J. exp. Biol. (1975), 62, 505–518
With 9 figures
Printed in Great Britain

THE OPTOKINETIC RESPONSES OF THE MYSID SHRIMP *PRAUNUS FLEXUOSUS*

By D. M. NEIL

*Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ**

(*Received* 14 *August* 1974)

SUMMARY

The optokinetic responses of the mysid shrimp *Praunus flexuosus* in the horizontal and vertical-transverse planes have been studied. The horizontal optokinetic nystagmus is fragmented, and eyestalk following speed is a function of stimulus speed. The vertical optokinetic response is not a nystagmus, but involves maintained eyestalk deviations. These deviations, and eyestalk following speed are both functions of stimulus speed. The velocity gain (eye speed/slip speed) of the responses in both dimensions has a constant value between drum speed 2°/sec and 40°/sec, which suggests that they subserve a simple rheotactic function. The vertical optokinetic response is modulated by statocyst input, and possible mechanisms underlying this effect are discussed.

INTRODUCTION

Optomotor reactions, in which movements of the body compensate for the displacement of images over the eye, are well known in higher crustaceans (Bethe, 1897; von Buddenbrock & Friedrich, 1933; Bröcker, 1935; Hassenstein, 1954; De Bruin, 1956). In stalk-eyed species nystactic eye movements, comprising slow following and rapid return phases, also occur independently of body movements. This particular category of optomotor reaction, the so-called optokinetic response, provides a convenient quantitative measure of the animal's response to moving stimuli (Kunze, 1964; Horridge & Sandeman, 1964).

One function of optomotor reactions is to stabilize the body in space, as in the rheotactic orientation of fish (Lyon, 1904; Harden Jones, 1963), larval lobsters (Hadley, 1906) and mysids (Fraenkel, 1940). De Bruin (1956) tested many animal species for their optomotor reactions, and found a good correlation between the development of a strong response and the ability to fly or swim freely.

Another function which derives from the optomotor reactions is the stabilization of the visual field on the eye, so that the precision of visual perception is increased. Horridge (1966*a*) considers this to be the primary function of the optokinetic system of *Carcinus*, and suggests that gross compensatory movements of the body represent by-products of this process.

In view of its close relationship to the optomotor reactions, the optokinetic response of *Praunus* has been studied in order to determine whether a stabilization of the eye and body, or an enhancement of slow movement detection is the more relevant biological function of optomotor reactions in this free-swimming animal. In addition,

* Present address: Gatty Marine Laboratory, University of St Andrews, St Andrews KY16 8LB, Scotland.

the optokinetic response of *Praunus* has been used as a reliable indicator of visual function in an extension of the study of interactions between the visual and statocyst systems in eyestalk position control (Neil, 1975*a*).

MATERIAL AND METHODS

The experimental animal was glued with a drop of gelatin-in-sea water solution on to a 'Perspex' bar, and mounted in the experimental chamber. For horizontal optokinesis this was a vertically mounted glass cylinder, $3\frac{1}{2}$ in. diameter, filled with sea water. For vertical optokinesis a $2\frac{1}{2}$ in. 'Perspex' cylinder, mounted horizontally and completely filled with sea water, was employed. In the latter case the animal holder was connected through a seal to a lever outside the chamber, so that the experimental animal could be rotated to different body positions.

Striped patterns were made by sticking lengths of $\frac{1}{2}$ in. wide insulation tape on to transparent cellophane sheets. These were mounted on a 6 in. diameter 'Perspex' drum and illuminated through a layer of 'Kodatrace' tracing paper. The repeat period of this striped pattern subtended 19° at the eye of the experimental animal when mounted in the middle of the drum. The striped drum was mounted on a pulley block which could be rotated about a vertical or horizontal axis, appropriate to the particular optokinetic stimulus required. Pulley drive from a Palmer 'Electric twelve' kymograph was employed. For experiments requiring oscillatory stimuli a heart-shaped cam was mounted on the kymograph spindle and deflected a lever which carried the drive to the drum pulleys. A large counterweight kept the lever hard up against the cam. Different combinations of frequency and amplitude of oscillation were produced by changing the kymograph speed and/or the drum pulley setting.

Eyestalk movements were followed by aligning a graticule in the eyepiece of a binocular microscope with one edge of the eyestalk. Rotation of the eyepiece was converted to a d.c. signal and recorded on a Smith 'Servoscribe' paper recorder. Details of the recording apparatus are given elsewhere (Neil, 1975*a*).

Terminology. The optokinetic response is well suited for quantitative analysis because both the stimulus and the response can be measured as angular velocities, and other parameters of the system can be derived indirectly from these values. The optokinetic system incorporates closed-loop control because the eyes are free to move. Under these conditions the difference between the eye speed (E) and the drum speed (D) is monitored continuously down the visual channel, and the true stimulus is the slip speed (S) of the striped pattern across the eye. The ratio of eye speed to slip speed, i.e. the velocity gain (G), gives a measure of the amplification of the stimulus signal which must take place within the optokinetic system in order to produce the observed response. The interrelationships of the system parameters are expressed in the terms:

$$S = D - E, \quad G = \frac{E}{S} = \frac{E}{D-E}$$

and are illustrated in Fig. 1.

Experiments were performed with a range of drum speeds covering four orders of magnitude (0·2–800°/sec), and at each speed setting the corresponding eye speed was recorded for over twenty cycles in each direction. No differences were observed in the eye speeds in opposite directions, so mean values were taken for each stimulus speed.

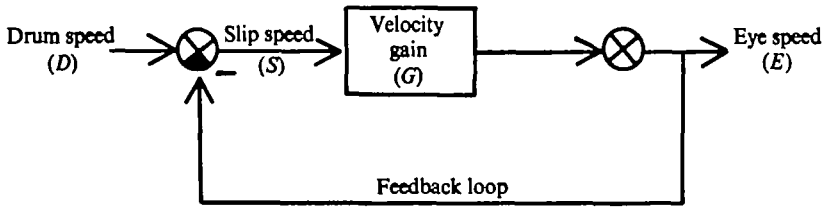

Fig. 1. General characteristics of the optokinetic control system. The feedback loop is negative, so that the effective stimulus for eyestalk following is Drum speed (D) − Eye speed (E) = Slip speed (S).

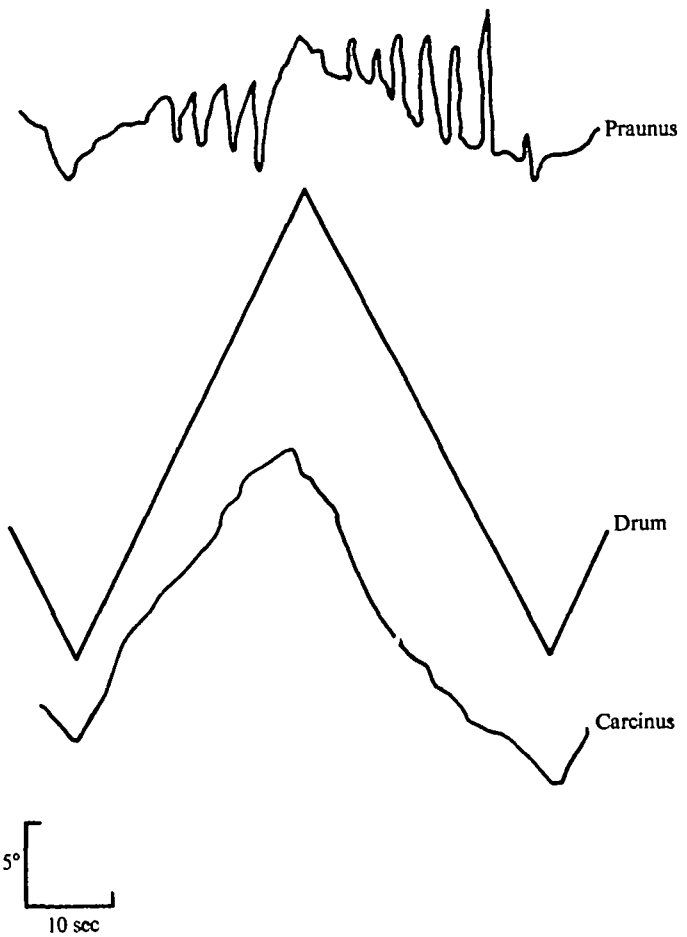

Fig. 2. Records of the horizontal optokinetic nystagmus responses of *Praunus* and *Carcinus*, produced by rotation of stripes about a vertical axis. Drum speed = 1°/sec.

RESULTS

Horizontal optokinetic response

A major objective of this study, the direct comparison of the optokinetic responses of *Praunus* and *Carcinus* was facilitated by recording the eyestalk movements of both species under the same experimental conditions. This overcame the difficulty of comparing results for the mysid obtained using graticule alignment with the well-

documented data for the crab obtained using an automatic recording device (Horridge & Sandeman, 1964).

Carcinus. The slow following phase of optokinetic nystagmus is a smooth prolonged response which most often goes to completion (up to 15° movement) before the rapid flick-back is initiated (Fig. 2). At speeds of stripe rotation above 10°/sec aberrant flicks appear, and the following response often fails completely. The latter effect is short-lasting, however, and the response returns if the speed of stripe rotation is reduced. The efficiency of the optokinetic following response varies as a function of drum speed, being greatest at the lowest stimulus speeds tested, when the eyestalks move at over 90% the velocity of the drum. As drum speed increases the efficiency of following is reduced, so that the maximum eye speed attained is only 4·6 °/sec (Fig. 3*a*). This velocity-dependence is reflected in the value of velocity gain (*G*), which is much greater than unity (6·3) at drum speed 0·22°/sec, but falls to less than 0·3 above 12°/sec drum speed (Fig. 3*b*).

Praunus. In response to moving stripes this mysid shows well-defined eyestalk following movements, although the slow phase is often interrupted by rapid eye flicks, and successive slow phases may start at points away from the rest position (Fig. 2). The fragmentary nature of slow nystagmus in *Praunus* contrasts strikingly with the smooth following of *Carcinus*, but nevertheless the mysid optokinetic response shows less tendency to fail at high stimulus speeds. Indeed eyestalk following speeds in excess of 20°/sec are reached by *Praunus* at stimulus speeds to which the eye of *Carcinus* fails to respond (i.e. > 45°/sec drum speed) (Fig. 3*a*). The highest drum speed which elicits a consistent nystactic response in *Praunus* is 380°/sec.

At low stimulus speeds the optokinetic performance of *Praunus* is far inferior to that of *Carcinus*, for in the mysid there is no sharp increase in velocity gain below drum speed 1°/sec, but rather a gradual decrease (Fig. 3*b*). The most significant feature of the mysid optokinetic system is the velocity-independence of *G* over the range of stimulus speeds 1°–45°/sec. Within this range the efficiency of eyestalk following remains relatively constant, and eye speed varies between 50 and 60% of drum speed, as indicated by values of *G* between 1·0 and 1·6 (Fig. 3*b*). Thus relatively low gain optokinetic system of *Praunus*, with its velocity-independent region, contrasts with the high gain, but strictly velocity-dependent system of *Carcinus*.

Vertical optokinetic response

Optokinetic responses can be elicited in *Praunus* by rotating stripes about a horizontal longitudinal axis. No nystagmus occurs, however, during the eyestalk response in the transverse vertical plane, in contrast to the many return flicks observed during eye tracking in the horizontal plane. The eyestalks follow the moving stripes for a short time, but then come to rest and maintain their angular displacements as long as the stripes are moving. If the direction of stripe rotation is then reversed, the eyes, in following the stimulus, move through their resting positions to deviate in the opposite directions by amounts equal to their initial displacements (Fig. 4). A useful measure of these eyestalk movements is the total angular deviation, which represents the angle subtended by the two extreme eyestalk positions for opposite directions of stripe rotation. Measurements of eyestalk deviations at different speeds of stripe rotation indicate that the maintained displacements of the eyestalks are velocity dependent

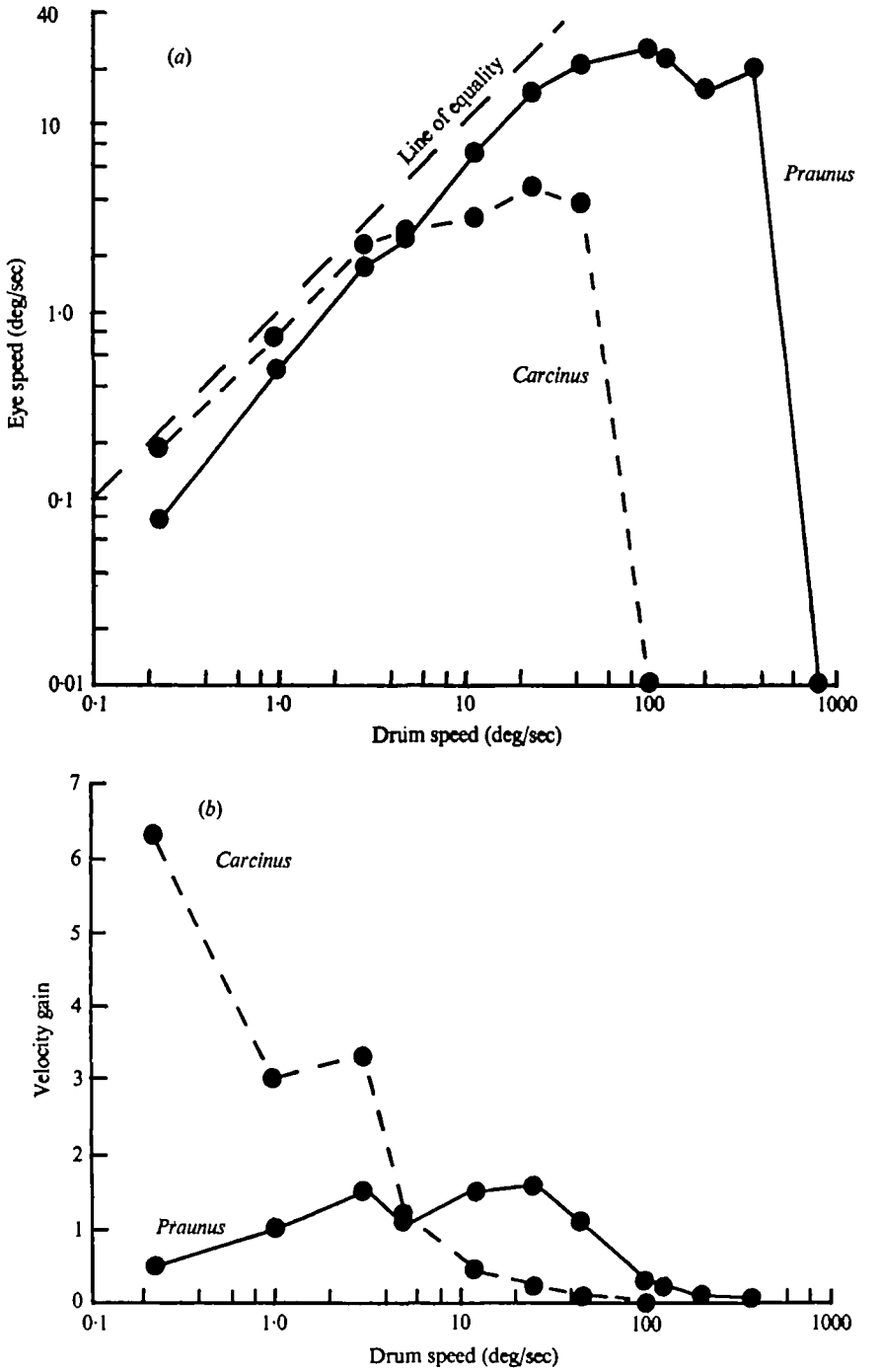

Fig. 3. Quantitative analysis of the horizontal optokinetic response. The data are mean values of the results obtained from three animals of each species. (*a*) Eyestalk following speeds of *Praunus* (●——●) and *Carcinus* (●– –●) over four decades of drum speed. (*b*) Velocity gain of the eyestalk following response over four decades of drum speed. The velocity independent region in the response of (*Praunus*) (between drum speeds 1 and 50°/sec) contrasts with the strict velocity dependence in the response of *Carcinus*.

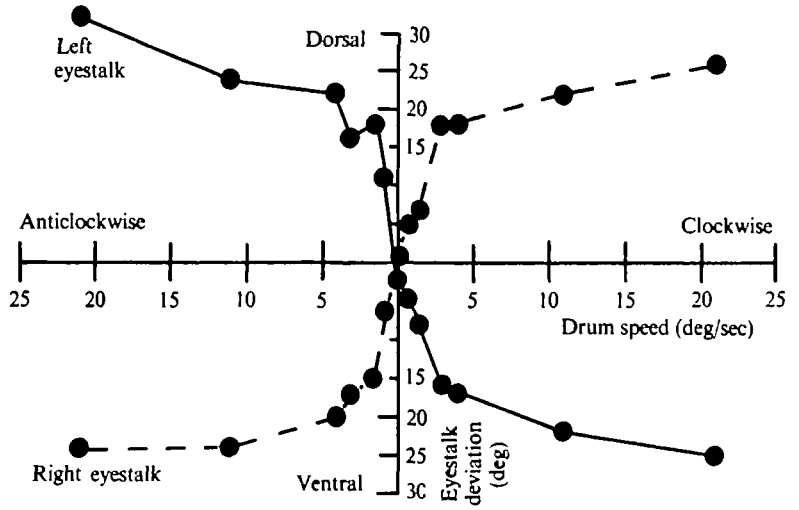

Fig. 4. Angular deviations of the eyestalks of *Praunus* in the transverse vertical plane, in response to rotation of the striped drum about the horizontal longitudinal axis in both clockwise and anticlockwise directions. Typical results, obtained from one individual (D4) are shown. The response is velocity dependent, and dorsal and ventral deviations of the eyestalks are symmetrical.

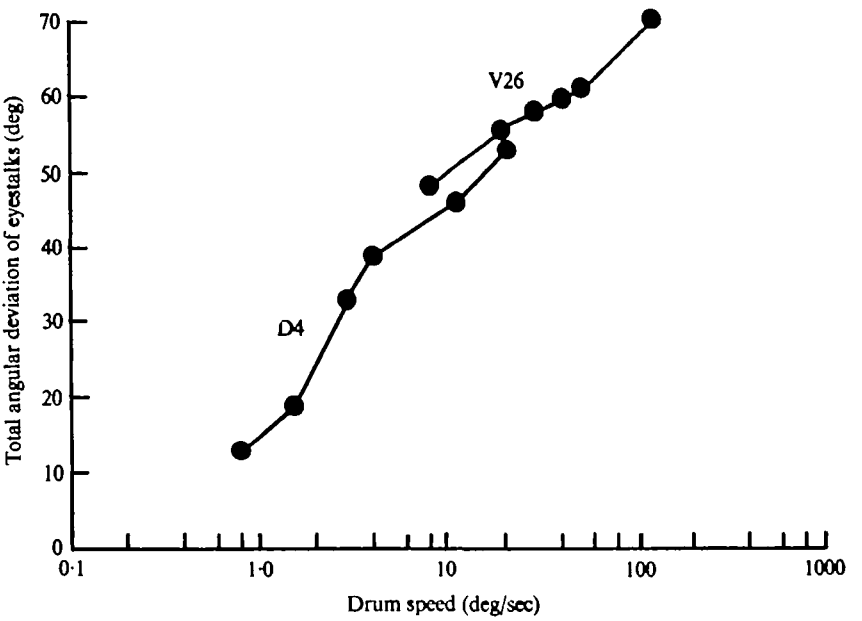

Fig. 5. Total angular deviation of the eyestalks in the transverse vertical plane over four decades of drum speed. The responses of two individuals over different speed ranges are shown. The total angular deviation has an approximately linear relationship to log drum speed.

(Fig. 4), and show a linear relationship to log. drum speed over the whole range tested (0·8–120°/sec) (Fig. 5).

Using oscillatory stimuli of amplitude less than that of the total angular deviation of the eyestalk, the speed of optokinetic following in the transverse vertical plane was measured. Over the range of drum speeds 1·5–40°/sec there is an almost linear

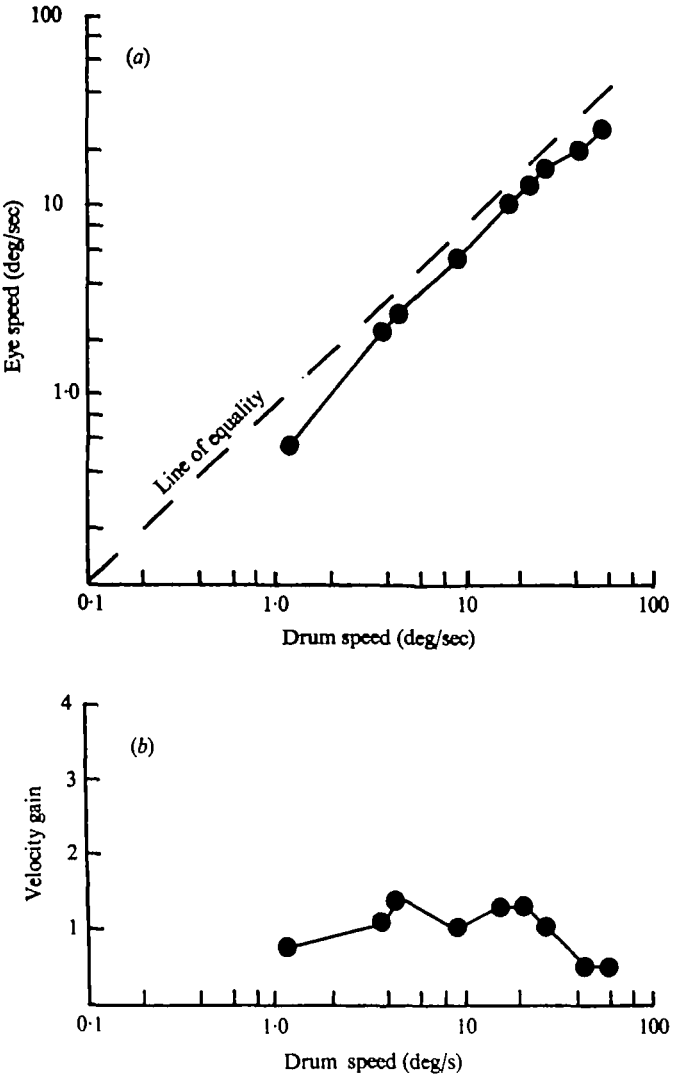

Fig. 6. Quantitative analysis of the vertical optokinetic response of *Praunus*. Typical results, obtained from one individual (V2), are shown. (*a*) Eyestalk following speed over two decades of drum speed. The response has an approximately linear relationship to drum speed. (*b*) Velocity gain of the eyestalk following response. Below drum speed 40°/sec the velocity gain remains close to unity.

relationship between eye speed and log drum speed (Fig. 6*a*), and in this region the velocity gain of the optokinetic system remains close to unity (Fig. 6*b*). In these features the optokinetic responses of *Praunus* in the vertical and horizontal planes are closely similar.

The effect of body position

In order to estimate the effect of statocyst input on the vertical optokinetic reaction of *Praunus*, the experimental animals were presented with standard stripe stimuli at different angles of body tilt. Measurements of both total angular deviation and eyestalk

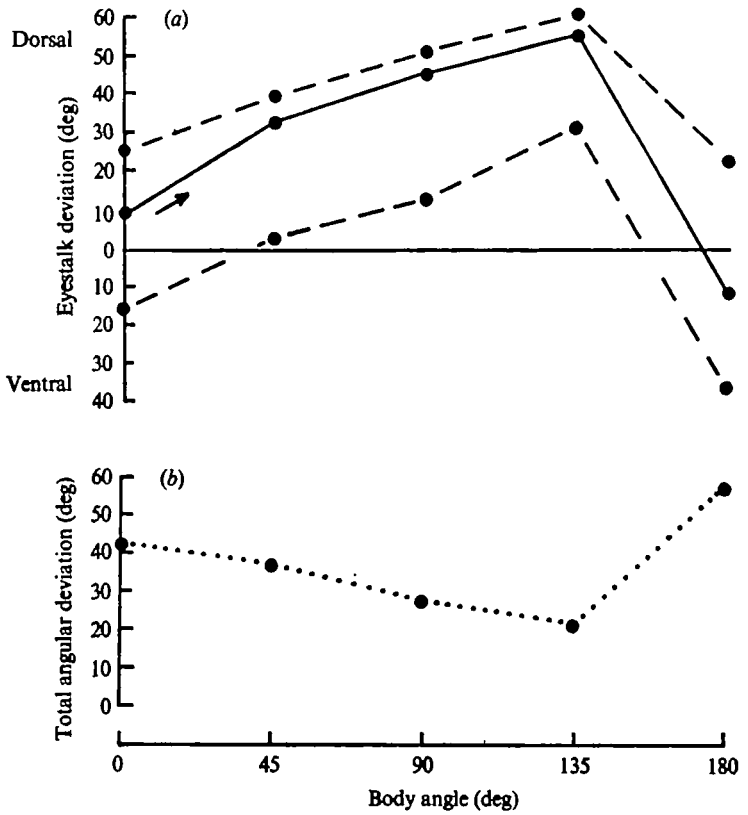

Fig. 7. The effect of body position on the vertical optokinetic response of *Praunus*. Eyestalk deviations at different angles of body tilt between the upright (0°) and the inverted (180°). Typical results, obtained from one individual (V25), are shown. (*a*) Compensatory responses of the left eyestalk at different angles of body tilt (——), together with the superimposed optokinetic responses (– – –). (*b*) Total angular deviations of the left eyestalk at different angles of body tilt (. . .).

following speed were made at five body positions between the upright (0°) and inverted (180°).

Total angular deviation. Using a single speed of stripe rotation (42°/sec), the response of the eyestalks to this stimulus was measured with the body first in the upright position. The lights were then switched off and the mysid rotated slowly to a body tilt of 45°. With the re-illuminated drum stationary the compensatory eyestalk deviation was measured, then the drum was rotated and the change in eyestalk position recorded.

Using the above procedure, the initial compensatory eyestalk deviation is similar to the one obtained under vertical illumination (Neil, 1975*a*), and the superimposed optokinetic responses show a position dependence such that the total angular deviation is reduced when the animal is turned on to its side (Fig. 7). In addition, there is an enhanced eyestalk response at the 180° body position, where the total angular deviation is greater than that recorded in the upright position. Taken together, these findings provide important evidence on the mode of interaction of the optokinetic and gravity-sensitive systems in *Praunus* (see Discussion).

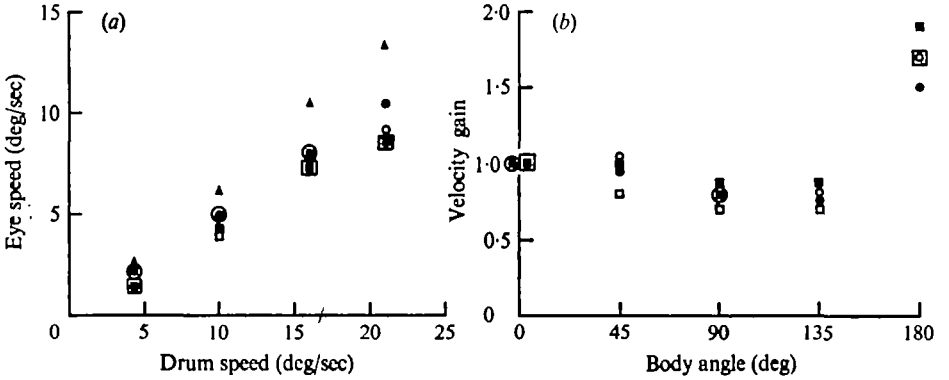

Fig. 8. The effect of body position on the vertical optokinetic response of *Praunus*. Eyestalk following speeds at different angles of body tilt between the upright (0°) and the inverted (180°). The data represent mean values for eight individuals obtained at five body positions with four drum speeds. (*a*) Eyestalk following speed at different drum speeds. ●, 0° (upright); ○, 45°; ■, 90°; □ 135°; ▲, 180° (inverted). (*b*) Velocity gain of response at different body positions. ●, drum speed 4·25°/sec; ○, 10°/sec; ■, 16°/sec; □, 21·25°/sec.

Eyestalk following speed. This parameter of the optokinetic response was measured at the five angles of body tilt in response to four different stripe rotation speeds. A linear analysis of the results was facilitated by choosing stimulus speeds within the range which elicited responses of constant velocity gain in the upright animal (i.e. the range 1·5–40°/sec drum speed in Fig. 6*b*).

As in the upright position, the velocity gain of the mysid optokinetic response at different angles of body tilt has a constant value over the range of stimulus speeds employed (Fig. 8*b*). However, eyestalk following speed does show a position dependence, being slightly lower at lateral body tilts than when the animal is upright (Fig. 8*a*). The effect of body position is most marked at 180°, where the eye speeds are significantly greater, being equivalent to velocity gains exceeding 1·5. Thus, with respect to both the general position dependence and the enhanced response in the inverted, the measurements of eyestalk following speed agree closely with those of total angular deviation.

Statocystless mysids

In an attempt to determine the nature of position dependence in the vertical optokinetic response of *Praunus*, experiments were carried out on animals without statocysts. Removal of both statocysts results in a loss of the position dependent effect (Fig. 9*a*), which suggests that the signals from the balance organs are its primary cause. However, since the maintained eyestalk deviations occur from an initial eye position close to the transverse body axis, rather than being superimposed upon an initial geotactic compensatory deviation, as in the intact animal (Fig. 7*a*), this result does not provide decisive evidence about the mechanism of the interaction between the statocyst and optokinetic systems.

Another consequence of statocyst loss is an increase in magnitude of the maintained eyestalk deviations, which become greater than those recorded at any body position in the intact animal (compare Fig. 9*b* and Fig. 7*b*). This suggests that the optokinetic reaction is in some way suppressed when the statocyst signals are present.

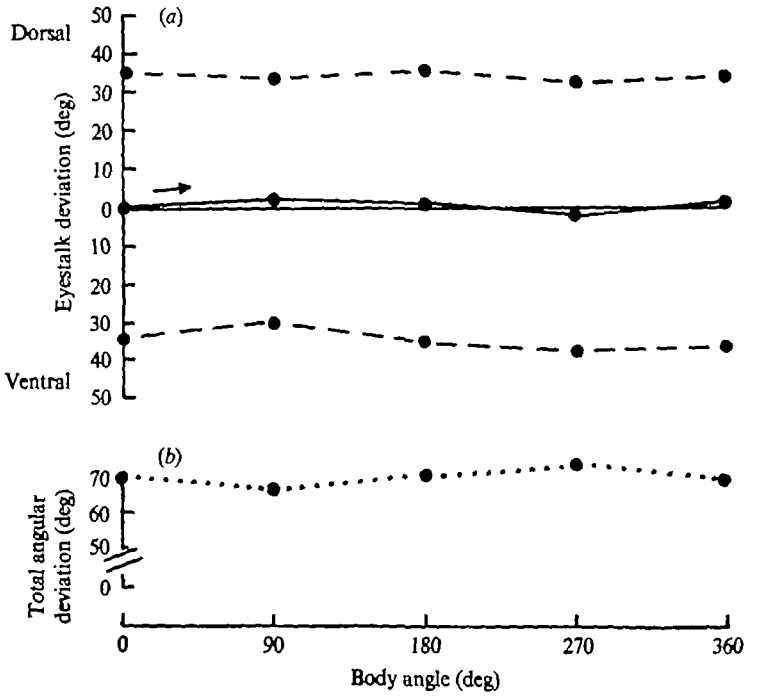

Fig. 9. The effect of body position on the vertical optokinetic response of statocystless *Praunus*. Eyestalk deviations at different angles of body tilt between 0° and 360°. Typical results, obtained from one individual (V36), are shown. (*a*) Although a compensatory response of the left eyestalk is almost completely absent (——) the optokinetic responses are of large amplitude (– – –). (*b*) Total angular deviations of the left eyestalk at different angles of body tilt. These values are larger than those obtained in the intact animal (cf. Fig. 7*b*).

DISCUSSION

Response in horizontal plane

The optokinetic response of *Praunus* in the horizontal plane shows both qualitative and quantitative differences from that of *Carcinus*. These indicate that the optokinetic system of *Praunus* is designed to operate in a higher range of stimulus speeds than the equivalent system in the crab. A fundamental difference is apparent in the capabilities of the crab and the mysid shrimp to detect very slow movements. The data presented here for *Carcinus* are consistent with the results of Horridge & Sandeman (1964) in demonstrating a sharp increase in the velocity gain of the optokinetic system at stimulus speeds below 1°/sec. This large amplification of the input signal by the optokinetic system is effective in stabilizing the eye, as in the smoothing of tremor, the return to the same point after a saccadic flick and the gross compensation for body movements (Horridge, 1966*a*). Additionally, it enables the crab to detect and follow very slow movements closely and consistently, and Horridge (1966*c*) and Barnes & Horrdige (1969) have demonstrated that *Carcinus* can track the movement of the sun across the sky. The behavioural significance of this last finding remains uncertain, however, in the absence of evidence that the crab uses the sun as a navigational cue.

The optokinetic performance of *Praunus* is poor below 1°/sec drum speed, but improves at higher stimulus speeds, and in the range 1–50°/sec drum speed the velocity gain of

the response has a relatively constant value close to unity. This indicates that the optokinetic system neither amplifies nor attenuates the input signal (i.e. the slip speed of the stripes over the eye) in converting it to a motor output (measured as eyestalk following speed). This is the expected property of a system for simple movement detection which generates compensatory movements for passive body displacements. Therefore, in contrast to the sophisticated visual abilities of the crab, the mysid optokinetic system appears to have a simple rheotactic function. However the possibility cannot be excluded that the eyestalk stabilization process is also concerned with improving the sensitivity of the mysid to polarized light (Waterman, 1960) by maintaining the ommatidial axes at optimal orientation to the *e*-vector (Waterman & Horch, 1966).

Response in the vertical plane

The form of the optokinetic response of *Praunus* in the transverse vertical plane contrasts with the eyestalk nystagmus in the horizontal plane. No rapid nystactic return flicks occur, and with continued drum rotation the eyestalks come to rest and maintain their angular deviations. However, a velocity-independent velocity gain setting of approximately unity is a common feature of the optokinetic responses in both planes. Therefore, in the range of stimulus speeds 2–40°/sec optokinetic movements of the eyestalks in both dimensions represent a compensation process in which there is neither amplification nor attenuation of the stimulus signal. This evidence alone is not sufficient to establish a single amplification point, upon which the different movement signals converge, and from which the appropriate motor commands arise, but it does suggest that movements of the eyestalks in the two dimensions subserve a common function.

Nystagmus is also absent in the optokinetic response about horizontal axes in the crayfish (Hisada, Sugawara & Higuchi, 1969) and the crab (Horridge, 1966*b*). In *Procambarus* stripes moving upwards in front of the animal are most effective as an optokinetic stimulus at drum speed 0·2°/sec, when the velocity gain of eyestalk following reaches 2·0 (Hisada *et al.* 1969). At higher speeds the efficiency of the response is reduced, and thus the crayfish optokinetic system in the vertical longitudinal plane has a restricted range, and low gain characteristics. In *Carcinus* the velocity gain of the optokinetic response in the transverse vertical plane reaches a value of 10 at low stimulus speeds (Horridge 1966*b*). Therefore, as in *Praunus*, the properties of the optokinetic responses in the horizontal and vertical planes are closely matched. The high gain characteristics of the crab system at low stimulus speeds facilitates close tracking of slow movements in two dimensions, such as the curved path of the sun across the sky (Barnes & Horridge, 1969).

High gain and low gain optokinetic systems

Although it is an indication of differences in the visual abilities of the crab and the mysid, the distinction between high gain and low gain optokinetic systems is to some extent arbitrary. This is suggested by studies on other animals. Analysis of the optomotor reactions of the insect *Stagmomantis* under open loop conditions has shown that the motor output can be up to one thousand times larger than the input at extremely low stimulus speeds (0·00065°/sec) (Mittlestaedt, 1964). The cephalopod eye

can also follow stripes moving at low speeds (0·035°/sec) but the velocity gain of the optokinetic system remains below unity (Collewijn, 1970). Therefore an ability to detect slow movements is not always matched by close following of the stimulus.

Among the vertebrates, optokinetic performance is equally diverse (Rademaker & Ter Braak, 1948). The eye of the goldfish is unable to follow at better than 70% the speed of a striped drum, which is equivalent to a velocity gain of 2·3 (Easter, 1972). The rabbit, which has an eye of the primitive mammalian type (i.e. non-foveate, with no macular vision, attention, prediction or saccadic tracking) is able to follow stripes to very low speeds (< 0·01°/sec), and below 1°/sec the velocity gain reaches values between 20 and 100 (Collewijn, 1969). In humans, however, the complexities of foveal vision affect eye tracking, which is poor at low target speeds (Young, 1971; Feldman, Atkin & Bender, 1969). The calculated velocity gain of the human opotokinetic system under these conditions is between 2 and 4.

On the basis of our present knowledge it is difficult to draw useful conclusions about optokinetic performance and function. A systematic comparative study within one group of animals may throw more light on the relationship between the properties of the visual system and the behaviour of the animal. The higher crustaceans, which display a variety of life habits, and for which neuronal basis of their visual responses is well understood (Wiersma, 1966) seem well suited for such a study.

The influence of body position

Measurements of two parameters of the optokinetic response of *Praunus* have demonstrated a position-dependence in the eyestalk following of stripes such that the response is reduced both in speed and amplitude when the body is tilted. This effect is statocyst-mediated, and disappears when the balance organs are removed. The mechanism underlying position-dependence is unknown, but may involve either a superposition of unequally weighted signals of visual and statocyst origin, or a more direct interaction such as inhibition of visual units by statocyst receptors.

Electrical recordings from optomotor fibres in various crustaceans have demonstrated a convergence of visual and statocyst inputs onto these final motor pathways (Wiersma & Yamaguchi, 1967; Wiersma & Oberjat, 1968; Wiersma & Fiore, 1971; York, Yanagisawa, & Wiersma, 1972). In the crayfish, visual stimuli cause changes in the firing frequency of optomotor fibres half as great as those produced by body rotation (Wiersma & Oberjat, 1968). Similar relationships may underlie the interaction of sensory modalities in *Praunus* (Neil, 1975*a*), and could cause the effect of visual inputs to be reduced when superimposed onto an ongoing gravitational optomotor discharge. This could occur through non-linearities and saturation effects in neuronal and neuromuscular transmission, or for the purely mechanical reason that the eyestalk offers an increased resistance to movement.

Although these explanations are consistent with the report that the gain of the crayfish optokinetic response is a function of eye position (Hisada *et al.* 1969), and with the finding that the optokinetic response of *Praunus* increases when the statocysts are removed, it is more difficult to explain the enhanced optokinetic response at the 180° body position in such terms. When the mysid is inverted the resultant turning tendency produced by the statocysts is close to zero (Neil, 1975*a*), and the component turning tendencies released from the two organs are in fact greater than those for the

upright animal (Neil, 1975*b*). Therefore the statocyst input onto optomotor fibres should be as great in the 180° body position as in the 0° position, and no increase in optokinetic performance should occur. The fact that eyestalk following is enhanced in the inverted mysid suggests that a more direct interaction of the signals from statocysts and eyes is involved.

Electrophysiological findings suggest that statocyst signals can act directly on the sensory side of the visual system. Abundant efferent activity is present in the optic tract of the crab *Podophthalmus* (Bush, Wiersma & Waterman, 1964), the crayfish *Procambarus* (Wiersma & Yamaguchi, 1966), and the rock lobster *Panulirus* (Wiersma & Yamaguchi, 1967*a*). In the crayfish, specific inhibition (Yamaguchi, 1967) and facilitation (Aréchiga & Wiersma, 1969) of visual movement units have been established, and are ascribed to direct efferent neuronal influences. Indeed the 'space constancy' of certain crayfish visual units (Wiersma & Yamaguchi, 1971*b*) is considered by Wiersma (1970) to result from the direct action of statocyst primary afferent fibres, without the interposition of interneurones. A less specific effect on visual units by the statocyst signal could explain some, or all, of the features of position-dependence in the optokinetic response of *Praunus*.

This work was supported by a Research Studentship from the Science Research Council. I am grateful to Professor T. Weis-Fogh for the facilities he provided in his laboratory. It is a pleasure to thank Dr H. W. Lissmann, my supervisor, for his advice and constant encouragement during the course of this work. I also wish to thank Mr D. Kusel for reading a draft of this manuscript.

REFERENCES

Aréchiga, H. & Wiersma, C. A. G. (1969). The effect of motor activity on the reactivity of single visual units in the crayfish. *J. Neurobiol.* **1**, 56–69.

Barnes, W. J. P. & Horridge, G. A. (1969). Two-dimensional records of the eyecup movements of the crab *Carcinus*. *J. exp. Biol.* **50**, 673–82.

Bethe, A. (1897). Das nervensystem von *Carcinus maenas*, ein anatomisch-physiologischer Versuch. I. Thiel, I. Mittheil. *Arch. mikrosk. Anat. EntwMech.* **50**, 460–546.

Bröcker, H. (1935). Untersuchungen über das sahvermögen der Einsiedlerkrebse. *Zool. Jb.* (*Zool.*) **55**, 399–430.

Buddenbrock, W. von & Friedrich, H. (1933). Neue Beobachtungen über die Kompensatorischen Augenbewegungen und den Farbensinn der Taschkrabben (*Carcinus maenas*). *Z. vergl. Physiol.* **19**, 747–61.

Bush, B. M. H., Wiersma, C. A. G. & Waterman, T. H. (1964). Efferent mechonoreceptive responses in the optic nerve of the crab *Podophthalamus*. *J. cell. comp. Physiol.* **64**, 327–45.

Collewijn, H. (1969). Optokinetic eye movements in the rabbit: input-output relations. *Vision Res.* **9**, 117–32.

Collewijn, H. (1970). Oculomotor reactions in the cuttlefish, *Sepia officinalis*. *J. exp. Biol.* **52**, 369–84.

De Bruin, G. H. P. (1956). Vision in the Crustacea. Ph.D. Thesis, University of Wales.

Easter, S. S. (1972). Pursuit eye movements in goldfish (*Carassius auratus*). *Vision Res.* **12**, 673–88.

Feldman, M., Atkin, A. & Bender, M. B. (1969). Oculomotor responses from visual input to an immobilised eye. Abstract in *4th International Congress of Neurological Surgery, 9th International Congress of Neurology, New York.*

Fraenkel, G. (1940). In *The Orientation of Animals* (ed. G. Fraenkel and D. L. Gunn), p. 253. Oxford: Clarendon Press.

Hadley, P. B. (1906). The relation of optical stimuli to rheotaxis in the American lobster *Homarus americanus*. *Am. J. Physiol.* **17**, 326–43.

Harden-Jones, F. R. (1963). The reaction of fish to moving backgrounds. *J. exp. Biol.* **40**, 437–46.

Hassenstein, B. (1954). Über die Sehschärfe von Superpositionsaugen (Versuche an *Lysmata seticaudata* und *Leander serratus*). *Pubbl. Staz. zool. Napoli* **25**, 1–8.

Hisada, M., Sugawara, K. & Higuchi, T. (1969). Visual and geotactic control of compensatory eyecup movement in the crayfish *Procambarus clarki*. *J. Fac. Sci, Hokkaido Univ. Ser.* 6, *Zool.* **17**, 224–39.

HORRIDGE, G. A. (1966*a*). Study of a system, as illustrated by the optokinetic response. *Symp. Soc. exp. Biol.* **20**, 179–98.

HORRIDGE, G. A. (1966*b*). Optokinetic responses of the crab *Carcinus* to a single moving light. *J. exp. Biol.* **44**, 263–74.

HORRIDGE, G. A. (1966*c*). Direct response of the crab *Carcinus* to movement of the sun. *J. exp. Biol.* **44**, 275–83.

HORRIDGE, G. A. & SANDEMAN, D. C. (1964). Nervous control of optokinetic responses in the crab *Carcinus*. Proc. R. Soc. (B) **161**, 216–46.

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

LYON, E. P. (1904). On rheotropism. I. Rheotropism in fishes. *Am. J. Physiol.* **12**, 149–61.

MITTLESTAEDT, H. (1964). Basic control patterns of orientational homeostasis. *Symp. Soc. exp. Biol.* **18**, 365–85.

NEIL, D. M. (1975*a*). The control of eyestalk movements in the mysid shrimp *Praunus flexuosus*. *J. exp. Biol.* **62**, 487–504.

NEIL, D. M. (1975*b*). The mechanism of statocyst operation in the mysid shrimp *Praunus flexuosus*. *J. exp. Biol.* (In press.)

RADEMAKER, G. G. J. & TER BRAAK, J. W. G. (1948). On central mechanisms of some optic reactions. *Brain* **71**, 48–76.

WATERMAN, T. H. (1960). Interaction of polarised light and turbidity in the orientation of *Daphnia* and *Mysidium*. *Z. vergl. Physiol.* **43**, 149–72.

WATERMAN, T. H. & HORCH, K. W. (1966). Mechanism of polarised light perception. *Science, N.Y.* **154**, 467–75.

WIERSMA, C. A. G. (1966). Integration in the visual pathway of Crustacea. *Symp. Soc. exp. Biol.* **20**, 151–77.

WIERSMA, C. A. G. (1970). Reactivity changes in Crustacean neural systems. In *Short-term Changes in Neural Activity and Behaviour* (ed. G. Horn and R. A. Hinde), pp. 211–36. London: Cambridge University Press.

WIERSMA, C. A. G. & FIORE, L. (1971). Unidirectional rotation neurones in the optomotor system of the crab, *Carcinus*. *J. exp. Biol.* **54**, 507–13.

WIERSMA, C. A. G. & OBERJAT, T. (1968). The selective responsiveness of various crayfish oculomotor fibres to sensory stimuli. *Comp. Biochem. Physiol.* **26**, 1–16.

WIERSMA, C. A. G. & YAMAGUCHI, T. (1966). The neural components of the optic nerve of the crayfish as studied by single unit analysis. *J. comp. Neurol.* **128**, 333–58.

WIERSMA, C. A. G. & YAMAGUCHI, T. (1967*a*). The integration of visual stimuli in the rock lobster. *Vision Res.* **7**, 197–204.

WIERSMA, C. A. G. & YAMAGUCHI, T. (1967*b*). Integration of the visual stimuli by the crayfish C.N.S. *J. exp. Biol.* **47**, 409–31.

YAMAGUCHI, T. (1967). Effects of eye motions and body positions on crayfish movement fibres. In *Invertebrate Nervous Systems* (ed. C. A. G. Wiersma). Chicago: University of Chicago Press.

YORK, B., YANAGISAWA, K. & WIERSMA, C. A. G. (1972). Input sources and properties of position-sensitive oculomotor fibres in the rock lobster, *Panulirus interruptus* (Randall). *J. exp. Biol.* **57**, 229–38.

YOUNG, L. R. (1971). Pursuit eye tracking movements. In *The Control of Eye Movements*, (ed. P. Bach-y-Rita, C. C. Collins and J. E. Hyde), pp. 429–43. New York and London: Academic Press.