

TWO-DIMENSIONAL RECORDS OF THE EYECUP MOVEMENTS OF THE CRAB *CARCINUS*

BY W. J. P. BARNES* AND G. A. HORRIDGE†

*Gatty Marine Laboratory, and Department of Natural History,
University of St Andrews, St Andrews, Scotland*

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INTRODUCTION

Although the optokinetic responses of arthropods have a wide significance in the analysis of the visual system (e.g. Reichardt, 1962; McCann & MacGinitie, 1965; Thorson, 1966*a, b*), and small movements of the head or eyecups are themselves effective in modifying the visual input to the animal (Horridge, 1966*a*), only one-dimensional records (usually horizontal) have been made of these movements. In the experiments to be described the eyecup movements of the crab, *Carcinus maenas*, have been recorded in two dimensions on an *X-Y* plotter. Although this method does not allow the velocity of the eyecup movement to be calculated at each moment of time, it provides a visual representation of the eye in space, which no previous studies have accomplished.

A single movable light in an otherwise dark room has been taken as the most convenient stimulus for two-dimensional studies, although any contrasting object or pattern will suffice so long as the crab sees nothing besides. A single moving light can be moved in any direction at a readily controlled speed and the results are relevant to the possible ability of the crab to resolve the movements of the sun, moon and stars as aids to orientation. The only other workers to use a single light as an optokinetic stimulus have been ter Braak (1936), Rademaker & ter Braak (1948) on the dog and rabbit, and Horridge (1966*b*, 1967) on *Carcinus*.

METHODS

Units consisting of a collimated light source and a pair of infrared-sensitive photocells were used to record eyecup movements as before (Barnes & Horridge, 1969). To record eyecup movements in two dimensions a vertical as well as a horizontal square of black paper was attached to the nylon bristle on the eyecup. One photocell-lamp unit registered horizontal, the other vertical eyecup movements. The outputs of the two photocells were fed into the two axes of an *X-Y* plotter, via differential DC amplifiers, and were separately calibrated when in position. Light visible to the crab was eliminated by a dark red filter.

The optokinetic stimulus was the movement of one or more subminiature bulbs

* Present address: Department of Zoology, University of Glasgow.

† Present address: Research School of Biological Sciences, P.O. Box 475, Canberra City, A.C.T. 2601.

in an otherwise dark room. The crab always faced the stimulus, which was 50 cm. away from it on the same level. Under these conditions, the bulb illuminated the eye surface with a brightness of approximately 0.05 lux (Horridge, 1966 *b*).

In some experiments, one or more white lights were rotated in a circle in front of the crab; in others, a white light was mounted on the end of the arm of a pen-recorder solenoid which was driven by a low-frequency waveform generator. This provides an accurate linear movement of small magnitude with a frequency response up to 10 Hz.

RESULTS

Small eyecup movements

In the absence of moving stimuli the eyecups of crabs are by no means stationary but exhibit a variety of oscillations over a wide frequency spectrum. The movements can be conveniently classified into four categories: tremor, drift, saccades (flicks) and waving movements.

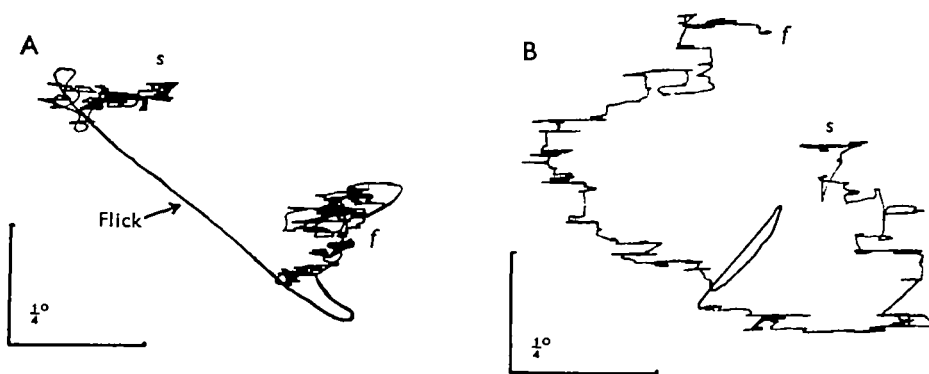


Fig. 1. Two-dimensional records of eyecup tremor. (A) Tremor over a period of 40 sec. with the eyecup stabilized upon a single stationary light. Note that a flick after about 20 sec. brings the eyecup to a new position. (B) Mainly horizontal tremor during a response to a light which moved in a clockwise circle from a 12 o'clock position. The cycle took 48 sec.; the stimulus diameter subtended 2.7° at the crab's eye. *s*, start; *f*, finish.

When eyecup movements are plotted in two dimensions, eyecup tremor can be seen to occur in both horizontal and vertical planes (Fig. 1). With the eye stabilized upon a stationary light in an otherwise dark room eyecup drift is reduced and tremor occurs continuously around the same place. Because of this, two-dimensional records of tremor alone are difficult to analyse, but close examination of plots such as Fig. 1 A shows that tremor in the horizontal plane predominates over tremor in other planes.

Tremor is more clearly observed during the response of the eye to a moving pin-light because, under these conditions, the record is not all superimposed on one spot (Fig. 1 B). Analysis of such records confirms that tremor, far from being a simple sinusoidal movement, is a complex irregular movement of several superimposed oscillations in different planes, and contains frequencies of up to 10 Hz. The dominant motion is, however, noticeably in the horizontal plane, and its amplitude there is within the range 0.01–0.2° peak to peak, as previously described (Horridge & Sandeman, 1964). This agrees with the finding that muscle 21 is the only muscle with a

phasic discharge when the eyecup is at rest (Burrows & Horridge, 1968), for this muscle moves the eyecup in the horizontal plane.

The sudden flick of the eyecup called a saccade is presumably caused by a short burst of motor nerve impulses. Saccades must be imposed independently of the control of eyecup position, since the eyecup usually returns quickly to near its original position after a flick (Fig. 1 B). Saccades occur with no particular preference for any plane, and therefore different muscles must be involved on different occasions.

Similarly, the eyecup drift that takes place when there are no contrasts in the visual field can occur in any direction. However, waving movements of the eyecups, described in the previous paper (Barnes & Horridge, 1969), occur predominantly in the horizontal plane.

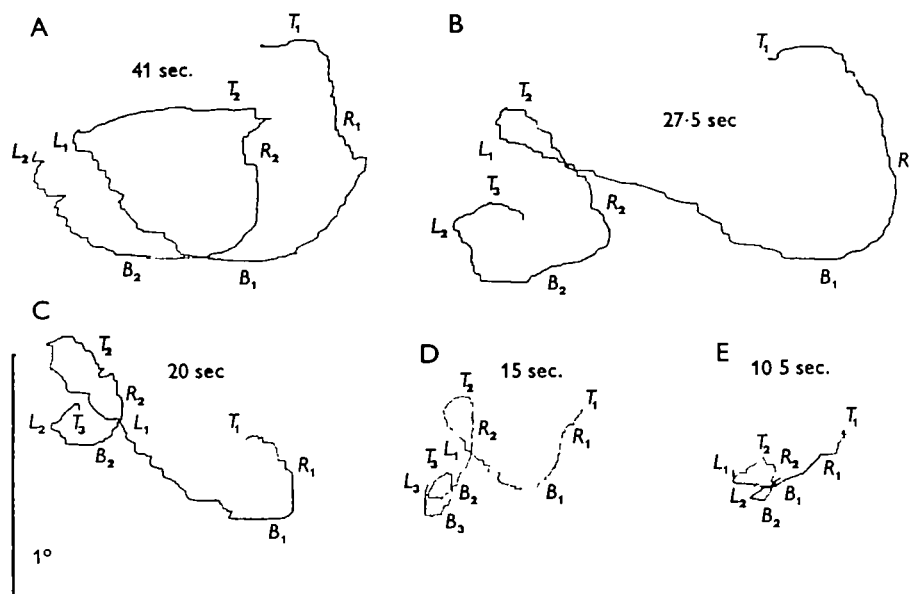


Fig. 2. Two-dimensional records of responses to a single light moved in a clockwise circle from a 12 o'clock position; the stimulus circle subtended 18.6° at the crab's eye; the period of rotation varied as follows. (A) 41 sec./cyc.; (B) 27.5 sec./cyc.; (C) 20 sec./cyc.; (D) 15 sec./cyc.; (E) 10.5 sec./cyc. T_1 , R_1 , B_1 and L_1 are, respectively, the 12, 3, 6 and 9 o'clock positions of the light during the first cycle. T_2 , R_2 , B_2 , L_2 , T_3 , R_3 , B_3 and L_3 are similar positions in the second and third cycles. Note the lower response amplitude and greater adaptation at higher frequencies of rotation.

Responses to moving pinlights

Stimulus moving in a circle

The movement of a light in a circle is a simple stimulus which incorporates both vertical and horizontal components. Although the movement of the eyecup in response to this stimulus is by no means an exact circle (Fig. 1 B), the eye responds by some kind of circular movement, demonstrating that the whole optokinetic system can follow a smooth transition between horizontal and vertical movement.

Although they show considerable variation of all kinds, the responses are often elliptical rather than circular, with horizontal extent of 15–35% of the stimulus, and vertical extent 10–25% of the stimulus. These values apply to stimulus circles sub-

tending less than 12° at the crab's eye, at periods of rotation of 30–200 sec./cyc. This is one aspect of the finding that the forward gain of the optokinetic response is greater in the horizontal than in the vertical plane.

The effect of changing the period of rotation of a stimulus circle of constant magnitude is illustrated in Fig. 2. With a stimulus circle subtending 18.6° at the crab's eye in the range of periods 30–200 sec./cyc., the only effect was a slight increase in the amplitude of the response at the lower frequencies of rotation. At decreasing periods of rotation from 30 to 10 sec./cyc., however, the horizontal extent of the response to the first circle or part of circle decreased from 7 to 2% of the stimulus diameter. Both of these effects can be attributed to known changes in the gain of the eye-movement

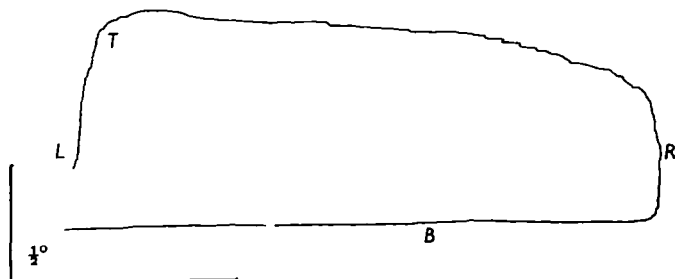


Fig. 3. Two-dimensional records of the almost rectangular response occasionally given by the crab's eyecups to the movement of a single light in a circle in front of the crab. The stimulus circle subtends 18.6° at crab's eye; the period of rotation is 60 sec./cyc. *T*, *R*, *B* and *L* are the 12, 3, 6 and 9 o'clock positions of the light respectively.

control system at various stimulus velocities. As well as the decrease at faster rotations, however, there was considerable adaptation of the response after the first half or the whole of one circle had been completed, for all periods of rotation of less than 30 sec./cyc. The effect is a spiral response rather than the usual circular or elliptical one (Fig. 2B–E). This is one aspect of the general finding that adaptation of the optokinetic response is not entirely attributable to the habituation of the particular facets which see the movement. There is involved a common pathway, possibly wide-field movement units such as those found in the crab, *Podophthalmus*, by Waterman, Wiersma & Bush (1964), which affects the response to movement across parts of the eye that have not previously been stimulated. Adaptation was never to zero, and the response persisted after many cycles of stimulation. A similar adaptation of the optokinetic response occurs to comparable one-dimensional oscillation of a striped drum which presents far more contrast than a single light (Horridge, 1966*d*).

Two of the many crabs studied gave almost 'rectangular' responses to the circular stimulus (Fig. 3). Such responses are only an extreme example of a very common phenomenon of which there were indications in many records. The eyecup appears to make vertical or horizontal responses more readily than oblique ones, and thus frequently moves in a stepwise fashion at times when a smooth diagonal movement would be expected (Fig. 2A–D). To analyse these 'rectangular' responses further, the pen of the *X–Y* plotter was intermittently lifted from the paper by a circuit driven by a metronome. This enabled the velocity of the eyecup in the different parts of the rectangle to be observed directly. The results were inconclusive, however, showing

only that the movement of the eyecup was rather irregular, speeding up and slowing down at different points in different rectangles.

The alternating horizontal and vertical movements that compose a 'staircase' response to an oblique stimulus have an amplitude of $0.05-0.1^\circ$. The 'steps' are the result of an alternation in the changes in tension between different muscles of the eye, for some of the eyecup muscles act in the vertical and others in the horizontal plane. The steps may arise from several possible causes which are not mutually exclusive. They may, for example, simply represent eyecup tremor superimposed on a purely diagonal movement; they may reflect an analysis, by interneurons on the sensory side, of perceived movement into its horizontal and vertical components; or they may be a sign of some kind of mutual exclusion in the action of horizontal and vertical muscles.

Only one-third of the crabs used in these experiments responded to the movements of a single light having an intensity of 0.05 lux at the crab's eye. The crabs which did not respond in these experiments appeared in no other way different from those that did, and all responded to a moving striped drum.

Stimulus moving at constant velocity at different angles to the horizontal

The velocity and amplitude of the crab's responses to a single light which is moved horizontally or vertically is proportional to the velocity and amplitude of the stimulus. Although Fig. 4 represents the responses of one crab, similar results were obtained from all animals on which measurements were made. As in the experiments described above these responses are variable and the amplitude of the response is low. In the horizontal plane the gain is about 0.3 , equivalent to responses of 25% of the stimulus, and in the vertical plane $0.2-0.3$, equivalent to responses of $15-25\%$ of the stimulus amplitude. The gain is presumably low because few facets of the eye are stimulated by a single light, as compared with a striped drum. The effect of the eyecup's own movement is taken into account in all calculations.

A constant-velocity movement of a light has also been used as a stimulus when the visual feedback loop has been eliminated. The movements of a blinded eye are recorded when the other eye sees but is fixed to the carapace. Whereas one-third of crabs responded to the movement of a pinlight when in the closed-loop condition, only two crabs, out of a total of more than twenty, responded in the open-loop condition. As there is no reason to suppose that the absence of visual feedback affects the ability of crabs to see the light and to respond, the poor performance must be attributed to the inability of the seeing eye to show tremor and thereby improve the contrast (Horridge, 1966*a*). The form of the open-loop responses of these two crabs does not differ from that of the closed-loop responses described above, although the gains of responses to both horizontal and vertical movements are even more variable than before. This was to be expected because the negative feedback loop decreases the response variability.

Under appropriate conditions the eyecups of *Carcinus* follow the movement of the sun across the sky. It is therefore reasonable to suspect that *Carcinus*, like several other crustaceans, orients by the sun (and moon). For rough direction-finding, in conjunction with an internal clock, the sun's azimuth is enough; for a more highly developed sense, the inclination of the sun's path may also be taken into account. In

order to test the ability of *Carcinus* to measure the angle of inclination of the path of a moving light, the single light was moved in front of the crab at a constant velocity of $1^\circ/\text{sec.}$ at different angles to the horizontal (Fig. 5). Repetition of the experiment with a stimulus velocity of $0.005^\circ/\text{sec.}$ (the same order of magnitude as the speed of the sun across the sky) gave similar results. The diagonal responses of Fig. 5, like those to a single light moved in a circle, are achieved in a stepwise fashion, as described above.

The angle of response to an oblique movement should be dependent upon the gains of the responses to horizontal and vertical stimuli taken separately, however the diagonal responses arise. When the gains for vertical and horizontal responses are

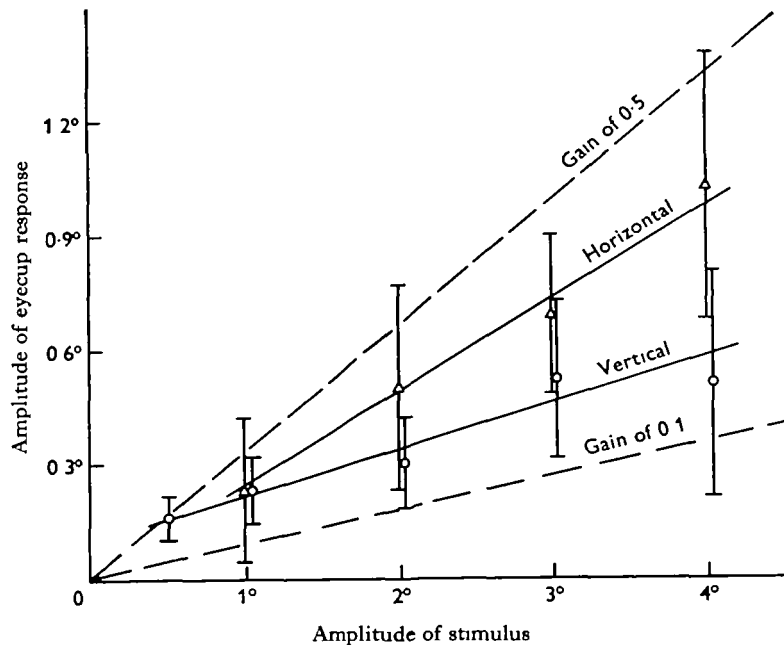


Fig. 4. The relation between stimulus amplitude and response amplitude for constant velocity horizontal (Δ) and vertical (\circ) movements of a single light over traverses of different extent. Velocity of stimulus, $0.1^\circ/\text{sec.}$ Vertical lines represent standard deviations, calculated on 4-14 responses. Theoretical lines representing gains of 0.5 and 0.1 are also shown.

equal, the responses given by the crab should be at the same angle as the stimulus. However, when the horizontal and vertical gains are unequal, as in most crabs, then a graph of stimulus angle against response angle should be a curve, stimulus angle only equalling response angle when the stimulus is either vertical or horizontal. Caution is necessary because the responses to vertical or horizontal movements of the stimulus are not necessarily vertical or horizontal, although tests show that they usually are so. The results of one set of measurements are shown in Fig. 6.

When the individual responses from which the graph, Fig. 6, was drawn are resolved into their horizontal and vertical components, and the mean horizontal and vertical gains calculated, the mean horizontal gain is 0.3, and the mean vertical gain is 0.2. This gives a V/H gain ratio of 0.67. The theoretical response curve for a V/H gain ratio of 0.67, shown on the figure, is close to the mean of 7 of the 11 different angles tested.

The data from other experiments fitted theoretical response curves with V/H ratios between 0.5 and 0.7, with the exception of one peculiar crab in which $V/H = 1.5$; i.e. in this crab the vertical gain was greater than the horizontal gain.

Though the results of these experiments approximately fit the different theoretical response curves, there was, nevertheless, considerable variation in the results, demonstrating that individual crabs can measure the angle of movement of a single light with

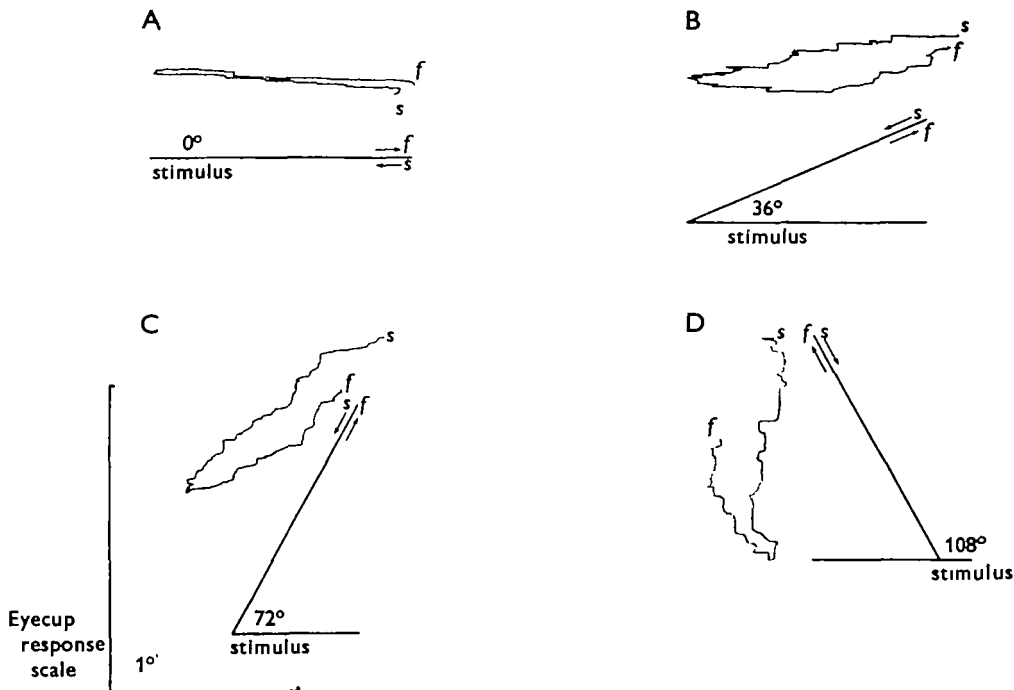


Fig. 5. Two-dimensional records of responses to constant velocity movements of a single light at different angles to the horizontal. The stimulus angles subtend 5° at the crab's eye; time from start (*s*) to finish (*f*) was 10 sec.; stimulus velocity was $1^\circ/\text{sec.}$ in each case. The vertical and horizontal eyecup response scales are unequal, and the lines representing the stimuli are adjusted to the same coordinates.

an accuracy of only $\pm 10-15^\circ$. The gains of the responses were similarly variable, so that any estimation by the crab of the velocity of the movement of the sun or moon across the sky would be liable to an error of $\pm 5-10\%$. In a behavioural response to striped patterns, honeybees do not discriminate between sets of black stripes whose slopes differ by less than 15° (Wehner, 1967). Crabs cannot resolve diagonal movements into their horizontal and vertical components with the accuracy that would be necessary for accurate computation of latitude and longitude; but on this test they perform as well as bees.

Experiments with two lights

The preceding experiments have shown that crabs can move their eyecups equally well in both horizontal and vertical planes, but nothing has been said about twisting or torsional movement. To test whether such a movement could be induced, two lights were mounted on opposite sides of the same circle, equidistant from the centre of

rotation and rotated in front of the crab. The responses were recorded in the horizontal and vertical planes as usual and were compared to eyecup tremor with the eye stabilized on a single stationary light and to the response to a single light rotated in a circle. Though the response given to the circular movement of a single light is normal, and the eyecup tremor is of the expected amplitude, there is no response to the rotation of the two lights. A response with torsional components cannot be elicited. Instead, the drift and tremor of the eyecup are enhanced. Though this may be a similar phenomenon to the increase in tremor often associated with any eyecup

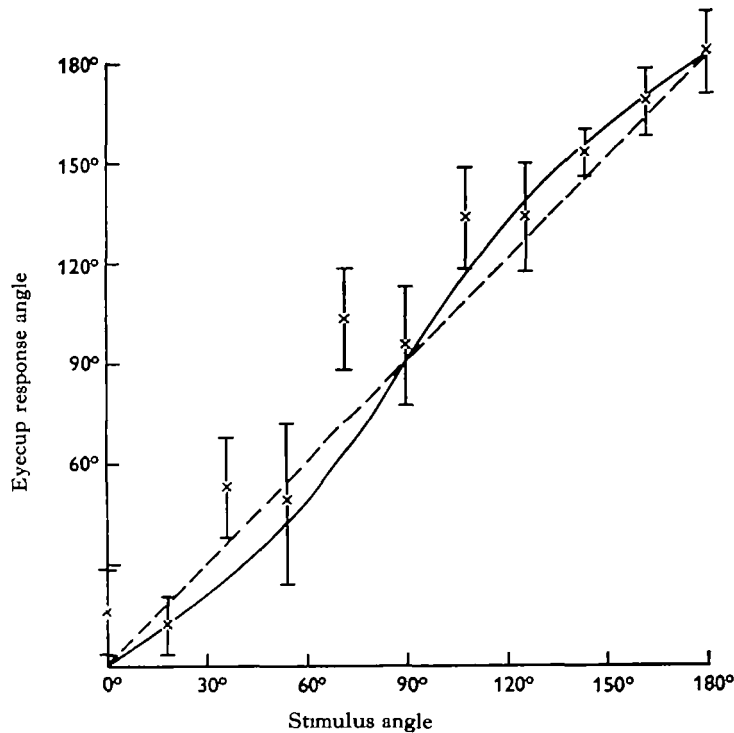


Fig. 6. Actual values for the angles of eyecup movement in response to constant-velocity movements of a single light at different angles to the horizontal. The stimulus amplitude subtended 5° at the crab's eye; its velocity was $1^\circ/\text{sec}$. Vertical lines represent standard deviations calculated on 4-14 responses. The dashed line represents a response equal to the stimulus. The continuous curve is a theoretical response curve for a vertical/horizontal velocity gain ratio of 0.67.

response, it may be more simply explained as the result of antagonism between the tendency to follow both lights which are always moving in opposite directions relative to the eye. The optokinetic mechanism sums the two movements in horizontal and vertical planes but has no means of dealing with the rotation of the pair of lights. The increased tremor is presumably the amplified difference between the two responses.

In all these experiments with single light stimuli, any stationary contrasting objects in the visual field inhibit the response. When a stationary light lies at the centre of the circular path of a second light, the amplitude of the response is reduced by up to 50% (average reduction 20%).

In a further experiment two lights were again rotated in clockwise circles in front of the crab. The two circles, which had the same centre, had diameters which subtended 16.8° and 5.6° at the crab's eye. The two lights were rotated at the same frequency (42 sec./cyc.), and always moved in opposite directions because they lie on opposite sides of the circle's centre. Both eyes of the crab could see both lights and nothing besides. In four out of eleven trials, the crab followed the direction of motion of the stimulus with the larger diameter, but with a response amplitude of only 40% of that given to a single light rotated in a circle of that diameter. In the other seven trials, there was no clear-cut response from the crab, though eyecup tremor and drift were enhanced.

Though not all crabs perform, these results agree with three principles. (a) The eye of the crab does not fixate on a light, but always slips behind. (b) The optokinetic mechanism responds to the net movement of all contrasting objects across the eye. Known previously for horizontal movement (Hassenstein, 1958), this conclusion can now be extended to two dimensional responses. (c) The crab responds to the horizontal and vertical motion but has no torsional component in its eyecup response to movement in a circle.

DISCUSSION

The two-dimensional records, though lacking a continuous measure of eyecup velocity, illustrate the eyecup movements of *Carcinus* in space in a way that no one-dimensional recording can do. They illustrate that eyecup tremor is a complex irregular movement of several superimposed oscillations in both planes, that saccades occur in all directions, and that following movements (optokinetic responses) are readily elicited in any direction. However, there is not even a limited torsional movement of the eye, as there is in the human eye.

From the form of the responses to diagonal movements of single lights, and the slope of the responses to movements of single lights at different angles to the horizontal, it is clear that *Carcinus* can approximately follow the angle of the track of the light. Although the eyecups respond to the movement of the sun across the sky (Horridge, 1966c), the behavioural evidence for any sun orientation is slight. Drzewina (1908) found that *Carcinus*, released on a beach, headed towards water, but demonstrated no mechanism for this hydrotropism. *Carcinus* orients to shadows (Alverdes, 1930), and a sun-compass reaction is known in the amphipods *Talitrus* and *Talorchestia* (Pardi & Papi, 1961). *Carcinus* turns so that it faces a single light source in an otherwise dark chamber (Wolter, 1936), but the crab's orientation to this light is not known to vary with the time of day, as would be expected if it possessed a sun-compass reaction. The mangrove crab, *Goniopsis*, exhibits a compass orientation to polarized light (Schöne, 1963), but the response of this crab to an unpolarized light source can only be interpreted as resulting from a tendency to avoid the hotter, drier and more brightly illuminated portions of the arena. Field tests are thus required to show whether *Carcinus* has a sun-compass orientation and, if so, whether it makes use of any aspect in addition to the azimuth of the sun.

SUMMARY

1. The eyecup movements of the common shore crab, *Carcinus maenas* L., have been recorded in two dimensions.
2. Saccades and eyecup drift occur in all directions. Eyecup tremor is a complex irregular movement although horizontal tremor predominates in most crabs.
3. Although the response to the movement of the light in a circle is usually an approximate circle or ellipse, rectangular responses are occasionally obtained and the eyecup often moves in a stepwise fashion in response to a smooth diagonal movement of the light.
4. The angle of response to a diagonal movement depends on the ratio of the response to horizontal and vertical movements alone. The eye is virtually stabilized in all planes by a contrasting object but never fixates upon a moving stimulus.
5. No torsional or twisting movements of the eyecups were obtained in response to light stimuli.

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