

PERCEPTION OF EDGES VERSUS AREAS BY THE CRAB *CARCINUS*

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The previous paper (Horridge, 1966) showed that a crab gives a directional eyestalk response to a striped drum which has been moved during a dark period. The crab's ability to do this shows that the former position of the stripes is remembered in some way for many minutes in the dark and is correlated with the new position on re-illumination. In that paper two aspects were omitted for simplicity. It was assumed that the crab perceives the stripes much as we do as areas of black and white, and that eye tremor can be ignored. In the present account it will be shown that neither of these assumptions is justified, and that both must be modified by one new fact, that eye tremor accentuates the perception of edges.

METHODS

The material and methods are exactly as described in the previous paper with the following modifications. Eye movements can be recorded throughout the dark period by the infra-red beam, flag and photocell, but for simplicity this can be dispensed with and only the final equilibrium positions of the eye need be measured with the flag reading directly on a fine scale.

The drum is moved by hand from one position to another during the dark period and at each position is held by a small magnet attached to a moving slide with a vernier calibration. These two slides, carrying their magnets, are bolted to a single platform which is mounted on flexible springs. This platform is mounted separately on a heavy stone slab so that its movement is not conveyed to the photocell, and is vibrated by a pen-recorder solenoid which in turn is driven by a low-frequency oscillator. This arrangement sets both magnets and the drum into oscillation with a frequency of 1 in 2-5 sec. A pin projecting from the side of the drum is moved from one magnet to the other during the dark period and this movement is superimposed on an oscillation amplitude of about $0.2-1.0^\circ$ of controlled frequency. In the other experiment there is no oscillation and one or other of the magnets holds the drum stationary for all the time that the crab sees it.

EXPERIMENTAL RESULTS

Open-loop conditions

The crab, with the right seeing eye firmly fixed to the carapace, and the left eye painted over, is held in its clamp in the illuminated drum for a few minutes, all lights are turned out for a standard time of 15 sec. and during the period of darkness the

drum is turned through a controlled angle. Upon re-illumination the left eye starts to move immediately and approaches equilibrium in a few seconds. Some crabs reach the final equilibrium position in about 30 sec. but others take at least twice as long. In the present experiments the left eye position was measured when the response had clearly come to an end. To make a number of measurements at numerous different angles with and without drum oscillation requires a run of several hours and

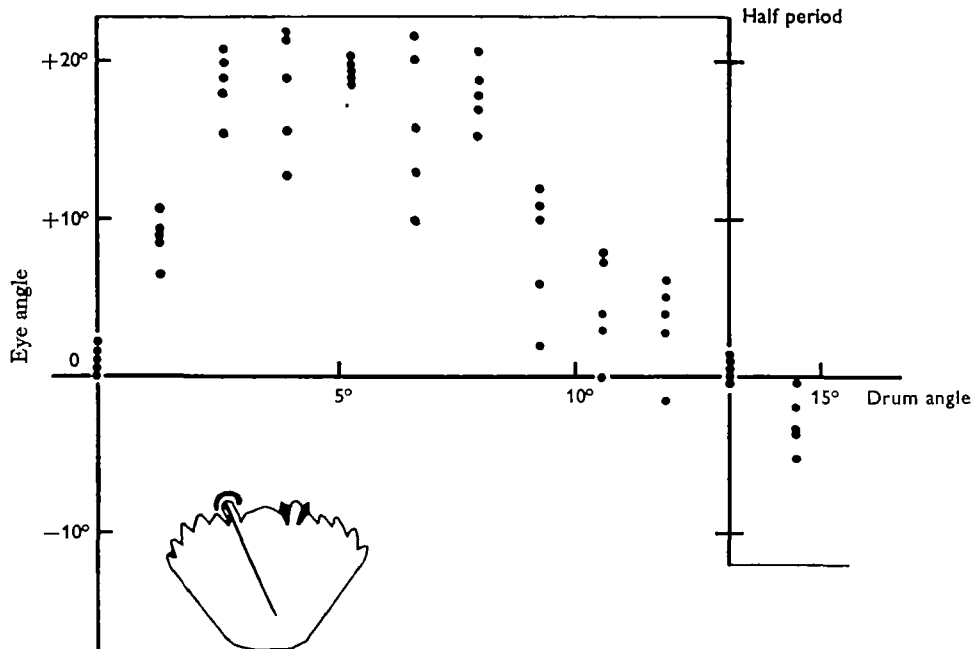


Fig. 1. Records from the left painted eye with the right eye clamped to prevent tremor. The drum was absolutely still before and after the dark period of 10 sec. The responses approximate to curve 1 of Fig. 6, showing no preference for edges as opposed to areas.

many crabs fail to sustain their responses for so long. However, Figs. 1 and 2 show results from one crab respectively without and with drum oscillation. For small drum angles the eye movements increase with increasing drum angle, rise to a maximum near $\frac{1}{4}$ stripe period and then fall. As described in the previous paper, the actual values of eye movements are greater than the drum movements because in open-loop conditions the true forward gain for small angles ranges from about 50 down to about 5, depending on the stimulus angle. However, a contrast appears between the two sets of results in the region of $\frac{3}{8}$ stripe period, i.e. near 10° . At $\frac{1}{2}$ stripe period with the stationary (clamped) eye seeing a stationary drum the results pass through zero in a downwards direction from top left to bottom right, i.e. with values up to $\frac{1}{2}$ stripe period all positive. However, with 0.5° of drum oscillation the eye angles pass through zero at $\frac{1}{2}$ stripe period from bottom left to top right with increasing drum angles.

One way to demonstrate the same result is to place a crab with one eye fixed and the other blinded in the drum with an imposed oscillation and then to move the

drum through an angle of $\frac{1}{3}$ stripe period during a dark period of a few seconds. Some crabs give an eye response in the same direction as the drum but others give a response in the opposite direction to the drum. This is the way to select a crab which responds strongly to edges; experience shows that crabs vary considerably in this way and also in the actual values of the forward gain.

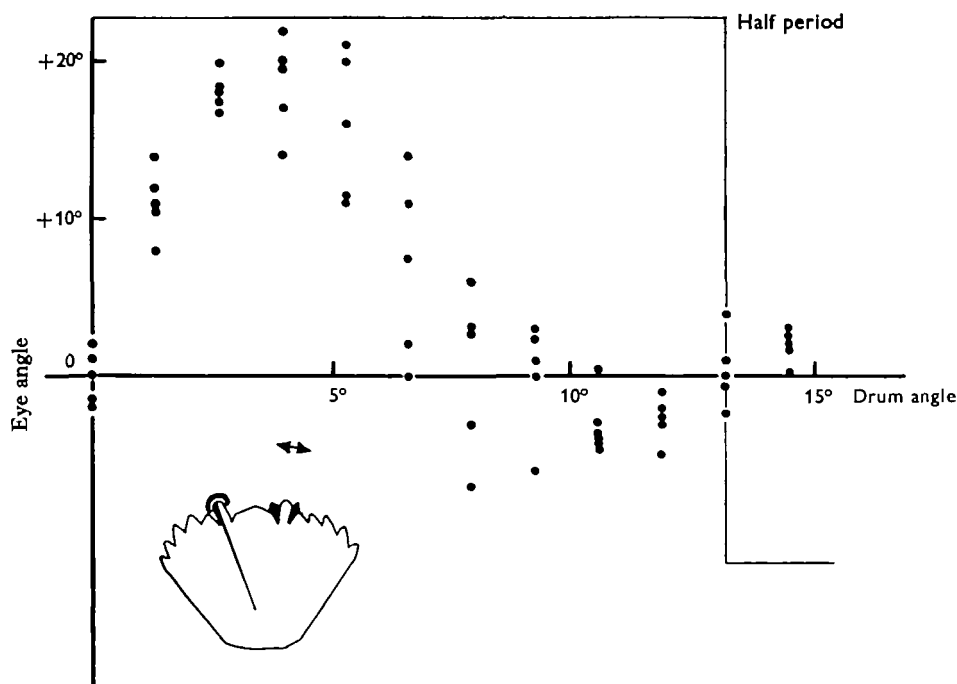


Fig. 2. The same arrangement, with the same crab as in Fig. 1 except that a constant tremor of 0.5° at a frequency of 1 in 3 sec. was imposed on the drum. The response now falls to zero at about $\frac{1}{3}$ stripe period, gives negative values for the $\frac{1}{3}$ stripe period, and approximates to curve 5 of Fig. 6. The larger scatter in the centre region suggests that the crab varies its attention between edges and areas.

Closed-loop conditions

When the seeing eye is allowed to move, the induced relative movement of contrasts in the visual field reduces the response as the eye sweeps across them. In the previous paper, where this effect was described for the optokinetic memory experiment, it was shown that the closed-loop response has the same periodicity as the open-loop response because when the response is zero in open-loop conditions it should also be zero at the same drum movement when the loop is closed. For all angles of drum movement the eye response is smaller than the drum movement because the gain in the feedback loop is not less than unity. Therefore an average curve drawn from results as in Fig. 2 can be used to predict the closed-loop responses of the same crab under the same conditions, exactly as was done in the previous paper (Horridge, 1966).

Actual closed-loop values, combined from several crabs, are shown in Fig. 3. These measurements are from a series of observations (Horridge & Shephard, 1965) which were recorded before their significance was realized and before any open-loop experiments were carried out. For these reasons not enough readings were taken in the

region of $\frac{3}{8}$ stripe period (around 10° drum movement), but nevertheless the responses are clearly negative in the region round $\frac{3}{8}$ stripe period and positive round $\frac{1}{8}$ stripe period.

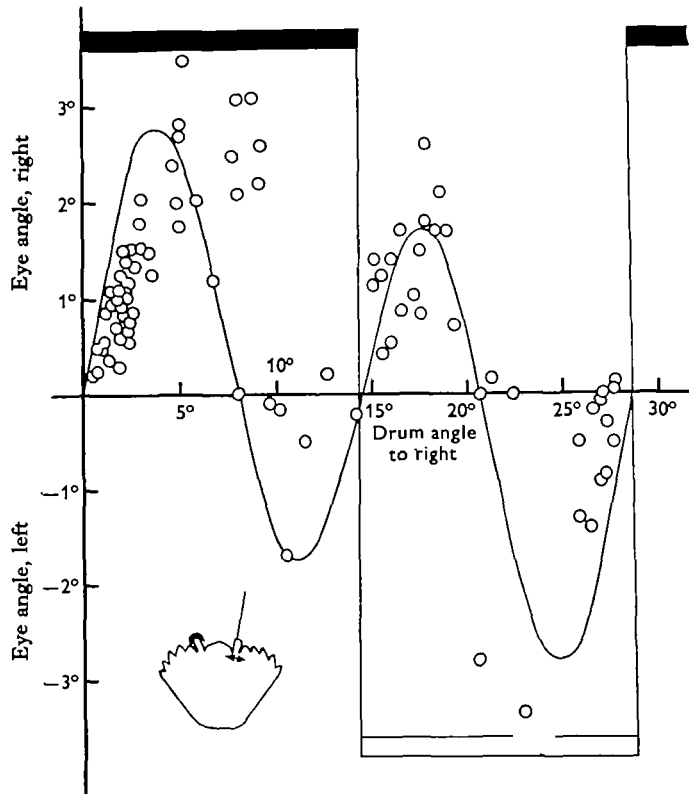


Fig. 3. Combined closed-loop results, from three crabs, of eye movements in response to various drum movements which were made in a dark period of 1 min. Records were taken from the free right eye with the left eye painted over. Note that responses in the region $\frac{1}{4}$ — $\frac{1}{2}$ and again in $\frac{3}{4}$ —1 stripe period are to the left for drum movements to the right. The smooth line is curve 6 from Fig. 6.

Edges versus areas in the perception of movement

The lower line of each pair in Fig. 4 shows the position of the drum following a dark period during which it was moved by a distance equal to $\frac{3}{8}$ stripe period. To our eyes there appears to have been a movement to the right, when the first two lines are compared, although it is possible with more difficulty to imagine a movement of $\frac{3}{8}$ stripe period to the left. When its seeing eye is clamped relative to the stripes the crab interprets this situation as a movement to the right, as we do. Suppose now that adaptation of the receptors causes the contrast of black and white areas to fade but that eye flicks or tremor reduces adaptation in those ommatidia facing the edges in the pattern. The crab will see something such as represented by Fig. 4B. Some parts of the pattern lead to interpretation as movement to the right while others favour movement to the left. The more that the contrast between centres of areas disappears the more the edges favour an interpretation as movement to the left for a drum movement of $\frac{3}{8}$ stripe period to the right, as in 4C. All intermediates are possible.

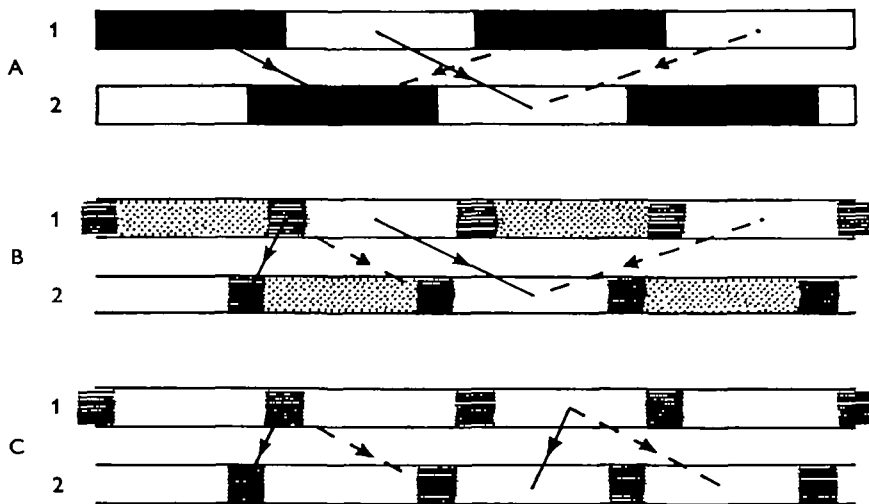


Fig. 4. The striped drum is moved three-eighths of the repeat distance during a period of darkness from the position in (1) to that in (2). A. If the animal sees stripes as areas, as we do, it will interpret the change as a movement to the right because the correlations in that direction are stronger than in the reverse. B, As in A but with the edges accentuated relative to the continuous areas. The correlation between edges would now suggest that B 2 has moved towards the left relative to B 1 whereas areas suggest the opposite. C, Only the contrast at edges now remains, and suggests a movement to the left. In all figures the short continuous arrows show stronger correlations than the corresponding broken arrows, which indicate an opposite movement.

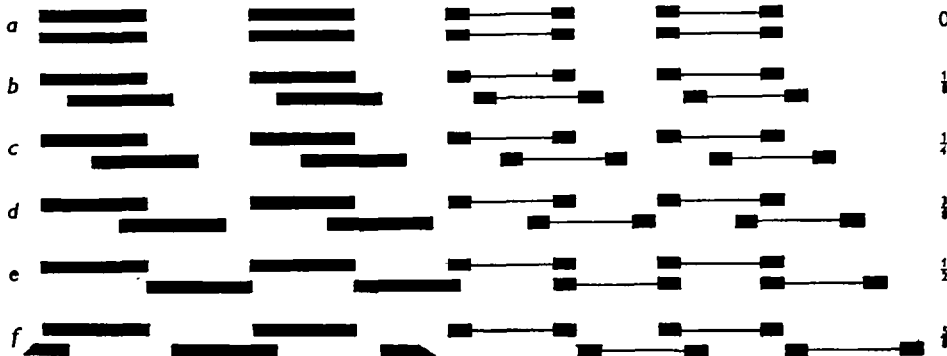


Fig. 5. Stimulus situations for various drum movements to show the origin of the periodicity in Fig. 6. The relative positions of the drum before and after the dark period is shown in the upper and lower line of each pair. Perception of areas is assumed on the left and of edges on the right. Lines (a)-(f) show successively larger drum movements at intervals of $\frac{1}{4}$ stripe period. In (a) and (e), for different reasons, no movement is apparent. In (b) there is little to distinguish the apparent distance moved when areas or edges are accentuated. In (c) there is maximum apparent movement of areas but no clue as to the direction of movement of edges. In (d) the movement of areas is to the right but of edges is towards the left, bringing the responses to these into different quadrants in Fig. 6. After responses to both edges and areas pass through zero (see Fig. 6) the apparent direction of movement is reversed in (f), where areas appear to have moved to the left while edges have moved to the right.

The way in which progressively increasing drum movements lead to a characteristic pattern of eye movements in one direction or the other for areas and for edges is shown by Fig. 5. When areas are considered the response should have a periodicity equal to the stripe period. When edges only are considered the response should have a periodicity equal to twice the stripe period. Intermediates can be worked out as follows.

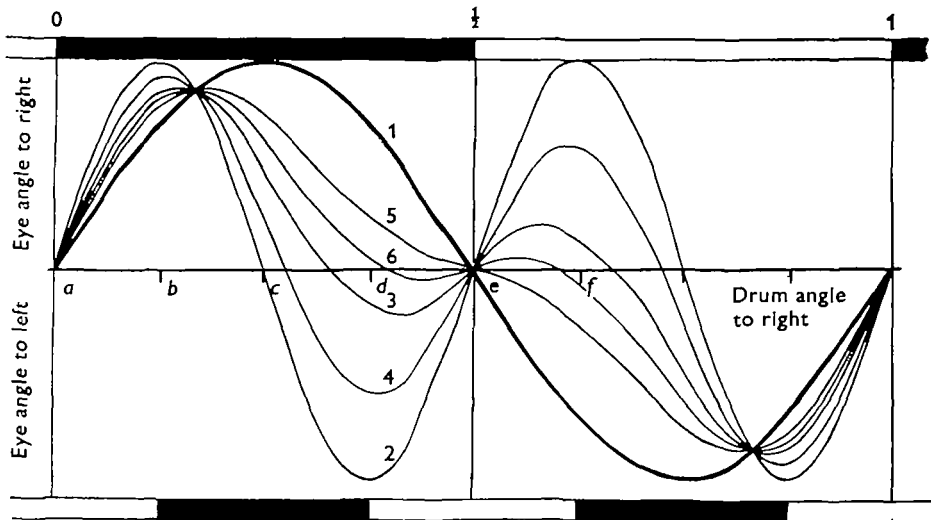


Fig. 6. Predicted patterns of responses which depend on the relative emphasis placed on edges versus areas in the inference of movement following a drum movement which took place in the dark. The letters (a)–(f) show the distances moved to the right in corresponding lines of Fig. 5. Eye movements are plotted vertically; drum movements on this figure are all to the right, increasing towards the right. Curve 1 shows the type of response to areas alone as in Fig. 5 left; curve 2 shows responses to edges. As explained in Fig. 5, responses to edges are zero at (c), while responses to areas and edges are in opposite quadrants at (d) and again at (f). Curves 5, 6, 3 and 4 show the predicted patterns of responses when successively more emphasis is placed upon edges and less upon areas.

Assuming that the responses approximate to sine waves, a theoretical curve can be drawn corresponding to the responses for areas (curve 1 in Fig. 6), and another, of half the wave-length, taking note only of edges (curve 2 in Fig. 6). An animal taking note of edges only, with no content referring to the areas, would make responses which pass through two periods in one stripe period. However, as shown in Fig. 4B, edges and areas are not mutually exclusive, and there must be all gradations combining them in different proportions. The intermediate curves of Fig. 6 are means between the two extreme curves, with different weighting, as follows: curve 1, $\sin \theta$; 2, $\sin 2\theta$; 3, $\frac{1}{2} \sin \theta + \frac{1}{2} \sin 2\theta$; 4, $\frac{1}{4} \sin \theta + \frac{3}{4} \sin 2\theta$; 5, $\frac{3}{4} \sin \theta + \frac{1}{4} \sin 2\theta$; 6, $\frac{5}{8} \sin \theta + \frac{3}{8} \sin 2\theta$. The curve which best fits the experimental data in Fig. 3 is 4 from Fig. 6. On this interpretation the crabs which gave the results in Fig. 3 were placing about three-quarters of their emphasis on edges and about a quarter on areas. The change from the results in Fig. 1 to those in Fig. 2, as a consequence of imposed tremor shows a change of emphasis from almost pure areas to about half and half (curve 3 in Fig. 6).

DISCUSSION

These experiments were designed to investigate the effect of eye tremor in the emphasis of contrasting edges. To control the tremor the eye was clamped and an oscillation was applied to the drum. This relative movement has the effect of causing some receptors to scan the edges which lie in line with them, whereas receptors which are all the time facing a white or a black area can be expected, from physiological properties of receptors in general, to adapt back towards a background frequency. In fact an even greater emphasis upon edges rather than areas appeared in eyes which were free to undergo tremor under closed-loop conditions than in eyes which saw an artificial tremor superimposed on the drum movement. Presumably, therefore, the amplitude and frequency of the artificial tremor were not the optimum. Perhaps the eye flicks at longer intervals are more effective.

Saccadic movements of the eye are important in the maintenance of vision in man, but this topic seems not to have been investigated in lower animals. No references to head or eyestalk tremor in arthropods have come to hand, and yet the subject is inseparable from the analysis of the mechanisms of vision in freely moving animals. Perhaps the evolution of stalked eyes came about for this reason. For a point source, eye tremor will take the stimulus up the region of steep slope in the curve of acceptance angle, while in retinula cells of neighbouring ommatidia, when there is overlap of acceptance fields, it will take it down the slope (Götz, 1965). This is the same effect as that produced by a small movement of 0.05° , to which we know that the stationary eye is sensitive. Therefore it appears that some components of the tremor are large enough to evoke a strong movement artifact from contrasting edges even if adaptation were not a factor. The objection that tremor is too rapid to be effective, or leads to habituation, does not apply to the larger and less frequent eye flicks, and the question is open to experiment by applying a range of different controlled tremors to the drum, with the eye fixed.

The effect of small movements in overcoming adaptation of the receptors, or of higher-order neurons in the memory experiment, is a more direct one. Some adaptation must occur, even if it is only partial. Most receptors will see either black or white all the time, for small angles of drum movement. Most information of movements will come from receptors which change from black to white or vice versa. With extreme adaptation we might expect that more information as to movement in the memory experiment would come from receptors which scan edges in the first position, as compared with those which scan edges in the second position. However, an extreme reliance upon edges is never found in practice, and most specimens seem to perceive mainly areas.

The enhancement of edges can be explained either by reference to the effect of eye movements on adaptation in a purely position-sensitive system or on the mechanism of movement perception, or on a combination of these possibilities. These questions require a more exact analysis, and invite electrophysiological investigation. The present account must be considered as only the first which utilizes the optokinetic memory as a technique of testing what the animal sees.

SUMMARY

1. In the previous paper it was shown how a crab remembers the former position of a drum which has been moved in the dark. The technique can be used to test what aspects of the visual field the crab has seen.
2. If the crab sees stripes as black and white areas, the responses with increasing drum movement will repeat themselves at each stripe period, but if only edges are seen the responses pass through two periods for each stripe period of drum movement.
3. With the seeing eye clamped and the moving eye painted over, a controlled amount of tremor can be imposed on the seeing eye by oscillation of the drum.
4. The perception of edges, as opposed to areas, of black and white stripes is enhanced by artificially imposed tremor.
5. Under closed-loop conditions, with movable seeing eyes, some crabs behave as if they perceive enhanced edges.

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