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Interactions of local movement detectors enhance the detection of rotation. Optokinetic experiments with the rock crab, *Pachygrapsus marmoratus*

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Abstract

Walking crabs move their eyes to compensate for retinal image motion only during rotation and not during translation, even when both components are superimposed. We tested in the rock crab, *Pachygrapsus marmoratus*, whether this ability to decompose optic flow may arise from topographical interactions of local movement detectors. We recorded the optokinetic eye movements of the rock crab in a sinusoidally oscillating drum which carried two 10-deg wide black vertical stripes. Their azimuthal separation varied from 20 to 180 deg, and each two-stripe configuration was presented at different azimuthal positions around the crab. In general, the responses are the stronger the more widely the stripes are separated. Furthermore, the response amplitude depends also strongly on the azimuthal positions of the stripes. We propose a model with excitatory interactions between pairs of movement detectors that quantitatively accounts for the enhanced optokinetic responses to widely separated textured patches in the visual field that move in phase. The interactions take place both within one eye and, predominantly, between both eyes. We conclude that these interactions aid in the detection of rotation.

Keywords: Crab, Flow field, Rotation detection, Optokinetic response, Nonlinear interaction

Introduction

Global image flow is a rich source of information to control locomotion, posture, and eye movements. It can guide the animal on its course, provides information about the three-dimensional layout of the environment *via* motion parallax, and governs the optokinetic response. The latter reduces rotational retinal image speed, thus minimizing blur and enabling the nervous system to extract the useful information contained in the residual flow.

The consequences of a mechanism that balances the net image flow in the visual field on both sides of an animal were demonstrated in experiments with walking *Drosophila* (Götz, 1975). These flies spatially integrate the outputs of local movement detectors. During rotation, the net sum over the total visual field provides the animal with the information necessary to perform a compensatory turning reaction while during translation the inputs from both sides effectively cancel each other. However, with such a mechanism the course of an animal would theoretically become unstable when objects are unevenly distributed in the environment. This is due to the properties of the elementary movement detectors and the fact that the local image speed during translation depends on the distance and angular positions of the objects relative to the animal.

Such instabilities can be prevented if an animal is able to decompose the image flow into its translational and rotational components and to rotate only in response to the latter. In freely walking crabs, it was shown that they indeed compensate for retinal image motion by moving their eyes only during rotation and not during translation, even when both components are superimposed as they usually are during locomotion (Barnes, 1990; Nalbach, 1990*a*; Paul et al., 1990). It has been demonstrated in theoretical studies that decomposition can unambiguously be achieved even on a local scale (Koenderink & van Doorn, 1976; Longuet-Higgins & Prazdny, 1980; Rieger, 1983). However, to make the computation robust against disturbances or imprecise measurement of retinal velocity, integration over larger parts of the visual field is necessary (Koenderink & van Doorn, 1987). The mechanisms which might be utilized in animals to perform this task have been studied in a few cases only (Collett, 1980; Rieger & Lawton, 1985; Nal-

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bach & Nalbach, 1987; Preiss, 1987, 1991; Junger & Dahmen, 1991; Warren et al., 1991).

In the present study, we propose that decomposition of retinal image flow might be improved by topographically organized interactions of local movement detectors. Our idea may be illustrated by the following gedanken experiment. Imagine a person sitting in a vehicle and looking out through a narrow side window. In this case, the person can hardly distinguish whether the vehicle is moving along a straight path or is rotating. However, if the person compares the view through two opposite windows, there will be no doubt about the course of the vehicle: during rotation the structures in front of both windows will be seen to move "in phase," i.e. both either clockwise or counterclockwise, during translation "in antiphase," that is both forward or backward. Accordingly, at least in animals with extended visual fields, like the rock crab, interactions of local movement detectors in opposite positions might play an eminent role in detecting rotation.

To test this hypothesis, we recorded the optokinetic eye movements in the rock crab, *Pachygrapsus marmoratus*, that were elicited by one or two horizontally oscillating vertical stripes and we varied the azimuthal angular separation between 20 and 180 deg. This poorly textured visual environment is appropriate for examining the crab's response to "global image motion" because crabs do not fixate and track single moving objects with their eyes (Horridge & Sandeman, 1964; Sandeman, 1978; Nalbach & Nalbach, 1987). Since optokinetic sensitivity varies over the eye of decapod crustaceans (von Buddenbrock & Friedrich, 1933; Kunze, 1963; Sandeman, 1978; Okada & Yamaguchi, 1985; Nalbach & Nalbach, 1987; Barnes, 1990; Fig. 1), the stripes were presented in a number of different positions around the crab. At elevations where the carapace or the opposite eye are not occluding the vision, each eye of *Pachygrapsus marmoratus* has a visual field of 360 deg in azimuth (Nalbach, 1987).

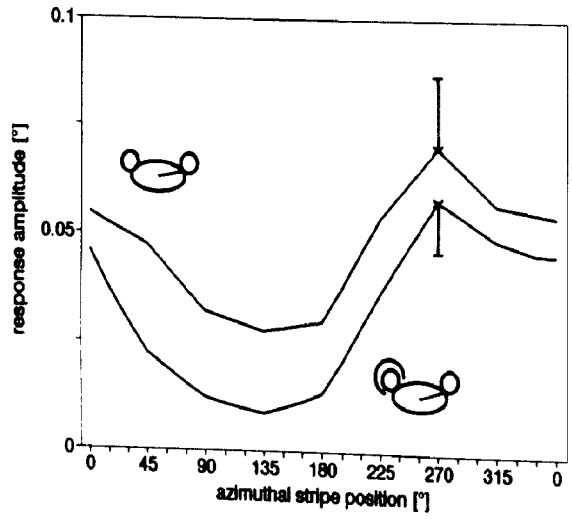

Fig. 1. Regional variation of the optokinetic response to a single stripe oscillating at various azimuthal positions around the eye of intact *Pachygrapsus marmoratus* (upper curve, left inset) and crabs with one eye covered by opaque paint (lower curve, right inset). Data from Nalbach and Nalbach (1987) are scaled by responses of four crabs of the present study with one black stripe (10 deg wide) sinusoidally oscillating at the position 270 deg (frequency 0.17 Hz, amplitude ±3.8 deg). Bars indicate standard errors.

This raises the question whether the expected interactions of local movement detectors take place within one eye only or also between the two eyes. We therefore compare the responses of intact and monocularly blinded crabs.

Material and methods

The experiments were carried out with seven rock crabs, *Pachygrapsus marmoratus*, with carapace widths ranging from 2.9–3.5 cm. During the experiments, the animals were fixed in space by a rod glued to their carapace and placed in the center of a drum (diameter 28 cm, height 35 cm). Their legs were supported by an air-cushioned styrofoam ball (diameter 10 cm) which could be rotated by the crab walking on the spot (Dahmen, 1980). Depending on the state of their activity, the animals sometimes lifted their legs and performed vigorous grasping movements. Since optokinetic gain varies with the state of the activity (Horridge, 1966; Nalbach & Nalbach, 1987), only the results of those experiments during which the animals were standing motionless on the ball were evaluated.

One or two vertical black stripes (10 deg wide, height 48 deg above and 52 deg below the equator of the eyes) were inserted into the drum and sinusoidally oscillated (frequency 0.17 Hz, amplitude ± 3.8 deg) around the yaw axis of the animal. Since each eye's lower visual field is occluded in the medial and posterior direction by the crab's own body (Nalbach, 1987), one or both of the stripes was only partly seen by one of the eyes, depending on the stripes' azimuthal positions. The optokinetic system of *Pachygrapsus* has, however, to cope with this incomplete visual field in its normal environment also. Therefore we did not restrict the stripes to the crab's upper visual field which covers the complete azimuth. The pair of stripes with varying angular distance (D) is named "stripe configuration." It is specified by the azimuthal positions of the stripes (e.g. 90 deg/270 deg) with 0 deg in front and 90 deg on the left side of the animal (see inset in Fig. 3b). Since the interval between two adjacent stripe configurations is 15 deg, the number of tested configurations is 24 with D = 20 deg or 12 with D = 180 deg, respectively (cf. abscissa in Figs. 3a and 3b). The background was a stationary white plastic cylinder. Narrow strips of white paper were glued to the eyecups the angular positions of which could be simultaneously recorded by means of a videotracker (for details see Fleischer & Pflugradt, 1977).

Response amplitudes were calculated by fitting a sine function with variable phase and amplitude but known (stimulus) frequency to the data plus a linear term to account for drift. With this method, an angular resolution better than 0.005 deg could be achieved.

Since the reactions of the two eyes should be the same under equivalent stripe configurations, we lumped corresponding raw data from the left and right eye. All response curves are drawn as if obtained with the right eye only (indicated by a line in insets). In some experiments, one of the eyes was reversibly blinded by covering it with opaque black paint. These animals will be named "monocular," and unimpaired crabs are called "binocular." As far as possible, a configuration with neighboring stripes was followed by one with widely separated ones to counteract a possible temporal trend in the reactivity of the animals. Furthermore, different parts of the eye were stimulated in consecutive experiments to prevent adaptation effects.

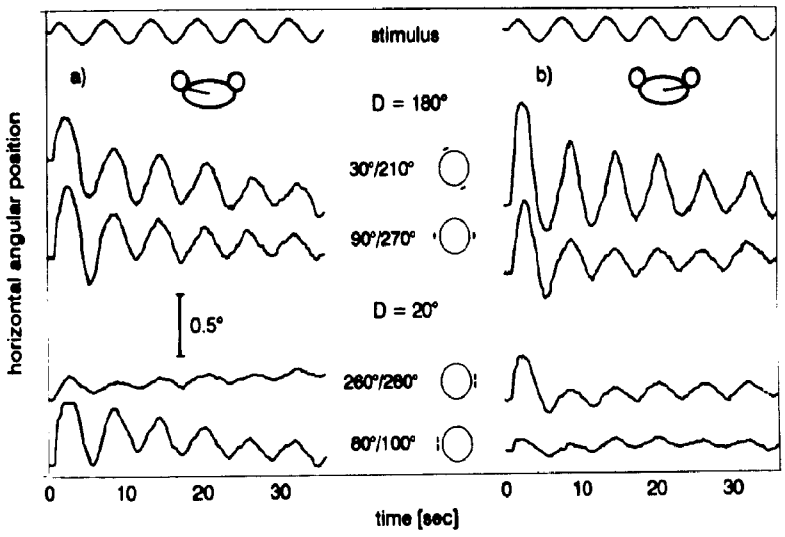

Fig. 2. Sample records of the optokinetic eye movements of the left (a) and right (b) eye of an intact crab stimulated by two vertical black stripes separated either by $D = 20$ deg or $D = 180$ deg placed at different azimuthal positions as indicated. Uppermost trace: stimulus (amplitude ±3.8 deg, not drawn to scale). Lower traces: eye position *vs.* time (see scale bar).

Results

Two stripes separated either by 20 or 180 deg

The oscillating stripes elicit weak, roughly sinusoidally modulated eye movements with a maximum closed loop gain of 0.23, but usually much less (Fig. 2). It should be noted that there is a strong habituation of the optokinetic response which has been observed previously only in response to high-frequency oscillations of densely striped patterns (Horridge, 1966; Nalbach, 1989). Especially the response during the first cycle is much stronger than during the following ones. Therefore only responses from cycle 2 to cycle 6 have been evaluated.

The sample records indicate firstly that the responses of binocular crabs to stripes separated by $D = 180$ deg are stronger than those to stripes presented with $D = 20$ deg. Secondly, the responses elicited with either one of the two principal configurations, $D = 20$ deg or $D = 180$ deg, respectively, depend on the positions of stripes in the crab's visual field. Furthermore, the response amplitudes of both eyes usually differ, most pronouncedly when the two stripes are on the same side (Fig. 2, bottom curves). This can be attributed to a variation in optokinetic sensitivity and the weak neural coupling of the eyes (Barnes & Horridge, 1969; Nalbach et al., 1985; Nalbach & Nalbach, 1987; Nalbach, 1989).

These qualitative observations were substantiated by systematically varying the position of the pair of stripes (Fig. 3). Regional variation of the response amplitude can most easily be read from the polar plots in the insets of Fig. 5. When the two stripes are separated by $D = 20$ deg, in both binocular and monocular crabs, the maximum response is elicited when the stripes oscillate in the lateral visual field, i.e. close to 270 deg, and the medial region of the visual field is the least sensitive, i.e. around the 90-deg position. These results are similar to those obtained in single-stripe experiments and thus reflect azimuthal variation of the optokinetic sensitivity (cf. Introduction, Fig. 1) due to both regional variation of eye parameters and neural wir-

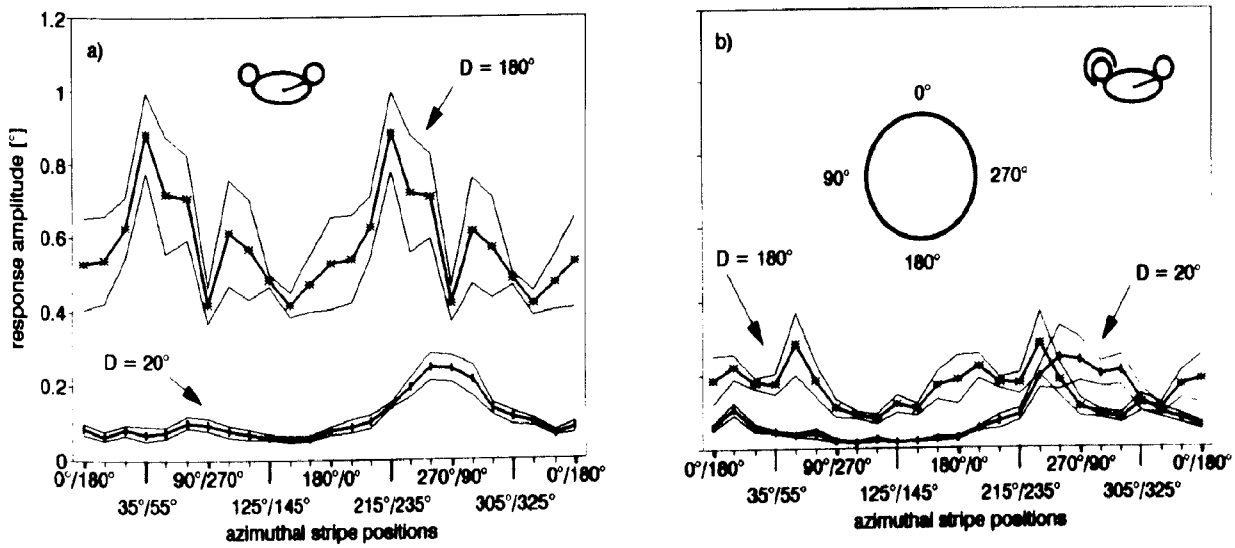

Fig. 3. Amplitude of the optokinetic response elicited by two oscillating vertical stripes separated either by $D = 20$ deg (short vertical lines) or by $D = 180$ deg (asterisks) and presented at various azimuthal positions in steps of 15 deg (abscissa: short ticks $D = 20$ deg, long ticks $D = 180$ deg). Average values with standard error of the mean (thin lines) determined with four crabs: (a) binocular and (b) monocular crabs.

ing (Sandeman, 1978; Nalbach & Nalbach, 1987). Furthermore, the responses in monocularly blinded crabs are slightly reduced compared to the corresponding responses in intact animals. When the two stripes are separated by $D = 180$ deg, the binocular animal's response is maximal when the stripe configuration is 45 deg/225 deg and minimal when the stripes are oscillating approximately at the positions 135 deg/315 deg. Similarly, monocularly blinded crabs respond best to the stripe configuration 60 deg/240 deg and weakly to stripes oscillating at the positions 120 deg/300 deg.

However, the optokinetic responses of intact crabs averaged over all azimuthal positions are by a factor of about 4 stronger than in monocularly blinded animals (Figs. 3a and 3b). Furthermore, the differences between the responses to widely separated and closely positioned stripes are less pronounced in monocular crabs than in binocular ones. When the two closely positioned stripes are presented to the optokinetically most sensitive lateral visual field of the seeing eye in monocular crabs, the responses are even larger than in a comparable experiment with stripes separated by $D = 180$ deg, that is when only one stripe oscillates in this most sensitive region (Fig. 3b). In binocular crabs, however, both the peak values and the responses averaged over all stripe configurations are about 4 to 6 times larger with $D = 180$ deg than with $D = 20$ deg (Fig. 3a).

The responses of binocular crabs to single stripes can be predicted from the responses of monocular crabs assuming an additive input from one eye to the other with a weighting factor of 0.36 (Nalbach & Nalbach, 1987). The same holds for the responses of binocular crabs to pairs of stripes separated by $D = 20$ deg (Fig. 4a). But the prediction fails when the stripes are separated by $D = 180$ deg. The responses of binocular crabs are far greater than those predicted by summing responses of monocular crabs (Fig. 4b), and the modulation of the experimental curve with azimuth is much more pronounced than expected.

Towards the underlying mechanism

These results suggest that there are indeed interactions between local movement detectors that increase the optokinetic response when the eyes are stimulated by two widely separated stripes, especially in binocular crabs. However, horizontal variation of optokinetic sensitivity might at least partly account for our results. We therefore compared the responses obtained in the present experiments with those that are to be expected on the basis of the "summation hypothesis" (Götz, 1975). According to this hypothesis, the response to two simultaneously presented stripes should be the sum of the responses obtained in separate experiments with a single stripe in the same positions as in the two-stripe experiment. To compare the results of the present experiments with the predictions of the summation hypothesis, we used the known responses of *Pachygrapsus* to a single stripe presented at different positions around the crab (Nalbach & Nalbach, 1987). To scale these data to the response strength of the present population, we sinusoidally oscillated a single stripe in the lateral visual field of the recorded eye at position 270 deg where the largest eye movements can be evoked (Fig. 1).

Fig. 5 demonstrates that the responses of both binocular and monocular crabs to stripes at various azimuthal positions and separated by $D = 20$ deg are fairly well approximated by the summation hypothesis. Only when the stripes are presented to the most sensitive part of the recorded eye is there a moderate amplification in the two-stripe experiments in both binocular and monocular animals (Figs. 5a and 5b). Thus, the expected responses are equal or smaller, but never larger than the measured ones.

However, when the stripes are separated by $D = 180$ deg, the summation hypothesis fails to describe the data in both binocular and monocular crabs (Figs. 5c and 5d). The measured responses are much larger than those predicted from the summation hypothesis. The only exception is in monocular crabs when one of the stripes is on the side of the blinded eye. The values predicted by summation are then close to the experimental data (Fig. 5d). However, this situation is effectively identical to a single-stripe experiment since the stripe contralateral to the seeing eye hardly elicits an eye movement (Fig. 1).

Since the responses elicited by a single stripe were obtained in experiments with a different population of crabs (Nalbach & Nalbach, 1987) from those in the present study, we tested our

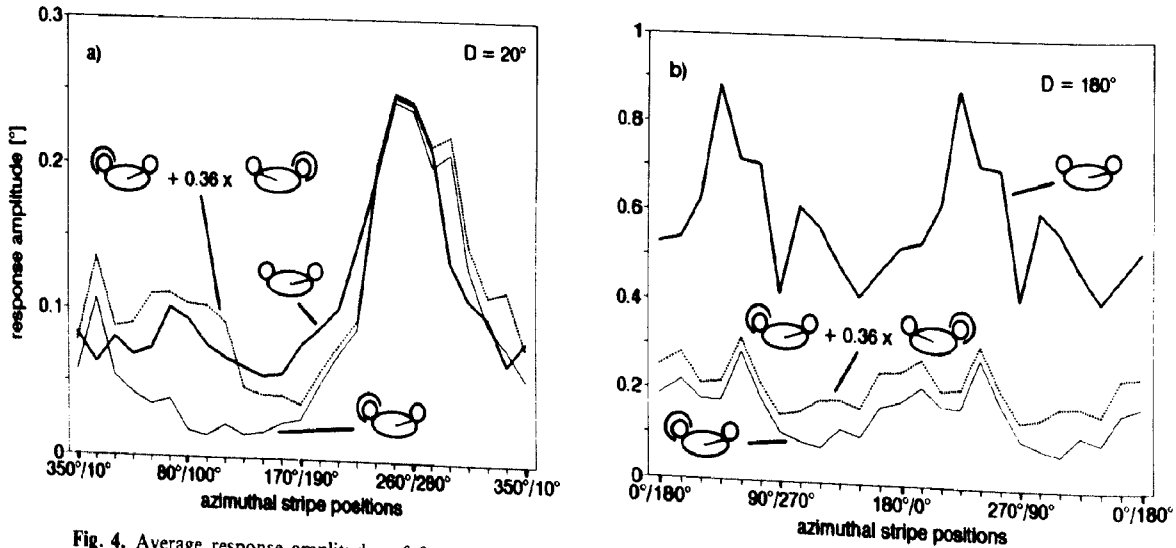

Fig. 4. Average response amplitudes of four binocular crabs obtained in two-stripe experiments (thick lines; data from Fig. 3a) compared to response amplitudes calculated (dotted lines) from the responses of monocular crabs in the same situations (thin lines; data from Fig. 3b) assuming additive eye coupling: (a) stripes separated by $D = 20$ deg and (b) stripes separated by $D = 180$ deg.

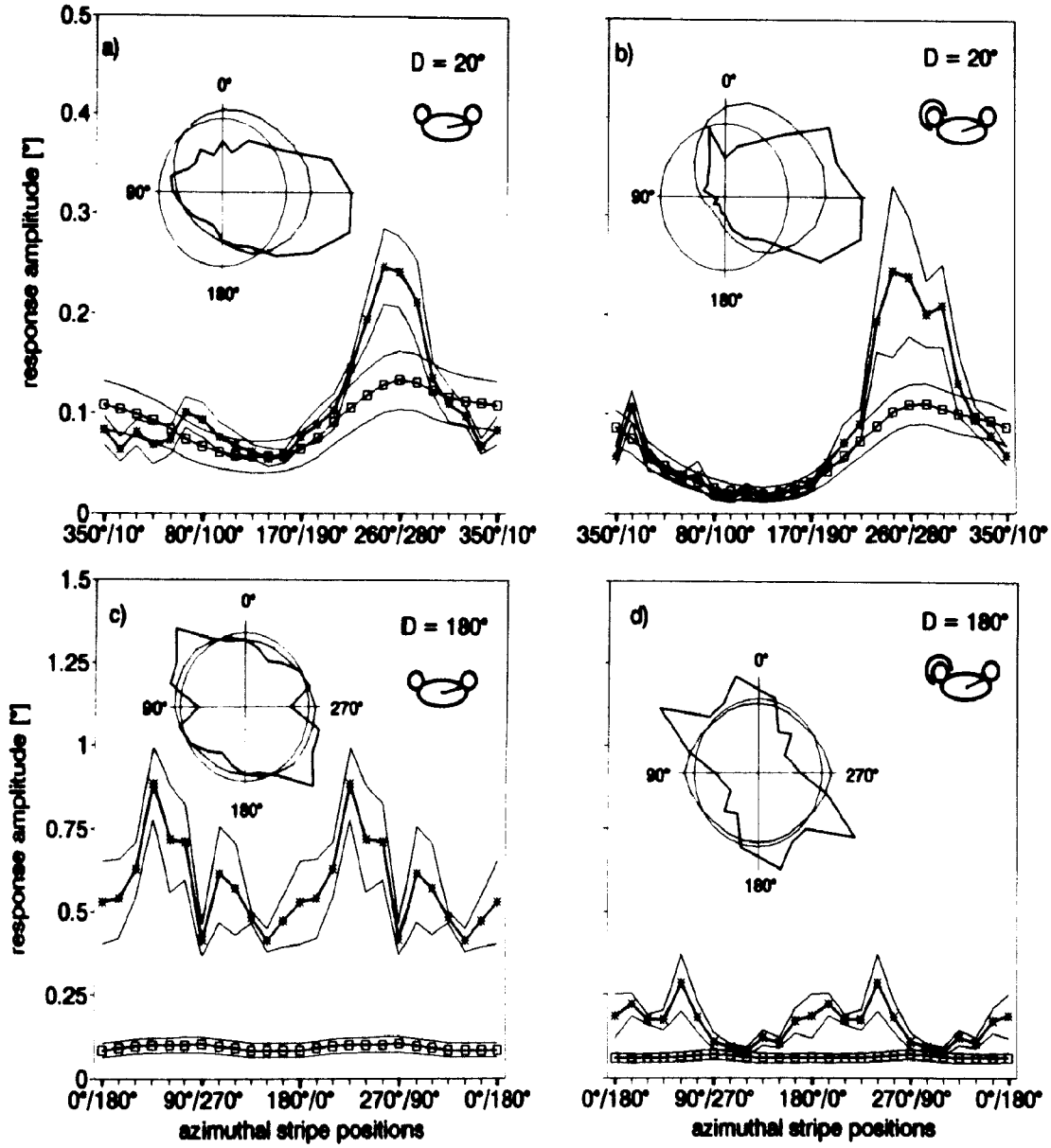

Fig. 5. Experimental results from Fig. 3 (asterisks) and responses expected on the basis of the summation hypothesis (open squares). Thin lines: standard errors of the mean. In insets, polar diagrams of the experimental data (thick lines) and the calculated values (dotted lines) are shown, both normalized to cover the same area as the unit circle (thin lines). These polar diagrams stress both the different azimuthal positions of the maxima and minima and the differences in the modulation of the curves. The stripes are separated either by $D = 20$ deg (a,b) or by $D = 180$ deg (c,d). The crabs are either binocular (a,c) or monocular (b,d).

animals in single- and two-stripe experiments during *one* experimental session. This procedure is essential to avoid the influence of temporal changes in reactivity of the crabs on the responses to be compared, but it restricts the number of experiments that can be performed in such a control experiment. We therefore chose a few positions in the lateral visual field of the crab since there the responses to a pair of stripes deviate most strongly from the values predicted by the summation hypothesis.

The responses in binocular crabs elicited by two stripes in the $D = 20$ deg configuration at selected azimuthal positions in this series of experiments are almost equal to the responses calculated according to the summation hypothesis (Fig. 6). However, as in the previous experiments, the response amplitudes to the widely separated stripes are larger than the predicted values by a factor of about 4. The quantitative differences between the results of the first (Fig. 5) and the second (Fig. 6) series of experiments might be due to the fact that in the latter the responses to the same stripe configuration are by about 50% weaker than in the first series which was performed with freshly captured crabs. However, at least qualitatively, the control experiment yields the same results as obtained in the first series of experiments.

Since the summation hypothesis cannot explain the response amplitudes in the two-stripe experiments, nonlinear interactions between the local movement detectors have to be postulated. These nonlinear interactions enhance the optokinetic response to widely separated contours in the visual field. In principle, two different mechanisms could generate such an enhancement. Either there is a "release from inhibition" when stripes are more and more separated, or a mutual "excitation" of the two sig-

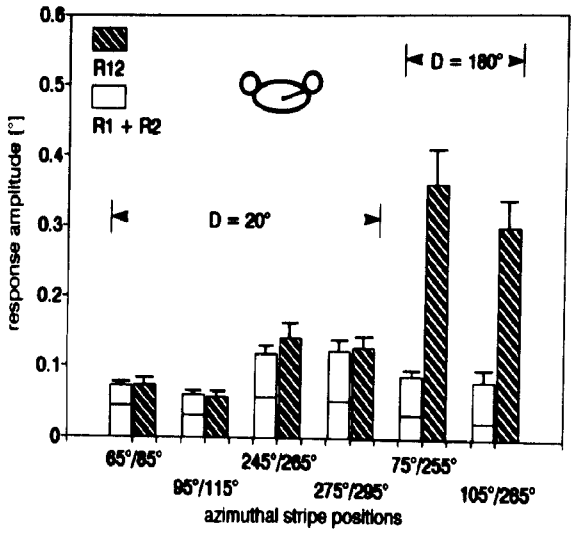

Fig. 6. Response amplitudes elicited in two-stripe experiments (hatched bars) and calculated from experiments with single stripes at the appropriate positions (white bars) as indicated by the stripe configurations along the abscissa. The horizontal line within the white bars separates the response amplitudes obtained in experiments with the single stripe in one of the two positions. The two stripes were separated either by $D = 20$ deg or by $D = 180$ deg, as indicated. Average values from three binocular crabs with standard error of the means; total number of stimulus presentations $n = 12$ in the experiments with $D = 20$ deg, $n = 24$ in those with $D = 180$ deg.

nals amplifies the optokinetic responses to widely separated stripes. Since the responses in the $D = 20$ deg situations (monocular and binocular crabs) are at least as large as predicted from the summation hypothesis, the first mechanism can be excluded, i.e. neighboring movement detectors do not inhibit each other when stimulated simultaneously. It is much more likely that the enhanced responses to stripes separated by 180 deg in both monocular and binocular crabs are due to facilitation.

Azimuthal separation of stripes between 20 and 180 deg

The results reported above lead us to ask how the optokinetic response becomes enhanced when the separation of the two stripes is increased from 20 to 180 deg. We chose pairs of stripes separated either by 45, 90, 135, or 180 deg. Since the number of all possible configurations is too large to be presented during one experimental session, we presented one of the two stripes (reference stripe) in either one of three azimuthal positions 0, 90, 270 deg, and varied the position of the other stripe. This series was meant to give a qualitative insight into the organization of the crab's optokinetic system. We mainly studied intraocular interactions, and thus most experiments were performed with monocularly blinded animals. These results are compared to data from a single, binocular crab which thus are preliminary but nevertheless safely demonstrate the main aspects to be shown.

When the reference stripe is positioned on the side of the blinded eye of the monocular crabs (Fig. 7a), the response am-

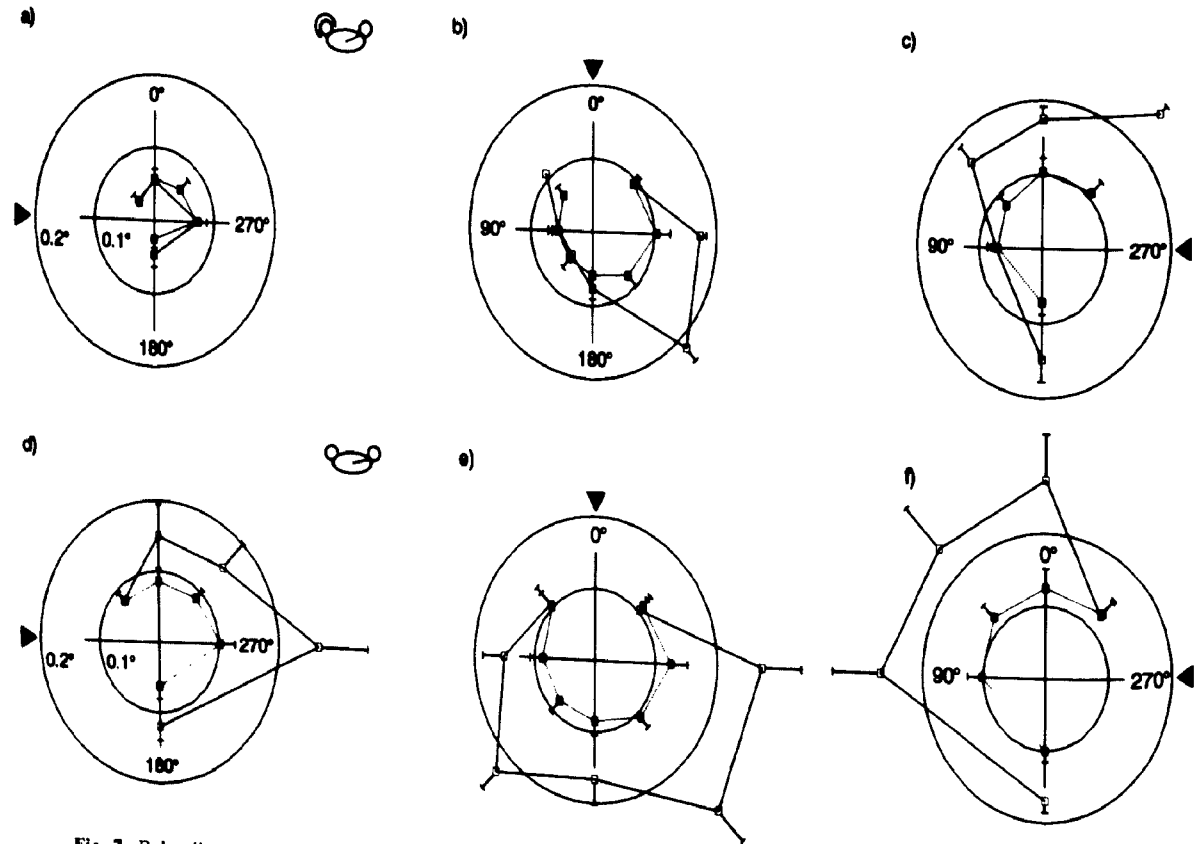

Fig. 7. Polar diagrams of average response amplitudes (open squares) with standard error and response amplitudes calculated according to the summation hypothesis (filled squares). Horizontal angular separation of the stripes varied from $D = 45$ deg to $D = 180$ deg. The position of the reference stripe is indicated by the filled triangle at position 90 deg (a,d), 0 deg (b,e), and 270 deg (c,f). The open squares are at the position of the second stripe. Scaling as indicated in (a,d). a-c: four monocular crabs; and d-f: binocular crab.

plitudes are small and do not deviate from those expected from the summation hypothesis. Since this is effectively a single-stripe situation (Fig. 1), no excitatory interaction is expected. When the reference stripe is positioned in the frontal visual field, which is moderately sensitive to optokinetic stimuli (Fig. 1), the responses are weak provided that the second stripe is placed contralateral to the seeing eye (Fig. 7b). However, when the second stripe is placed on the side of the seeing eye and the stripes are separated by more than 45 deg, the responses are much stronger than predicted by the summation hypothesis. Finally, when the reference stripe is placed in the optokinetically most sensitive lateral part of the seeing eye (Fig. 7c), the responses are enhanced even if the stripes are separated only by 45 deg. Again, when the second stripe is placed lateral to the blinded eye at 90 deg, it does not contribute to the response although the stripes are separated by 180 deg.

Also in the binocular crab, the optokinetic response depends on the azimuthal position of the stripes and their separation (Figs. 7d–7f). In this crab, stripes separated by 45 deg never elicited eye movements larger than predicted. Otherwise, the responses were enhanced, particularly when one stripe was positioned ipsilaterally to the recorded eye (compare Figs. 7d and 7f).

In summary, these experiments with monocular and binocular crabs demonstrate that the optokinetic response in *Pachygrapsus* becomes pronouncedly enhanced when the two stripes are separated by at least 45 to 90 deg and when each stripe is presented at positions (Fig. 1) where it evokes a strong response even in a single-stripe experiment.

Discussion

When stimulated by a pair of sinusoidally oscillating stripes, the strength of the optokinetic response of *Pachygrapsus marmoratus* depends on both the azimuthal position and the separation of the stripes. This is much more pronounced in binocular crabs than in monocular ones (Fig. 3). Thus we conclude that both intraocular and interocular interactions of elementary movement detectors contribute to the enhancement of the optomotor response. Furthermore, we can exclude that neighboring movement detectors inhibit each other since the responses of both binocular and monocular crabs in the $D = 20$ deg configuration (Figs. 5a, 5b, and 6) are at least as large as predicted from the summation hypothesis. Thus, the enhanced responses of both binocular and monocular crabs to stripes separated by 180 deg cannot be attributed to a "release from inhibition" but are due to an excitatory interaction (Figs. 5c, 5d, and 6).

Our results substantiate the earlier finding that the optokinetic response elicited by two vertically oscillating *horizontal* stripes is larger than predicted by summation of single-stripe response amplitudes when the stripes are separated by $D = 180$ deg and stimulating the eye within a narrow region around its equator (*Heloecius* and *Pachygrapsus*: Nalbach et al., 1989). Thus, from the earlier and the present results, we conclude that in *Pachygrapsus* a similar organization of wide-range interactions of movement detectors for all three axes of rotation seems to exist.

Experiments similar to ours were performed first with the fly *Pollenia*. In this species, two widely separated stripes on the wall of a continuously rotating drum elicit stronger optomotor responses than two stripes which are close to each other (Gaffron, 1934; Hertz, 1934). Recently in another insect species, the waterstrider *Gerris*, dramatic effects of separating two oscillating stripes on regional variation of optokinetic sensitivity were demonstrated (Dahmen, personal communication). Similar effects have been observed also in pigeons (Nalbach, 1990*b*). Thus, in a wide range of species interaction of movement detectors with widely separated receptive fields enhances the optokinetic response to rotating panoramas. In addition, it was shown in pigeons standing in the center of a rotating textured drum that translational head movements are reduced (Nalbach, 1990*b*). Thus, long-range interactions of local movement detectors seem to enable animals to decompose optic flow into its rotational and translational components.

Our results allow us to speculate on possible neural mechanisms underlying such interactions. Our hypothesis has been inspired by a proposal of von Buddenbrock and Friedrich (1933) nearly 60 years ago. They demonstrated that the optokinetic responses of *Carcinus maenas* increase drastically when the width of a moving stripe pattern is expanded just beyond 180 deg. Similar results were obtained in the fiddler crab, *Uca pugnax* (Kunze, 1963). Although open to several alternative hypotheses, von Buddenbrock and Friedrich came up with a model of excitatory interactions between movement detectors with roughly opposite receptive fields. Indeed, both in insects (Ibbotson, 1991) and in birds (Wylie & Frost, 1990, 1991) recent electrophysiological recordings demonstrated movement-sensitive cells whose receptive fields are divided into subfields that receive input from about opposite receptive fields.

We propose a specific four-layer-model to explain both the regional and separation-dependent strength of the crab's optokinetic responses (Fig. 8): local, directionally selective movement detectors of the correlation type sense the pattern motion (Reichardt & Varjú, 1959; Fleischer, 1980; Nalbach, 1989). Their outputs are integrated in second-stage neurons with overlapping receptive fields. Such a layer of neurons with moderately broad receptive fields will reduce the number of neurons necessary to mediate the interactions that take place in the next layer. Motion-sensitive cells with appropriate width of their receptive fields (30 to 40 deg) have been recorded in the optic tract of the crab *Podophthalmus* which seem to cover the entire visual field of the animal (Waterman et al., 1964; Wiersma et al., 1964). To account for regional variation in optokinetic sensitivity (Sandeman, 1978; Nalbach & Nalbach, 1987; Barnes, 1990), the outputs of these cells are weighted by the factors g_i, g_j ... (see Fig. 8). They are the input to the cells of the third stage where the essential, excitatory intraocular interactions take place. Specifically, we propose a multiplication-like operation between pairs of layer 2 cells whose receptive fields are separated by a certain angle. The products are integrated by the layer 3 cells whose outputs are weighted according to the "separation label" (factors K_a, K_b, ...). That is, cells receiving input from areas separated by $D = 20$ deg have a low weighting factor, and those receiving input from areas separated by $D = 180$ deg have the highest weighting factor. These layer 3 interactions account for the separation-dependent increase of the optokinetic response. The weighted signals are integrated in layer 4 (possibly not neurons but muscles) to give rise to an eye movement in the appropriate direction.

The suggested multiplication-like operation in pairs of layer 2 cells is derived from a fit to the experimental data of responses calculated under this assumption (Fig. 9). In our calculation, we assume that the output signals of the second-stage neurons

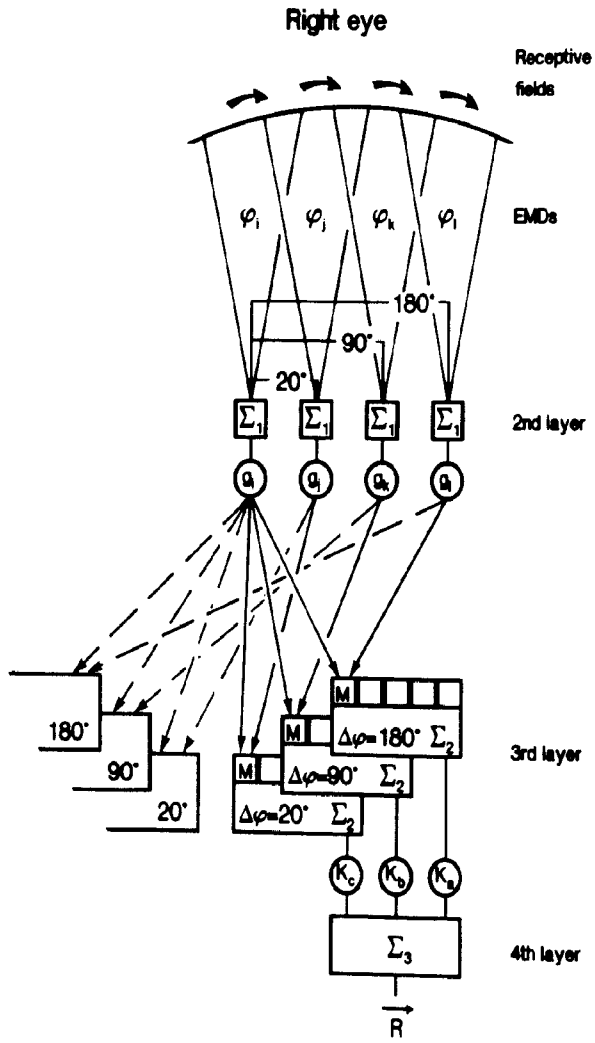

Fig. 8. Four-layer-model to describe position and separation-dependent strength of the optokinetic response. The first layer consists of direction-sensitive local movement detectors (EMDs) which are not shown individually. The output of these EMDs is integrated by layer 2 cells with overlapping receptive fields. Their output is weighted (factors g) according to the azimuthal position of the cells' receptive field. The weighted output is fed to layer 3 cells in the following manner. Pairs of signals of those layer 2 cells are combined, whose receptive fields are separated by a specific angle, for example by 20, 90, or 180 deg. Of course, there are much more interacting pairs of output signals from the layer 2 cells onto the layer 3 cells than shown in the figure but for the sake of clarity they are omitted. At the layer 3 cells the excitatory, intraocular amplification takes place by a multiplication-like interaction (M). The products of all interacting signal pairs are integrated by the layer 3 cells. In the next step their output is weighted by a factor K, which depends on the separation between the receptive fields of layer 2 cells feeding onto the specific layer 3 cell. Finally, the weighted signals of all layer 3 cells are integrated in the fourth-layer cell whose output represents the motor-output (R) for one direction of eye movement. The broken lines indicate that both eyes interact.

are proportional to the response amplitudes obtained in single-stripe experiments (Fig. 1). We shift them in azimuth according to the configuration in the two-stripe experiment, and calculate their product. Although we propose a multiplication as the essential nonlinear interaction in this step of information processing, our results demonstrate that the crab moves its eyes sinusoidally with the same frequency as the oscillating pattern (Fig. 2). Multiplication of two sine functions results in a strong component of the twofold frequency. Since, however, the interaction of second-layer cells is restricted to cells with identical preferred direction, their output differs from zero only during one-half period of the stimulus cycle. Movement into the opposite direction is coded by a parallel pathway of opposite directional sensitivity. The resulting curve is fitted to the experimental data by a least-square procedure, which yields the different weightings K_a, K_b, K_c ... of the output signals of the third-layer cells (Fig. 8).

Considering the experiments with monocular crabs, to which the model is primarily adapted, the data are closely approximated by the proposed multiplication-like interaction with respect to both the depth of modulation and the position of minima and maxima (Fig. 9). At first view, the latter is somewhat astonishing in the case of 180-deg separated stripes, since the peak response is displaced from the position of the maximal response to a single stripe. However, this is a consequence of the multiplication stage in the model. For example, the response to a single stripe oscillating in the 270-deg position is relatively strong (0.059 deg) but that one to a stripe in the 90-deg position is weak (0.012 deg). Consequently, the multiplication of these two values yields a smaller product (0.00071 deg) than the multiplication of the moderately strong responses to stripes oscillating in the 45-deg (0.023 deg) or the 225-deg position (0.037 deg), respectively, which results in a larger value (0.00085 deg).

We have demonstrated (Fig. 4) that the simple additive model that originates from experiments with monocular crabs (Nalbach, 1989) is not adequate to describe optokinetic eye coupling when both eyes receive visual input and stripes are widely separated. This result led us to conclude that binocular interaction depends on both stripe separation (compare results obtained with $D = 20$ deg and $D = 180$ deg, Figs. 4a and 4b) and stripe position within the visual field (compare modulation of response curves and linear predictions in the $D = 180$ deg situations, Fig. 4b). This suggests that interocular interactions similar to the intraocular mechanisms are effective in binocular crabs. Thus, we propose that linkage of both eyes is achieved by neurons originating from layer 2 cells of our model (Fig. 8). They converge onto layer 3 neurons of the contralateral eye that represent the adequate angular separation of receptive fields. This means that the crab possesses a cyclopean eye with regard to the optokinetic response. A somewhat related model was proposed by Barnes and Horridge (1969).

The most suggestive hints, however, come from experiments of Kunze (1964) with a species of ghost crabs, *Ocypode*. When he allowed the crab to see one hemifield of a continuously rotating drum with one eye only, very weak optokinetic responses were elicited. When the crab could see a small additional part of the second hemifield, the responses dramatically increased. The outcome of the experiments was qualitatively the same independently which of the two eyes saw the additional part, i.e. intraocular and interocular interactions equally enhanced the optokinetic gain.

Recordings from the optic tract that connects the optic ganglia of both eyes and the brain demonstrate movement-selective neurons with properties that make them likely candidates to represent layer 2 cells of our model: they are directionally selective, have receptive fields 30–60 deg wide, and transfer information from one eye to the other (Wiersma et al., 1964). Furthermore, in *Carcinus*, direction-selective interneurones in the medulla have been identified which receive input from both eyes (Sandeman et al., 1975). More detailed analysis of their

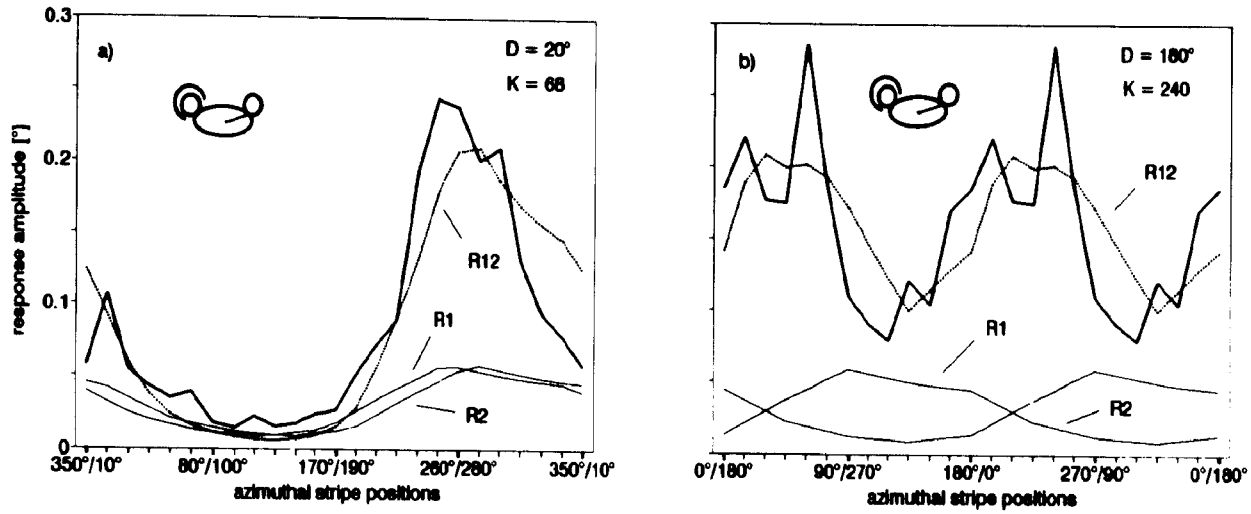

Fig. 9. Average response amplitudes of four monocular crabs obtained in two-stripe experiments (thick lines; data from Fig. 3b) compared to responses (R12) calculated according to the proposed four-layer-model (Fig. 8) by multiplication of the responses to single stripes (R1, R2) at the appropriate positions (from Fig. 1). Using the least-square method, the weighting factor K was calculated which gave the best fit to the experimental data: (a) 20-deg stripe separation, and (b) 180-deg stripe separation.

properties is needed, however, to identify them as layer 3 neurons of our model.

In our study, we set out to explore a possible mechanism in crabs that responds only to the rotational component of the optic flow field with compensatory eye movements. Recently, in a study of visual orientation in waterstriders Junger and Dahmen (1991) proposed a different mechanism for the visual discrimination between rotational and translational self-motion. They suggest that animals might discriminate between rotation and translation by exploiting the fact that in specific areas of the visual field the directions of the flow-field vectors generated during translation differ strongly from those generated during rotation. These differences are most pronounced at roughly 45 deg above and below the horizon and at azimuthal positions that depend on the direction of translation. Flow-field components could be distinguished by comparing overall horizontal and vertical components in these areas. An important property of this scheme is that discrimination is possible with monocular information alone although it should improve whenever image motion is seen at opposite positions in the visual field.

The latter corroborates our results. The idea that specific parts of the visual field might play a particular role in discriminating rotation and translation has been put forward before to explain azimuthal variations in optokinetic sensitivity. According to a hypothesis of Collett (1980), animals might react with a rotational optomotor response when they perceive motion across that part of the eye that looks forward into the direction of locomotion, i.e. into the "pole" of the translational flow field. Since crabs predominantly run sideways, the peak of motion sensitivity in their lateral visual field has consequently been taken as an indication that crabs might use such a mechanism to respond to rotational image motion only (Wehner, 1981; Barnes, 1990). However, in this case we would expect that with two stripes separated by $D = 180$ deg the maximum of motion sensitivity still in the crab's lateral visual field. Our data demonstrate, however, that in this situation the peak sensitivity is shifted to an oblique axis in both binocular and monocular crabs (inset in Figs. 5c and 5d). Accordingly, it seems unlikely that regional variation of optomotor sensitivity is a specific adaptation in order to cope with the requirements of decomposing the optical flow field and alternative hypotheses gain more weight (Sandeman, 1978; Nalbach & Nalbach, 1987).

In the Introduction, we outlined a gedanken experiment that illustrates the use of far-ranging interactions of local movement detectors to distinguish between the translational and rotational component in the optic flow. We have demonstrated that indeed the response to pattern rotation increases with stripe separation. However, additional experiments have to be performed to study whether such a mechanism effectively suppresses erroneous responses to translational optic flow. A critical test would be, for example, to confront the crab with simultaneous translational and rotational optic flow of a pattern consisting of either closely spaced or widely separated stripes. From our results, we would predict that in the latter case crabs will rotate their eyes only with respect to the rotational and not the the translational component.

Present knowledge suggests that, in a range of species, elementary movement detectors in diametrically opposite positions in the animals' visual field form a very efficient rotation detector. We expect that such an arrangement represents a general strategy to decompose optic flow into its rotational and translational component.

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