARGS grant to D.C. Sandeman, University of NSW, Kensington, Australia; by grants to H.O.N. and G.N. from the Studienstiftung des Deutschen Volkes, and by a DFG grant to D. Varjú (SFB 307).

References

Barnes WJP (1985) Introduction to The control of equilibrium. In: Barnes WJP, Gladden MH (eds) Feedback and motor control in invertebrates and vertebrates. Croom Helm, London, pp 253–258

Buddenbrock W von, Friedrich H (1933) Neue Beobachtungen über die kompensatorischen Augenbewegungen und den Farbensinn der Taschenkrabben (*Carcinus maenas*). Z Vergl Physiol 19:747–761

Cameron AM (1966) Some aspects of the behaviour of the soldier crab, *Mictyris longicarpus*. Pacific Sci 20:224–234

Dahmen HJ (1980) A simple apparatus to investigate the orientation of walking insects. Experientia 36:685–687

Glantz RM, Nudelman HB, Waldrop B (1984) Linear integration of convergent visual inputs in an oculomotor reflex pathway. J Neurophysiol 52:1213–1225

Götz KG (1975) The optomotor equilibrium of the *Drosophila* navigation system. J Comp Physiol 99:187–210

Hengstenberg R (1984) Roll-stabilization during flight of the blowfly's head and body by mechanical and visual cues. In: Varjú D, Schnitzler HU (eds) Localization and orientation in biology and engineering. Springer, Berlin Heidelberg New York, pp 121–134

Hengstenberg R (1988) Mechanosensory control of compensatory head roll during flight in the blowfly *Calliphora erythrocephala* Meig. J Comp Physiol A 163:151–165

Hengstenberg R, Sandeman DC, Hengstenberg B (1986) Compensatory head roll in the blowfly *Calliphora* during flight. Proc R Soc Lond B 227:455–482

Horridge GA, Sandeman DC (1964) Nervous control of optokinetic responses in the crab *Carcinus*. Proc R Soc Lond B 161:216–246

Hughes A (1977) The topography of vision in mammals. In: Crescitelli F (ed) The visual system of vertebrates. (Handbook of sensory physiology vol 7/5). Springer, Berlin Heidelberg New York, pp 613–756

Kunze P (1964) Eyestalk reactions of the ghost crab *Ocypode*. In: Reiss RF (ed) Neural theory and modelling. Stanford University Press, Stanford, pp 293–304

Nalbach H-O (1987) Neuroethologie der Flucht von Krabben (Decapoda: Brachyura). Doctoral thesis, University of Tübingen

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

Nalbach H-O, 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, 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 DM (1975) The optokinetic responses of the mysid shrimp *Praunus flexuosus*. J Exp Biol 62:505–518

Neil DM (1982) Compensatory eye movements. In: Sandeman DC, Atwood HL (eds) The biology of Crustacea vol 4: Neural integration and behavior. Academic, New York, pp 133–163

Reichardt W, Poggio T (1976) Visual control of orientation behaviour in the fly. Part I. A quantitative analysis. Q Rev Biophys 9:311–375

Rossel S (1980) Foveal fixation and tracking in the praying mantis. J Comp Physiol 139:307–331

Sandeman DC (1968) A sensitive position measuring device for biological systems. Comp Biochem Physiol 24:635–638

Sandeman DC (1983) The balance and visual systems of the swimming crab: their morphology and interaction. Fortschr Zool 28:213–229

Sandeman DC, Erber J, Kien J (1975) Optokinetic eye movements in the crab *Carcinus maenas*. Eye torque. J Comp Physiol 101:243–258

Varjú D (1975) Stationary and dynamic responses during visual edge fixation by walking insects. Nature 255:330–332

Wiersma CAG (1970) Neuronal components of the optic nerve of the crab, *Carcinus maenas*. Proc K Ned Akad Wet Amsterdam 73C:25–34

Wiersma CAG, Hou L-HR, Martini EM (1977) Visually reacting neuronal units in the optic nerve of the crab *Pachygrapsus crassipes*. Proc K Ned Akad Wet Amsterdam 80C:135–143

Yarbus AL (1967) Eye movements and vision. Plenum, New York

Zeil J (1983) Sexual dimorphism in the visual system of flies: the free flight behaviour of male Bibionidae (Diptera). J Comp Physiol 150:395–412

Zeil J, Nalbach G, Nalbach H-O (1986) Eyes, eye-stalks and the visual world of semi-terrestrial crabs. J Comp Physiol A 159:801–811