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LIGHT-DEPENDENT EYE COUPLING DURING THE OPTOKINETIC RESPONSE OF THE CRAB *CARCINUS MAENAS* (L.)

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SUMMARY

1. The movements of both distal eye stalks in the horizontal plane, elicited by optokinetic stimuli, have been recorded simultaneously.

2. A panorama was split into two separate halves and was either oscillated around the animal in a sinusoidal fashion or displaced in a stepwise manner. Both eyes could be stimulated independently.

3. The stimuli on both sides differed either (a) in the illumination, or (b) in the total amount of light impinging upon the eyes or (c) in the relative phase of the sinusoidal stimuli to either eye.

4. As the illumination decreases the optokinetic response weakens.

5. If one eye has no or only weak optokinetic input, it will be driven by the other eye. The response mediated by the contralateral optokinetic stimulus diminishes if the amount of light impinging upon the driven eye is increased.

6. There is a logarithmic relationship between the response of the driving eye and that of the driven eye.

7. The possible biological significance of these relationships is seen in the enhanced coupling at low light intensities.

8. The variable strength of coupling and possible roles of movable eyes are discussed.

INTRODUCTION

When decapod crustaceans turn around the yaw axis, their eyes rotate in the opposite direction relative to the body, so that they remain almost stationary with respect to the surroundings. Depending on the circumstances, the eye movements are mediated by the visual input itself *via* the well-known optokinetic response (see e.g. Dijkgraaf, 1956; Kunze, 1963; Horridge & Sandeman, 1964), by the eye-leg-reflex (Varjú & Sandeman, 1982) or by statocyst organs (Sandeman & Okajima, 1972). While compensating for body rotations, both eyes usually move synchronously, that is to say in the same direction and with the same angular velocity.

When eye movements are elicited in laboratory experiments by moving vertically-striped patterns around the animal, both eyes see the same panorama. Under such circumstances synchronous eye movements would be expected, even if both eyes were

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driven by their own, independent optomotor pathways. Yet bilateral interaction has been demonstrated in previous experiments: even if only one eye (driving eye) receives optomotor input while the other (driven) eye is blinded, both move more or less in synchrony. Also, motor neurone activity to the blinded eye has been recorded while stimulating the contralateral eye (Horridge & Sandeman, 1964; Wiersma, Bush & Waterman, 1964). It has therefore been concluded that both visual inputs are integrated to generate a common motor programme of central origin (Horridge & Sandeman, 1964). It should not be overlooked, however, that during synchronous eye movements one eye moves towards the midline of the body and the other away. Thus, different sets of muscles are excited on both sides by different groups of motor neurones. Furthermore, the synchrony of eye movements can be abolished, at least temporarily, by conflicting stimuli to both eyes (Barnes & Horridge, 1969).

One of the major problems the eye has to cope with under natural conditions is the change in light intensity during the day. It is now known that the eyes of crabs undergo large diurnal alterations in structure and short-term pigment migrations (Henkes, 1952; Leggett & Stavenga, 1981). Although it is known that the optokinetic system becomes less effective at low light intensities (Korte, 1966; Varjú & Sandeman, 1982), the influence of illumination on the optokinetic reaction has been widely ignored. Only the optokinetic response to a moving pinlight of varying intensity has been studied (Horridge, 1966). The present study is therefore addressed to the effects of illumination on the optokinetic reaction, with particular attention paid to the role of binocular coupling.

MATERIALS AND METHODS

Specimens of the shore crab *Carcinus maenas* (L.), of 3–5 cm carapace width, were clamped by their carapace in the centre of a stimulus drum. The animal's inclination to the vertical resembled the most frequently observed natural posture. All experiments were carried out in moistened air and care was taken to keep the air temperature below 20 °C (see Fleischer, 1980).

The panorama subtended a visual angle of ± 52 °C above and below the crab. A partition subdivided the visual field along the long axis of the animal. It was tightly fitted to the carapace so that neither eye could see the panorama presented to the other. On one side a standard pattern was presented consisting of equidistantly spaced black and white stripes, each 15 ° wide (see inset to Fig. 2). The other side was either homogeneously white or contained black stripes of varying number and width. The drum was illuminated from outside through a diffusing cylinder by a mosaic of 32 small d.c.-driven incandescent light bulbs. The illumination could be independently varied on both sides by introducing neutral density filters into the space between bulbs and drum. The degree of light modulation within the pattern amounted either to 50 % or to 95 %, not affected by changing the illumination.

On both eyes narrow strips of paper were fastened. Their angular positions were simultaneously recorded every 20 ms by means of a videocamera, and the data were transferred to a computer for further processing. Details of this device are described elsewhere (Fleischer & Pflugradt, 1977; Fleischer, 1980). The angular resolution was better than 0.01 °, limited mainly by spontaneous random eye movements.

RESULTS

The results are described in two sections. Section A deals with a 'one way' situation, in which a driving eye receives a strong optokinetic input, and a driven eye receives none or only a weak one. Thus a signal is generated only by one (driving) eye. This set of experiments allowed us to study separately the effect of a signal emitted from the driving eye, and its acceptance by the driven eye.

In the experiments reported in section B, both eyes receive a strong optokinetic stimulus. Both eyes are able to influence each other. We define this process as 'binocular crosstalk'.

Section A

The effect of overall illumination on the response of the driving eye and on the signal it sends to the driven eye

We first examined to what extent illumination affects the ability of the crab to perceive the relative velocity between eye and surroundings. This ability determines the optokinetic response of the driving eye and the signal it sends to the contralateral eye.

The driving eye was stimulated with a sinusoidally-oscillating standard panorama (frequency 0·1 Hz, amplitude U = 0·25 °) at two light intensities (I = 0·045 lx and 7·8 lx). The driven eye was blinded by coating it with black paint. Pooled data from these experiments (Table 1) show that the response amplitude (A_a) of the driving eye decreases dramatically as the illumination is reduced (cf. Horridge, 1966). The excursions (A_b) of the driven eye, however, remain almost the same.

In order to interpret this result we have to consider possible neural paths mediating eye-coupling in crabs. Barnes & Horridge (1969) proposed that the *input* to the optokinetic control system of each eye is superimposed on the input to the contralateral side. However, the underlying experimental results can equally well be understood if we assume (i) that the *output* of the motion detecting system on one side is superimposed on the output of the contralateral system, and (ii) that both are

Table 1. *The influence of illumination of the driving eye on the response to oscillatory stimuli*

U (degrees)	I (lx)	A_a	A_b	A_b/A_a
0·25	0·045	0·07 ± 0·01°	0·023 ± 0·006°	0·34
0·25	7·8	0·223 ± 0·012°	0·038 ± 0·009°	0·162
1·25	7·8	1·03 ± 0·04°	0·063 ± 0·013°	0·06

The driven eye was blinded with black paint, the driving eye was free to move and faced the standard panorama (a grating with basic wavelength of $\lambda = 30°$ and 50 % modulation). The drum was sinusoidally oscillated around the vertical axis with amplitude U (0·25° and 1·25°) at a frequency of 0·1 Hz. The illumination, I, of the pattern was varied from 0·045 lx to 7·8 lx. The numbers give the amplitude of the basic Fourier component of the time course of eye position for the driving eye (A_a) and for the driven eye (A_b), calculated from several periods. Average responses obtained with three animals, ± standard deviations of the means. The ratio A_b/A_a gives the transfer ratio of the coupling signal.

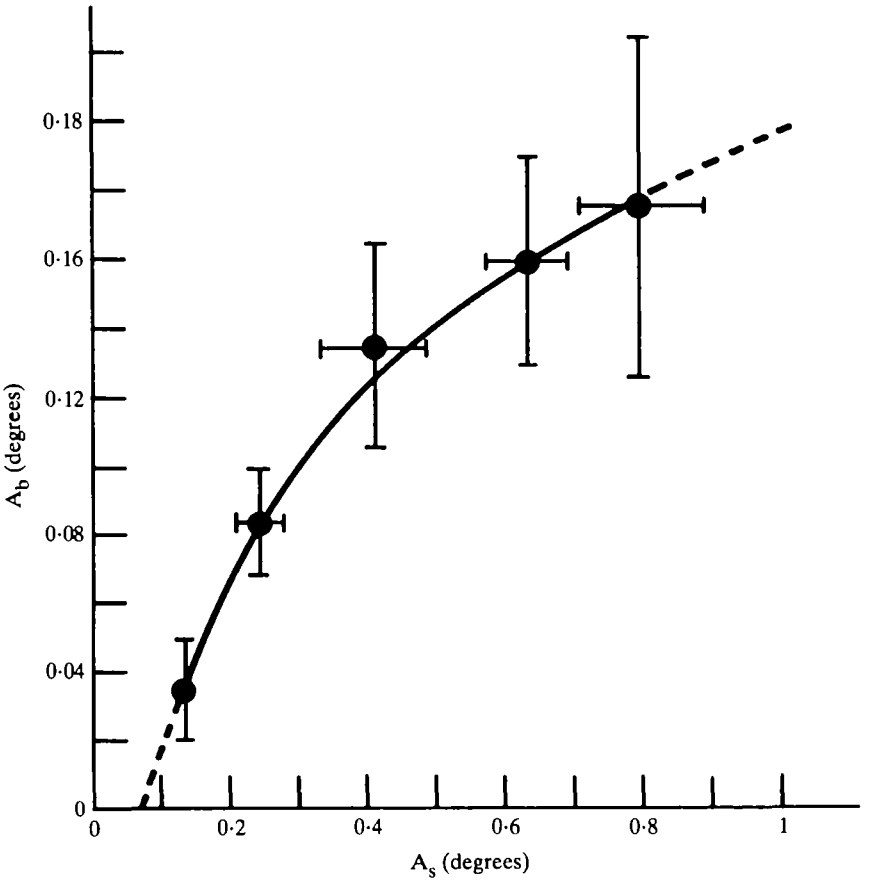

Fig. 1. Response amplitude of a driven (blinded) eye (A_b) as a function of the response amplitude of the driving eye (A_s) which faced a striped drum with basic wavelength $\lambda = 30°$. The pattern was sinusoidally oscillated around the vertical axis with the amplitudes 0·25, 0·5, 0·75, 1 and 1·25°; illumination, I = 7·8 lx. Average values obtained with three animals, ± standard deviations of the means. The parameters of the regression curve $A_b = a \log A_s + b$ are: $a = 0·183$, $b = 0·197$, regression coefficient $r = 0·997$.

subject to spontaneous variation. We adopt this alternative, since it can explain observations which cannot be understood on the basis of the Barnes-Horridge proposal (Nalbach, 1982). Consequently, the strength of coupling between both eyes is given as the ratio of the excursions of the driven (A_b) to the driving (A_s) eye. Examination of our data (Table 1) shows that this transfer ratio A_b/A_s increases as the illumination decreases.

The above experiments were repeated at the higher illumination (I = 7·8 lx) with a larger stimulus amplitude (U = ± 1·25°). The data obtained with two stimulus amplitudes but with the same illumination (Table 1) show that the transfer ratio (A_b/A_s) declines as the response of the stimulated eye (A_s) increases.

In fact, the data in Table 1 indicate a logarithmic relationship between A_b and A_s. This is confirmed by an additional experiment in which we changed the stimulus amplitude in several steps at high illumination (I = 7·8 lx) (Fig. 1). From further evidence we conclude that this logarithmic relationship originates from non-linear

processing of the signal which is transmitted from the driving to the driven eye (Nalbach, 1982).

In summary the above experiments show that with low overall illumination (1) the ability of the crab to perceive velocity is strongly impaired, and (2) as the response of the driving eye becomes stronger, the driving eye will less effectively influence the driven eye.

The effect of overall illumination on the response of the driven eye

We have shown that the response amplitude of the driving eye increases, and the coupling becomes less effective, while the illumination of the pattern presented to the driving eye is increased. Next we examined whether the overall illumination only of the driven eye influences the coupling as well. In these experiments the driven eye faced the homogeneous half of the drum whose illumination (I_h) was varied. This eye was either seeing or coated with white or black paint. The driving eye was looking at the standard panorama. The illumination on this side (I_s) remained unchanged. The driving eye was either fixed to the carapace or free to move. Fig. 2 shows sample records of the angular position of the driven eye during repeated stepwise angular

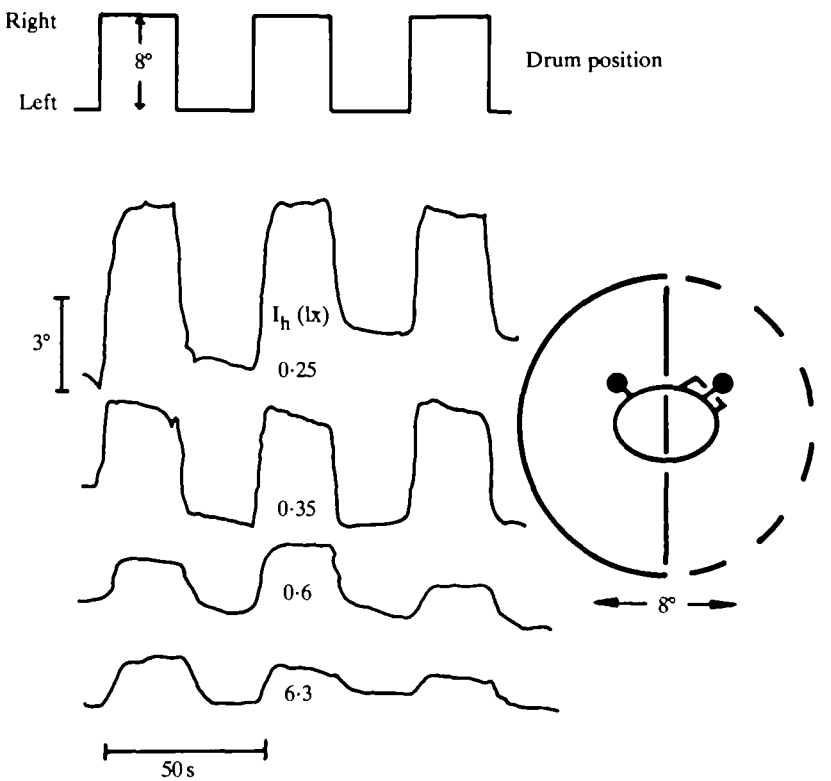

Fig. 2. Sample records of the angular position of the (left) eye facing the homogeneously illuminated half of the drum. It is driven by the visual input to the contralateral (right) eye which is fixed to the carapace and looks at the standard panorama, (a grating with basic wavelength of $\lambda = 30°$). The stimulus was an 8° step-like angular displacement of the drum around the vertical axis. Parameter is the illumination, I_h, of the homogeneous half of the pattern (lx), as measured at the crab's eye. Average brightness, I_s, of the standard pattern: 9·5 cd m^{-2}.

Table 2. *The influence of illumination of the driven eye on the step response*

	Driving eye	I_h (lx) : 0·25	0·35	0·60	6·30
1	fixed	3·63 ± 0·23°	3·06 ± 0·21°	1·69 ± 0·18°	1·01 ± 0·06°
2	free	1·97 ± 0·12°	1·61 ± 0·15°	—	0·38 ± 0·05°
		blinded	coated	—	seeing
3	fixed	4·80 ± 0·64°	3·24 ± 0·87°	—	0·72 ± 0·07°

Panorama and stimulus as described in the legend to Fig. 2. The luminance, I_h, of the homogeneous half of the pattern is varied. The driving eye was either fixed to the carapace (1) or free to move (2). (3) The driven eye was either seeing (the homogenous part of the pattern, luminance 6·3 lx), coated with white paint or blinded by black paint. The numbers give the final angular displacement of the driven eye after the step-like stimulus (8°). Averages of 16–33 responses obtained with three animals (1), seven responses obtained with 1 animal (2), and responses obtained with four animals (3), ± standard deviations of the means. Average luminance, I_s, of the standard panorama = 9·5 cd m^{-2}.

Table 3. *The influence of illumination of the driven eye on the response to oscillatory stimuli*

		ν: 0·01 Hz		0·5 Hz	
	U	I_h (lx) : 0·007	10·6	0·007	10·6
A_b	0·25°	0·088°	0·045°	0·022°	0·024°
	1·25°	0·291°	0·094°	0·042°	0·052°
A_s	0·25°	0·155°	0·154°	0·088°	0·090°
	1·25°	0·668°	0·694°	0·223°	0·280°
A_b/A_s	0·25°	0·57°	0·29°	0·25°	0·27°
	1·25°	0·44°	0·14°	0·19°	0·19°

The eyes faced panoramas as described in the legend to Fig. 2; the driving eye was free to move. The drum was sinusoidally oscillated around the vertical axis with amplitude U (degrees) at frequencies (ν) of 0·01 Hz and 0·5 Hz. The illumination, I_h, of the homogeneous part was varied. The numbers give the amplitude of the basic Fourier component of the time course of eye position for the driven eye (A_b), for the driving eye (A_s), and the transfer ratio A_b/A_s calculated out of several periods. Average responses obtained with six animals. Average luminance, I_s, of the standard panorama, 7·8 lx.

displacements of the panorama which amounted to 8°. Pooled data are presented in Table 2. Whether the driving eye was fixed or free to move, the response of the seeing, driven eye decreased as it was more strongly illuminated. The response was strongest when the driven eye was blinded with black paint and the driving eye was fixed to the carapace. Coating the driven eye with white paint, which transmitted some light but prevented the crab from seeing borders, also significantly reduced the response.

Similar results were obtained when the drum was oscillated sinusoidally around the vertical axis (Table 3). Here, the driving eye was always free to move, and the driven eye could see. Again, the response of the driven eye diminished as the illumination (I_h) of the homogeneous panorama was increased, especially at low oscillation frequencies ($\nu = 0{\cdot}01$ Hz). With increasing frequencies ($\nu = 0{\cdot}5$ Hz) the coupling between the two eyes became weaker, as previously observed (Barnes & Horridge,

Table 4. *The influence of stationary contour lines in the visual field of the driven eye on the response*

U (degrees)	Stripe no	Stripe h
0·25	0·038°	0·040°
1·25	0·069°	0·078°
0·25	0·188°	0·178°
1·25	0·779°	0·614°

Similar experiments to those described in the legend to Table 3. Average responses of the driven (upper part) and of the driving eye (lower part) obtained with three animals. Columns headed 'no': the driving eye faced the standard panorama, the driven eye the homogeneously illuminated part of the pattern. In the other experiments, a 15° wide stationary black stripe was introduced into the lateral part of the visual field of the driven (h) eye.

1969; Nalbach, 1982). The response of the freely moving, driving eye was not altered by changing the illumination (I_h) of the homogeneous half of the drum, which was seen only by the driven eye (Table 3).

In our experiments it was impossible to eliminate all contrasts from the visual field of the driven eye. The border line between the inner surface of the drum and the partition, as well as parts of the clamp and the animal's body were probably seen. When the driven eye moved, these stationary contour lines could generate optokinetic input to this eye, which could act as a 'brake' for its own movement as well as for that of the driving eye (Barnes & Horridge, 1969). One might argue that with increasing illumination these borders would become more and more visible and that the resulting optokinetic input could cause the effects described above. However, the response of the driving eye was not diminished (Table 3), indicating that the few stationary contrasts in the visual field of the driven eye did not affect the responses in our experiments. This was investigated further by introducing a stationary vertical stripe, 15° wide, (two strongly contrasted contour lines) into the lateral part of the visual field of the driven eye, which is most sensitive to optokinetic stimuli (cf. inset in Fig. 3).

The data obtained without a stripe (column headed 'no' in Table 4) and with a stripe on the homogeneous side (column 'h'), show that the additional contour lines had a negligible influence on the response of the driven eye. It cannot be excluded that a slight braking effect will be counteracted by the reduced amount of light after introducing the black stripe (see next section). One might also argue that the optomotor braking effect is already saturated without an additional black stripe due to unavoidable stationary contours. However, this appears to be very unlikely, because the optomotor response itself (e.g. to stepwise angular displacements of the panorama) increases monotonically with increasing numbers of black stripes up to at least eight (Fleischer, 1978).

In summary, the above experiments show that alteration of the illumination of the driven eye influences the strength of coupling from the driving eye. The driving signal has less effect when the homogeneous visual surround of the driven eye is strongly illuminated.

Pattern differences and the total amount of light

To examine whether these light-dependent changes in coupling were due to changes in the brightness of the pattern or to the total amount of light, which can be changed independently of the overall illumination (e.g. by varying the ratio of the black and white areas within the panorama), we examined the effect of pattern differences. The driving right eye of the crab faced the standard pattern. The total amount of light on the left eye was gradually reduced by increasing the black areas while the overall illumination of the left side was kept constant. The pattern contained two vertical contour lines resulting from a black stripe in a light surround or a bright

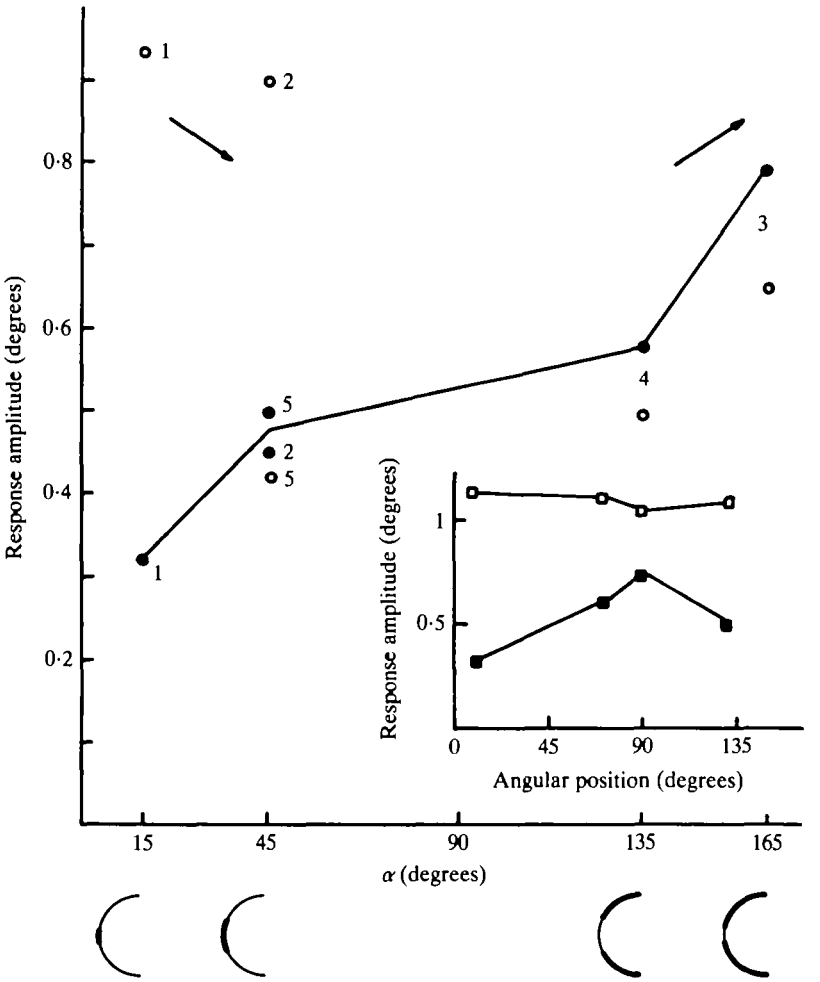

Fig. 3. Response amplitude of the left eye facing panoramas with increasing black portions (filled circles). Abscissa: total angular extent, $\alpha°$, of the black stripe, in positions as indicated by the pictograms below the abscissa. The right eye (open symbols) faced the standard panorama. The drum was oscillated at a frequency of 0·1 Hz, amplitude 1·25°. Inset: response amplitude *versus* angular position of the midline of a single black stripe of 15° width within the left visual field. Numbers indicate the temporal order of the measurements. The tilted arrows indicate whether the shift of contour lines would decrease or increase the response.

stripe in a black surround, as shown by the pictograms below the abscissa in Fig. 3. The drum was sinusoidally oscillated around the animal.

Increasing the black portion of the panorama caused the response of the left eye to increase (Fig. 3). This suggests that the total amount of light impinging upon the eye influences the bilateral interaction in the same way as the illumination, i.e. less light leads to a stronger contralateral influence.

When evaluating these results we have to consider that increasing the black portion of the panorama also shifts the contour lines within the visual field. Since contour lines in the lateral part of the visual field are particularly effective in eliciting optokinetic responses (Kunze, 1963; Sandeman, 1978*a*), we examined the possible role of this shift by changing the position of a single black stripe on the left (driven) side. In spite of the strong optokinetic input to the right (driving) eye, the amplitude of the response of the left (driven) eye increased considerably as the black stripe was moved from a frontal or caudal position towards a lateral one (inset in Fig. 3). The tilted arrows in Fig. 3 illustrate whether the response would decrease or increase due to the shifting of the borders of the black areas. The actual course of the curve in Fig. 3 leads us to conclude that changing the amount of light impinging on a driven eye has a much stronger effect than shifting the edges within its visual field.

Section B

The effect of illumination on the binocular crosstalk

Finally we examined whether the influence of illumination on the coupling also exists when *both* eyes receive a strong optokinetic input: here we are no longer dealing with the 'one way' situation of the previous experiments with a driving and a driven eye. With equivalent stimuli to both eyes binocular crosstalk can take place.

A standard pattern was presented to each eye, and the patterns were oscillated sinusoidally but independently from each other. While frequency (ν) and amplitude (U) on both sides were equal, the relative phase of the two stimuli ($\triangle\phi$) was set to 0°, 90° and 180°. (At $\triangle\phi = 180°$ both patterns moved simultaneously towards or away from the animal's midline.) For the sake of clarity we made the stimulus on one side the reference, against which the phase ($\triangle\phi$) of the pattern movement on the other side was measured.

In Fig. 4 the response amplitude A/A_o (normalized to that obtained with $\triangle\phi = 0°$) is plotted against $\triangle\phi$. Increasing $\triangle\phi$ reduced the response amplitude. With decreasing illumination (I) this effect became stronger. At $\triangle\phi = 0°$ and $\triangle\phi = 180°$ the response amplitudes on both sides were identical. The difference at $\triangle\phi = 90°$ can be explained by assuming a delay in the cross-connection between the two eyes (Nalbach, 1982). Note also that the response amplitude (A_o) relative to the stimulus amplitude (U) strongly decreased with decreasing illumination (I).

From these results we conclude, therefore, that the interaction between both eyes is mutual and becomes stronger as the overall illumination decreases. This is most clearly seen at low stimulus frequencies ($\nu = 0{\cdot}1$ Hz), where the optokinetic input is particularly effective. The result is independent of stimulus amplitude (U).

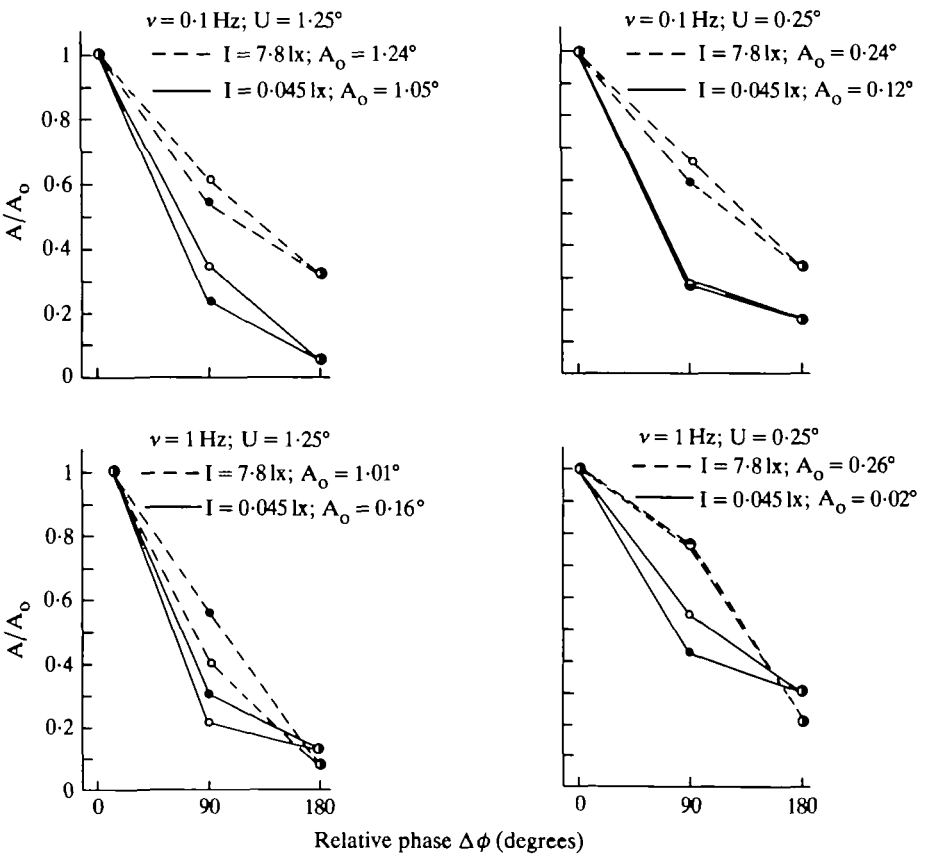

Fig. 4. Normalized response amplitude (A/A_o) plotted against the relative phase $\Delta\phi$ between the sinusoidal pattern movements on both sides. Parameters are: frequency (ν), amplitude (U) of pattern oscillation, and illumination (I). A_o is the response amplitude at $\Delta\phi = 0°$. Open circles represent the reference pattern.

DISCUSSION

At high overall illumination the optokinetic response is strong and coupling between the eyes is weak. At low illumination, however, the optomotor response is weak and coupling is strong (Fig. 2). Experiments where one eye drives the other show that two effects contribute to this change in the strength of coupling. (a) Due to logarithmic signal transformation in the coupling pathway (Fig. 1), the relationship between response amplitudes of the driven and the driving eye is not proportional (Table 1). (b) The overall illumination of the driven eye influences the strength of the coupling: as the total amount of light increases, the contribution of the contralateral eye to the optokinetic response becomes weaker (Fig. 4), regardless of whether the increase is brought about by higher illumination (e.g. homogeneous panorama, cf. Tables 2, 3; Fig. 2) or by reducing the surface area of the dark portion of the surround (while the level of illumination is kept constant, cf. Fig. 3). The binocular coupling, therefore, depends on visual input parameters, on the optokinetic input itself and on the total amount of light integrated over the eye.

We suggest that there is a system-inherent reason for the weak coupling with high illumination and strong optokinetic input: the optokinetic response is generated *via* a feedback loop with unavoidable delays. When the optokinetic gain is high this could lead to instabilities. Small-amplitude eye-scanning in a walking crab has been interpreted as feedback oscillations (Sandeman, 1978*b*; Nalbach, 1982). Strong coupling would amplify instabilities and long-lasting oscillations with high amplitude could arise.

At low light levels, when visual information is no longer readily available to the animal, pooling becomes important. As the optokinetic input is weak, the coupling between the eyes is enhanced and so the effective optokinetic sensitivity increased. Furthermore, this will no longer impair the stability of the system, as the optokinetic gain is low. Also the eye-leg-reflex (Varjú & Sandeman, 1982) and the input from the statocyst organs (Janse & Sandeman, 1979) contribute more to eye stabilization. These mechanisms help the crab to maintain visually guided behaviour even under poor light conditions.

We have discussed the control of coupling strength as a mechanism for gain control of the optokinetic system, preventing instability under bright light when optokinetic gain is high, and raising the overall gain under dim light when the optokinetic gain is low. This still leaves us with the problem of the consequence this design has on the possible functions of the optokinetic response. To us, there seem to be two main roles for optokinetic eye movements in crabs, which are supported also by the eye-leg-reflex (Dijkgraaf, 1956; Varjú & Sandeman, 1982) and the input from the statocyst organs (Dijkgraaf, 1956; Sandeman & Okijama, 1972). One role is image stabilization. The optokinetic system works against inevitable eye drifts due to the lack of proprioceptive control of eye position. It also compensates for relative movements during passive rotation of the animal (caused, for example, by water currents, cf. Dijkgraaf, 1956) or during active body turns. The diminution of the 'background movement' in the latter case might enhance the detectability of moving objects such as predators (Varjú & Sandeman, 1982). The other role is removing the rotational component of the visual flow pattern across the retina during locomotion. This serves to obtain information about the three-dimensional structure of the environment and also course control. The separation of the rotational and translational components has been shown theoretically to be crucial for the interpretation of the flow pattern (Longuet-Higgins & Prazdny, 1980). As far as we can see, there is no need for strong eye coupling under conditions of good vision. High optokinetic gain, eye-leg-reflex and input from the statocyst organs, as well as the stimulus condition ('coupled' movement of the environment) could be sufficient to ensure almost synchronous eye movements. Therefore, matching of both retinal images might also be possible.

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REFERENCES

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

DIJKGRAAF, S. (1956). Über die kompensatorischen Augenstielbewegungen bei Brachyuren. *Pubbl. Staz. zool. Napoli* **18**, 341–358.

FLEISCHER, A. G. (1978). Analyse der optokinetischen Reaktion der Krabbe *Carcinus maenas*. Dissertation, Universität Tübingen.

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

FLEISCHER, A. G. & PFLUGRADT, M. (1977). Continuous registration of X-Y-coordinates and angular position in behavioural experiments. *Experientia* **33**, 693–695.

HENKES, H. E. (1952). Retinomotor and diurnal rhythm in crustaceans. *J. exp. Biol.* **29**, 178–191.

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

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

JANSE, C & SANDEMAN, D. C. (1979). The role of the fluid-filled balance organs in the induction of phase and gain in the compensatory eye reflex of the crab *Scylla serrata*. *J. comp. Physiol.* **130**, 95–100.

KORTE, R. (1966). Untersuchungen zum Sehvermögen einiger Decapoden, insbesondere von *Uca tangeri*. *Z. Morph. Ökol. Tiere* **58**, 1–37.

KUNZE, P. (1963). Der Einfluß der Größe bewegter Felder auf den optokinetischen Augennystagmus der Winkerkrabbe (*Uca pugnax*). *Ergebn. Biol.* **26**, 55–62.

LEGGETT, L. M. & STAVENGA, D. G. (1981). Diurnal changes in angular sensitivity of crab photoreceptors. *J. comp. Physiol.* **144**, 99–109.

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

NALBACH, H.-O. (1982). Reaktionen der Krabbe *Carcinus maenas* auf monokulare und binokulare optokinetische Reize. Diploma-thesis, University Tübingen.

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

SANDEMAN, D. C. (1978*b*). Eye-scanning during walking in the crab *Leptograpsus variegatus*. *J. comp. Physiol.* **124**, 349–357.

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

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

WIERSMA, C. A. G., BUSH, B. M. H. & WATERMAN, T. H. (1964). Efferent visual responses of contralateral origin in the optic nerve of the crab *Podophthalmus*. *Cell. comp. Physiol.* **64**, 309–326.