

OPTOKINETIC MEMORY IN THE CRAB, *CARCINUS*

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For many lower animals the optokinetic response of the eye or head to a movement of the whole visual field is a useful indication that the movement has been seen. The lower velocity limit of the optokinetic response is extraordinarily low in some animals. In the dog, ter Braak (1936) reports responses to drum movements at $6.4^\circ/\text{hr.}$, which is comparable to the lower limit in the crab. The question arises as to whether a memory of successive positions is involved.

It has been shown (Horridge & Sandeman, 1964) that the eye of the crab *Carcinus* responds to movements of a brightly illuminated drum as low as $0.0017^\circ/\text{sec.}$; the eye then responds with a movement of about $0.001^\circ/\text{sec.}$ so that the *average* movement of the stimulus across the eye is a slip speed of $0.0007^\circ/\text{sec.}$ This corresponds to an angular movement of 0.17 rev./24 hr. period. At low stimulus speeds in the range $0.0008-0.02^\circ/\text{sec.}$ the percentage following of the drum by the eye can be 90-95%, so long as no stationary objects remain in the visual field. It must be stressed however that these are average movements, for the eye is free to move and it makes continual tremor movements of an amplitude of $0.04-0.2^\circ$ at a frequency of around 1/sec. Besides the tremor there are occasional flicks and slower deviations. The optokinetic response is superimposed on these other movements and is seen only when they are averaged out over a period of several seconds; latencies are usually less than 10-20 sec. The question as to how the crab observes slow movements then includes the question as to how it performs the averaging process in order to see them with an eye that is in tremor. This would be possible if the animal could compare the position of contrasts in the visual field with their positions at an earlier period of time relative to the array of receptors. A system with some form of persistent signal from each retinal element should be able to perform this feat. In order to test whether there is some form of persistence the movements were made during a short period of darkness. A preliminary account has already appeared (Horridge & Shepherd, 1966).

METHODS

The experimental arrangement was designed to be as flexible as possible because the same apparatus (Fig. 1) has been used to provide a large variety of stimuli, as described in succeeding papers. The crab is rigidly held by the carapace in a standard flask clamp which is provided with two flanges to prevent the legs from reaching the eyes in efforts to clean off the flag, eye-shields or clamping wedges. A light flag (weight 3 mg.) is made from fishing nylon with a 4 mm. square of thin black paper at the end. The flag is secured to the top of the eye by a touch of warm insect wax

(beeswax, lanolin and rosin mixture) which must be as cool as possible when applied. The flag lies behind the eye and moves over a pair of photocells arranged in opposition to each other. This is a composite miniature unit (Texas type LS. 221), housed on a thin probe suspended over the heart region of the carapace. The photocell is excited by a parallel beam of infra-red light from a 45 W. tungsten lamp and a

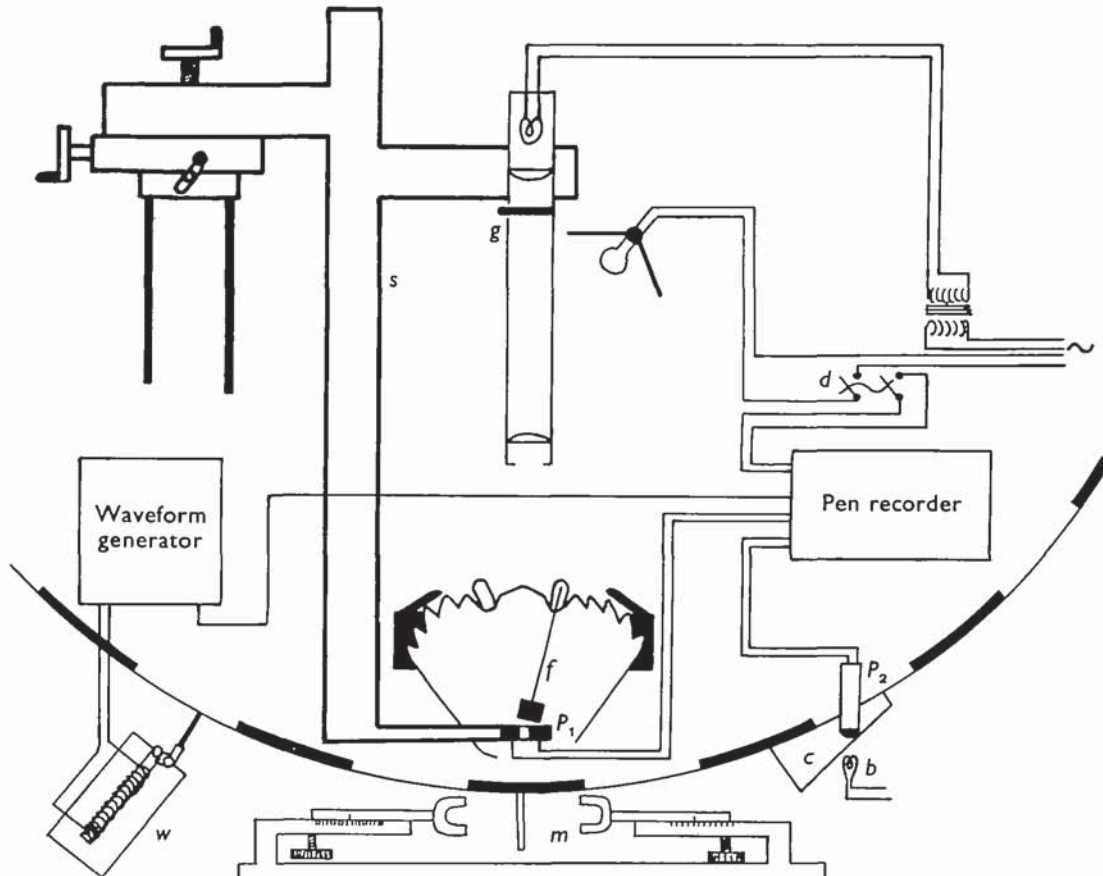


Fig. 1. Arrangement for making and recording the drum and eye movements. The crab is clamped relative to the drum with the eye at the centre. A flag, *f*, cuts a parallel beam of infra-red light which impinges on a pair of photocells, *p*₁. The photocells are clamped to the same adjustable support, *s*, as the lamp, which contains a filter of black glass, *g*. The drum movement can be caused by the modified pen-writer *w*, which is activated by an l.f. waveform generator, and may be limited by adjustable magnetic stops, *m*. Drum movement is recorded by the photocell *p*₂, which is shaded from a bulb *b* by an obliquely cut card *c*. The dark period is marked on the recorder with the double switch *d*.

filter of black glass in a lamp-house which allows no light to escape. The lamp and the photocell are mounted together on the same support so that after adjustment the beam is always focused evenly on the photocell, while, with the help of a calibrated lathe cross-bed, the photocell and lamp can be moved together relative to the flag and remain accurately calibrated. This arrangement measures eye movements to 0.01° over a range of $3-4^\circ$, depending on flag length, and adjustment of the zero

does not move the crab relative to the stimulus. Larger angles were measured by moving the zero by a definite amount, or by direct reading on a protractor.

Movements of the drum are controlled either by hand, by a linear pen-recorder actuator or by a 150-tooth gear engaged by a worm. The pen-recorder solenoid is the most useful because it is driven by a low-frequency waveform generator (Servomex type LF 51) which provides sine waves, and rising or falling ramp-functions, in single half-cycles or continuously down to one cycle in 2000 sec. To make controlled movements between two stationary positions in the dark with an accuracy of 0.01° , a steel peg on the drum is moved between two small magnets which are mounted on calibrated micro-manipulators, all heavily mounted on the same support. Drum movements are indicated by a photocell at the lower edge of the drum. A piece of card, attached to the outside of the drum with one straight edge inclined to the tangent, shades this photocell to various extents as the drum moves. Different cards or a series of notches or pinholes in the card allow drum movements to be recorded over large or small ranges, and the system is calibrated directly by measurement of the length of arc. The two sets of photocells, the switch which controls the general illumination by a 60 W. pearl bulb, and a line to indicate switching of the waveform generator, all feed into a pen recorder which has a response up to 90 cyc./sec.

Crabs can be treated in different ways according to the experimental requirements. There are four visual situations, as follows. (a) Both eyes free to move and see. (b) The flag on a seeing eye and other eye left free to move but painted over to eliminate possible binocular effects; this is the single-eye closed-loop condition. (c) As in (b) but with the flag on the blinded eye; this is the closed-loop situation with output through the brain. (d) One eye sees but is firmly fixed to the carapace and therefore fixed relative to the drum. This eye drives the other, to which the flag is attached and which is painted over to prevent visual feedback as a result of its movement. This is the open-loop condition with output through the brain.

RESULTS

With visual feedback

Actual movements in various types of responses are shown in Fig. 2. When the light is switched off the eye usually moves away from the position in which it had become stabilized over the previous period of time in the light (Fig. 2a). Drift can be in either direction. When the light is then restored the eye may first make a sudden jerk in either direction as a direct result of the sudden stimulus but thereafter it commonly returns over many seconds with a characteristic slow movement towards its former position (Fig. 2a). If the drum oscillates through a small angle for the whole duration of this experiment the eye response to the oscillation fails when the light goes out and the eye drifts away as before. When the light is restored the response to the oscillation starts at once and continues during the correcting movement of the eye back towards its former position. This is of fundamental importance in showing that vision is not impaired but continues with characteristic input-output relations during the correction movement.

On re-illumination the eye recovers from its drift in the dark by a movement towards its former position, but it does not recover the position entirely. The percentage

recovery varies with the nature of the visual field, with the angle turned through by the eye, and with the duration of the dark period, besides being subject to considerable variation between crabs and between similar occasions with the same crab. The effects of some of these variables will be treated in a subsequent paper. In general, for brightly illuminated striped drums of stripe repeat period 30° and duration of darkness up to a few minutes, the percentage recovery of a seeing eye which is free to move is about $60 \pm 20\%$. The new eye angle is measured at the new equilibrium, which is reached in 1–2 min.

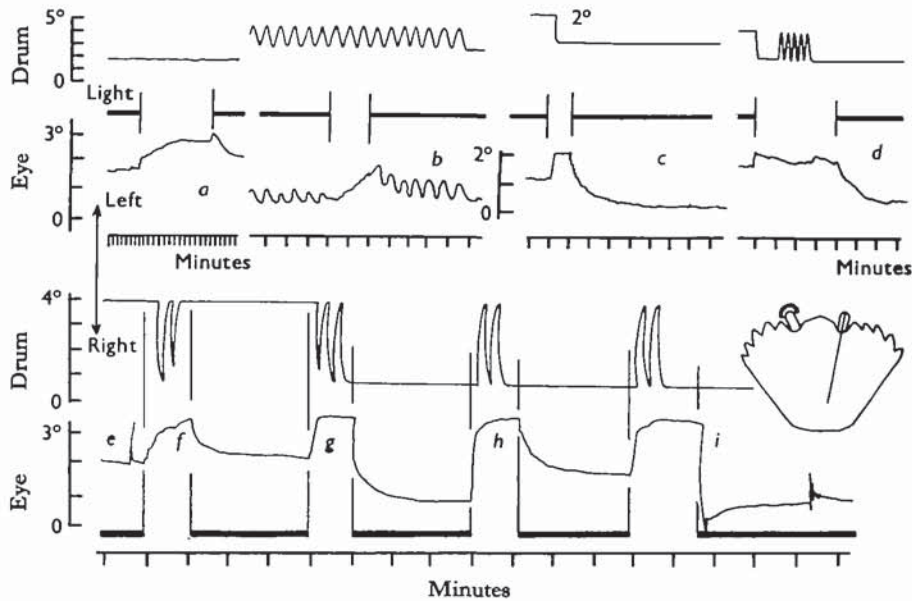


Fig. 2. Eyestalk movements (lower traces) in response to drum movements (upper traces) which are completed during a period of darkness. (a) Drift of the eye when the light is turned off without drum movement. (b) As before but with a small oscillation of the drum. The eye recovers from the drift which occurred in the dark and at the same time responds to the oscillation. (c) A drum movement is made in the dark; the eye drifts in the dark and then responds in the light to both drift-induced movement and true movement of the drum. (d) As before with a longer period of darkness and slower movement on re-illumination. The eye fails to respond to drum oscillations which were made in the dark. (e) Spontaneous eye flick with return to base-line. (f) Drift in the dark, failure to respond to oscillations in the dark, and recovery on re-illumination. (g, h) As before with or without drum movement. (i) The eye movement on re-illumination is in the opposite direction on account of a large retraction to the right at 'on'.

Movement of the drum through a small angle during the dark period also has the effect of moving the visual field relative to the eye, and the response to this movement sums with that due to the drift (Fig. 2c). By using short controlled periods of darkness of 5–15 sec. the drift can be reduced until it is negligible, especially when the eye is kept near to its preferred resting position in darkness. With longer periods of darkness the response takes longer to complete (Fig. 2d). Whether the animal can see the drum movements in the dark is readily tested by slowly oscillating the drum during the dark period. Typical subsequent responses are shown in Fig. 2f–i. The last of these, 2i, is notable because on re-illumination the eye made a sudden flick (probably

a retraction reflex to the unexpected stimulus) which carried it beyond the former position relative to the drum in the light so that it now made the recovery movement from the direction opposite to that which would have been expected from the position which it occupied during the dark period. This, and many similar observations, confirm that the eye is visually and not proprioceptively controlled. Small flicking movements of the eye are normally followed by recovery to, or almost to, the former position (Fig. 2e). From the above findings it is clear that the recovery movement from a flick could be induced by memory of the former eye position as well as by the assumption of a flow of motor impulses which were temporarily prevented or inhibited during the flick.

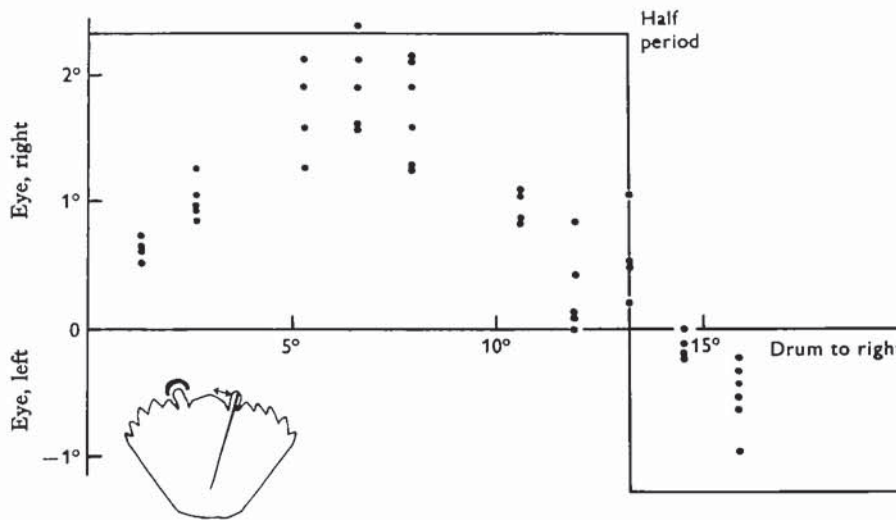


Fig. 3. Results of the memory experiment upon one particular crab which seemed to give no emphasis to edges although the seeing eye was free to move in tremor.

Eye movements for various drum movements are plotted for a freely moving, seeing eye in Fig. 3. For equally spaced black and white stripes the size and even the sign of the response depend on the relation between the drum movement and the stripe width. Qualitatively the explanation of the fall in the response at drum angles greater than $\frac{1}{2}$ stripe period and the negative response at drum angles of $\frac{1}{2}$ -1 stripe period is as follows. Consider the stimulus presentations at different drum movements as illustrated in Fig. 4. For no movement in the dark (4a) the situation on re-illumination (second line) is the same as the initial situation. For a shift of $\frac{1}{8}$ stripe period (4b) and $\frac{1}{4}$ stripe period (4c) the apparent movement is greater for the greater drum angle. At $\frac{1}{2}$ stripe period, as in 4e, there is no apparent *direction* of movement because to the left is as likely as to the right. Experimentally it is found that this situation gives zero responses and not 50% full responses in each of the two directions, as might have possibly happened. Knowing this experimental result, it is not surprising that a movement of $\frac{3}{8}$ stripe period, as in 4d, elicits a response which is less than that at $\frac{1}{4}$ stripe period and is in fact about intermediate between the responses at $\frac{1}{4}$ and $\frac{1}{2}$ stripe period. For a movement of $\frac{5}{8}$ stripe period (4f) the situation *to the crab* is as in 4d with apparent movement of $\frac{3}{8}$ stripe period to the left. For increasing drum

angles between $\frac{1}{4}$ and $\frac{3}{4}$ of stripe period, the responses progress from the quadrant ($< \frac{1}{2}$, eye right) through zero (at $\frac{1}{2}$, no response) to the opposite quadrant ($> \frac{1}{2}$, eye left) as in Fig. 3. For drum movements to the right in the interval $\frac{1}{2}$ -1 stripe period the response is to the left, falling to zero at a movement of exactly 1 period, which is indistinguishable from no movement. For any drum angle the movement inferred by the crab from its memory of the first position is therefore an approximately sinusoidal response varying from a positive to an equal negative value with periodicity equal to the stripe period. As will appear in the succeeding paper, the situation can be more complicated than this because eye tremor may accentuate edges relative to areas.



Fig. 4. The stimulus situations (*a-f*) for drum movements of 0, $\frac{1}{8}$, $\frac{1}{4}$, $\frac{3}{8}$, $\frac{1}{2}$ and $\frac{5}{8}$ of stripe period. For different reasons no movement is apparent in *a* or *e*, and the movement in *f* appears to the human eye to have been to the left, i.e. $-\frac{3}{8}$. As will be shown in the succeeding paper the actual stimulus situation is more complicated than this because edges can be accentuated relative to areas.

The amplitude of the eye movement varies, as mentioned, with conditions which have yet to be explored. In the present arrangement, with black stripes of repeat period about 30° painted in black on shiny hard white card, illuminated by a 60 W bulb about a metre distant, the maximum eye movement is about 70% of the drum movement when the duration of the dark period is only a few seconds. The most important factors which affect this, apart from the differences between crabs, are contrasting objects which remain stationary in the visual field, and the duration of the dark period.

Some contrasting objects which are stationary to the crab in this experimental arrangement are not important. Only horizontal eye-movements are recorded and therefore the top edge of the drum is neglected as it makes no relative movement across the eye during the response. For this reason the light which provides the general illumination is placed centrally over the seeing eye. The drum edge and this light in fact help to stabilize the eye against vertical drift. The recording photocell and the flag are behind the eye but the crab has a wide field of view and can see almost directly behind. Altogether the only serious stationary objects relative to the crab's

eye is its own chela (if in sight), its antennal flagellum (if not cut off), its carapace edge and the photocell support (if not well placed). There is, however, no reason to suppose that responses of freely moving eyes in memory experiments will ever be 100% of the drum movements, because when eyes follow the slow movements of self-luminous

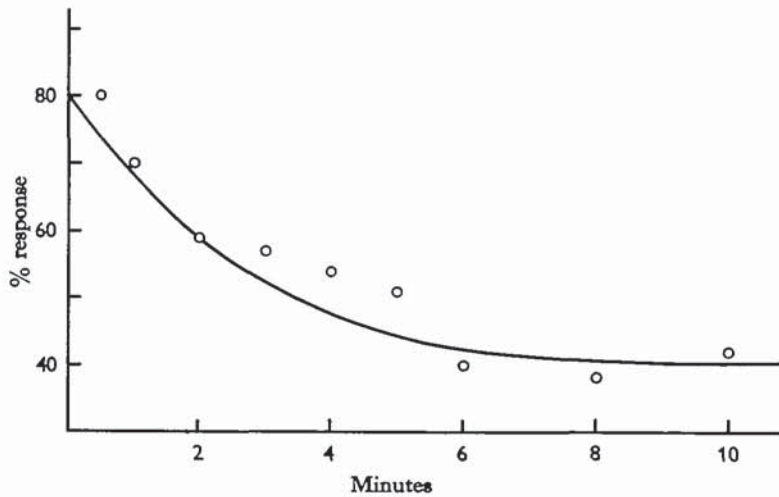


Fig. 5. Eye movement as a percentage of the drum movement after different periods of darkness, during which time the drum is moved through any angle up to 5°. For comparison, the continuous curve shows the exponential decay from 80 to 40% with a time-constant of 150 sec. (from Horridge & Shephard, 1965).

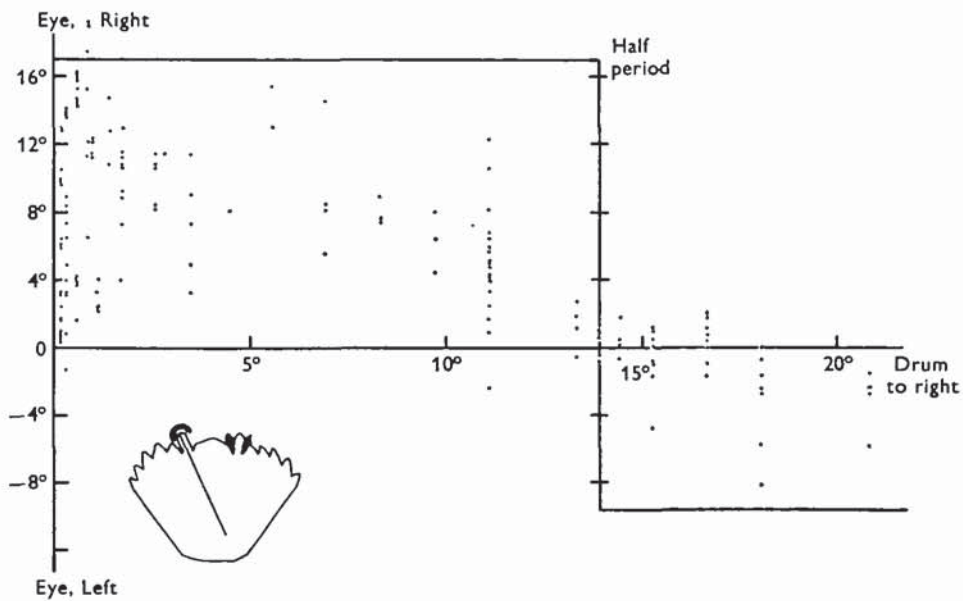


Fig. 6. Observations upon one crab showing eye movements in response to drum movements made in a dark period of 10 sec. The seeing eye was clamped so that there was no tremor of the eye relative to the drum in either the old or the new position. Under open-loop conditions the response at small drum angles is larger than the stimulus.

objects in complete darkness the eye movements never reach the stimulus movement under closed-loop conditions. In fact the velocity gain is never infinite.

Increasing the duration of the dark period affects the response in two ways: the percentage following at equilibrium is reduced and the period for completion of the response is lengthened. In addition, drift during the longer dark period causes an increased variability in the results. The average percentage following falls off with duration of dark period approximately exponentially (Fig. 5), but results are uncertain for periods of more than 10 min. However, it is remarkable that the crab, with one

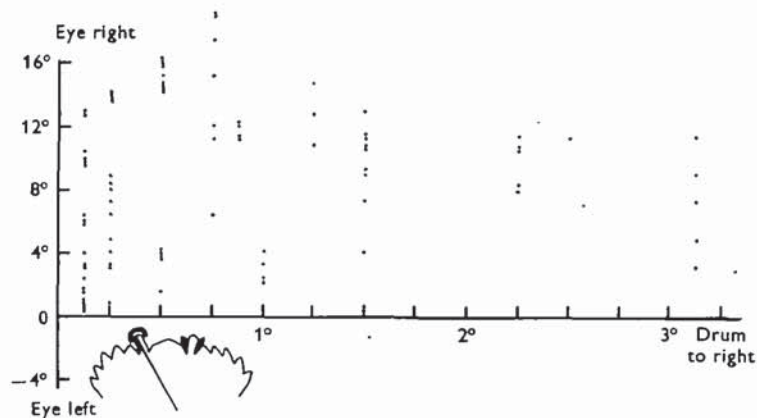


Fig. 7. Detail of the left side of Fig. 6, showing eye movements for small drum movements with a clamped eye driving a blind eye. There was therefore no eye tremor and no visual control of the movement. The period in the dark was 10 sec.

eye, shows a directional response to a movement of the drum by 0.5° after a dark period of 2 min., and to a movement of 1° for up to 15 min. Continuous movements at the same overall speed would be at 0.004 and $0.0011^\circ/\text{sec.}$, which correspond reasonably well with the lower limit of effective slip speeds in the crab. With a memory mechanism of this type the slowest movements need never be actually seen in progress, and, considering the eye tremor, it is now doubtful if their instantaneous velocities across the eye are ever important.

Removal of visual feedback

The memory experiment can be repeated with crabs having one eye seeing but fixed while the response is recorded from the other eye, which is painted over. The seeing eye makes no movement and the responding eye sees no consequence of its own movement. With this arrangement the eye angles are larger than the drum angles (Fig. 6). This reflects the situation in the perception of movement, when the speed of the eye is several times the relative speed of the stimulus across the eye (Horridge & Sandeman, 1964). The results do not show a symmetrical rise and fall with increasing angle; instead, for small angles in the region of 1° of stimulus the responses are surprisingly large, as shown in the enlarged detail for the first 3° of drum movement (Fig. 7). For this data, all from one crab, the ratio of the average eye-movement to the drum movement falls from 50 at drum movements of 0.125° to 30 at 0.25° and 0.5° to 12–20 in the region of 1° . Average figures are not justified on

account of the scatter and the uncertainty in weighting the good performances. These ratios show, qualitatively, that the stationary eye conveys to the brain a message which represents a much larger displacement than that which actually occurs across the stationary retina. Experimentally it is difficult to avoid producing a nystagmus in the moving eye unless one can coax the crab to work from one side of its full range of eye movement to the other. Starting in the centre of the range of the eye movement, a response of 15° includes one fast phase, so bringing the eye back near to the middle of its range. As much as possible this was avoided. Incidentally, since there is no relative movement of the stimulus during these movements of a blinded eye, and the nystagmus can be arranged to come at any time in the response, the onset of the fast phase presumably cannot be controlled by the visual input.

THEORETICAL TREATMENT

The eye movement is an indication of an inference of drum movement. After a drum movement of 1° in a dark period of 15 sec. performed in front of a clamped eye, the brain excites the muscles to make a response up to 50 times as great as the drum movement. However, the painted eye does not go on moving indefinitely in a futile effort to correct the displacement of the image on the fixed eye. There are two possible types of explanation for this finding. (a) The two stationary drum positions are correlated by a mechanism which infers movement exactly as in movement perception. This in turn is amplified as for a signal of the equivalent low velocity, and passed to the brain, to emerge as a change in frequency of motor impulses to both eyes, only observable in the movement of the blind eye. (b) The old and the new drum positions are projected to a reference grid which preserves them spatially and simultaneously, Mismatch in this grid provides an eye movement in the direction of the best correlation in this mismatch until the projection of the first drum position fades or until the eye is restored to its former position. These two possibilities are not exclusive, but may participate side by side, or the second may provide the input for the first. Finally, other types of explanation may not have been thought of. However, the suggestion that the crab compares the new position with a spatially remembered version of the old position is nothing more than a statement of the experimental finding in other words, by suggesting that within the animal there are hypothetical constructs which correspond to the experimental situation. The hypothesis of a spatially arranged memory system might be accepted for a crab only as a last resort, when other mechanisms cannot be found to explain the experimental findings. One definite finding which is against the idea that the eye is driven towards its old position as long as the mismatch persists is that in the open-loop situation the movement by the blinded eye is completed in less than a minute (for a 10 sec. dark period) whereas the memory, and therefore the mismatch, persists for many minutes, at least in the dark.

The theory that the drum shift is converted to movement is supported by several observations of a varied nature to be described in the succeeding papers. It is evident that a mechanism in the optic lobe, with long time-constants, is able to retain some kind of pattern of excitation. Let us suppose that this is peripheral to the one-way movement fibres, which are excited when the drum is re-illuminated. The optic tract would then carry a sequence of impulses which falsely signal that *movement is*

occurring on re-illumination. An angular velocity would be signalled briefly as some measure of impulse number or frequency in line-labelled pathways, each of which fires over its own range of stimulus velocities. This is the period during which the eye makes its response.

As found from open-loop and closed-loop measurements on responses to steady motion of the same type of drum (Horridge & Sandeman, 1964), the ratio of eye speed to the slip speed (the true stimulus speed across the eye) is greater than unity

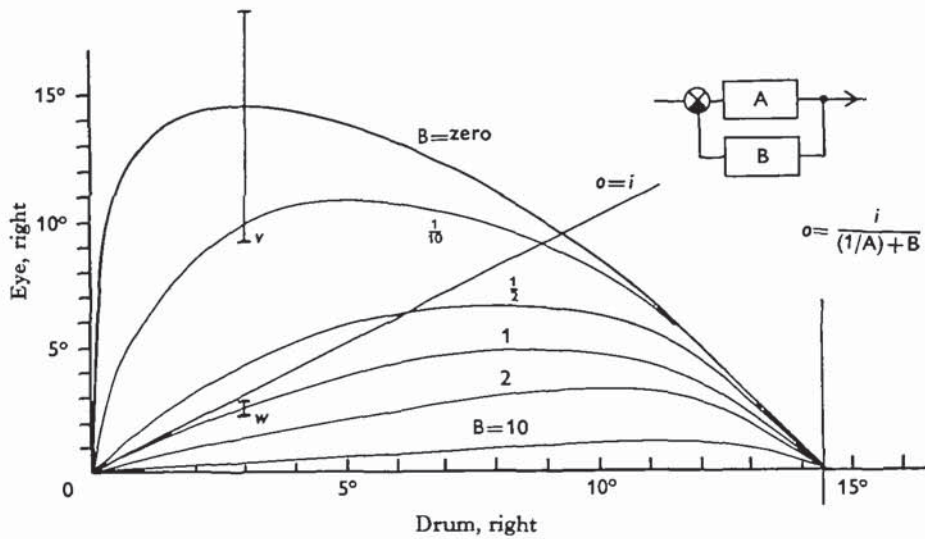


Fig. 8. Eye angles at the new equilibrium plotted against drum movements for various amounts of visual feedback. Eye angle equals drum angle at the straight line ($o = i$). The curve $B = \text{zero}$, for open-loop conditions, is drawn from representative experimental data from crabs with one eye fixed and the other eye blind. The other curves are calculated from this by insertion of various values of B into the equation $o = i / \{(1/A) + B\}$, where the symbols have the meanings shown in the inset. Experimental closed-loop conditions agree best with the curve for $B = 1$. The range of variability shown by v in the open-loop curves gives on calculation the range shown by w on the closed-loop curve.

in the range $0.1-0.005^\circ/\text{sec}$. In the closed-loop memory situation the crab behaves as if this forward gain remains as the same function of the slip speed, while a visual feedback loop of unity gain is added.

Now let us transpose from velocities to angles moved in the memory experiment and fit together the open-loop and closed-loop results in the same way. In Fig. 8 the ratio of eye angle (o) to drum angle (i) for any particular value of drum angle is A , called the forward gain. In the closed-loop situation, with seeing eye free to move, there is negative feedback, of gain B , because in its response the eye sweeps across the stationary drum. An average curve from open-loop experiments is drawn in slightly thicker line ($B = \text{zero}$). For small drum angles the large values of A are obvious when compared with the straight line when $o = i$. The other curves are calculated by putting various values of B into the equation $o = i / \{(1/A) + B\}$ for each observed value of A at each drum angle. As B increases the response is reduced, and a curve similar to the experimental one for closed-loop conditions is found when B is about unity. With $B < 1$ the closed-loop responses are larger than drum angles, which

never happens; on the other hand, with $B > 1$ the curve is skewed towards the right, whereas the experimental closed-loop curve is nearly symmetrical, though only superficially resembling a sine wave. In addition, the calculated magnitudes of eye angle fall close to the experimental values when $B = 1$, and are too small when $B = 2$. If this theoretical treatment is a fair representation it shows that the angle which the eye moves across the stationary drum in a memory experiment is neither magnified nor reduced by the system which reduces the response when the loop is closed.

The variability of the response to small drum angles in the open-loop state can now be seen as completely compatible with the small variability when the visual

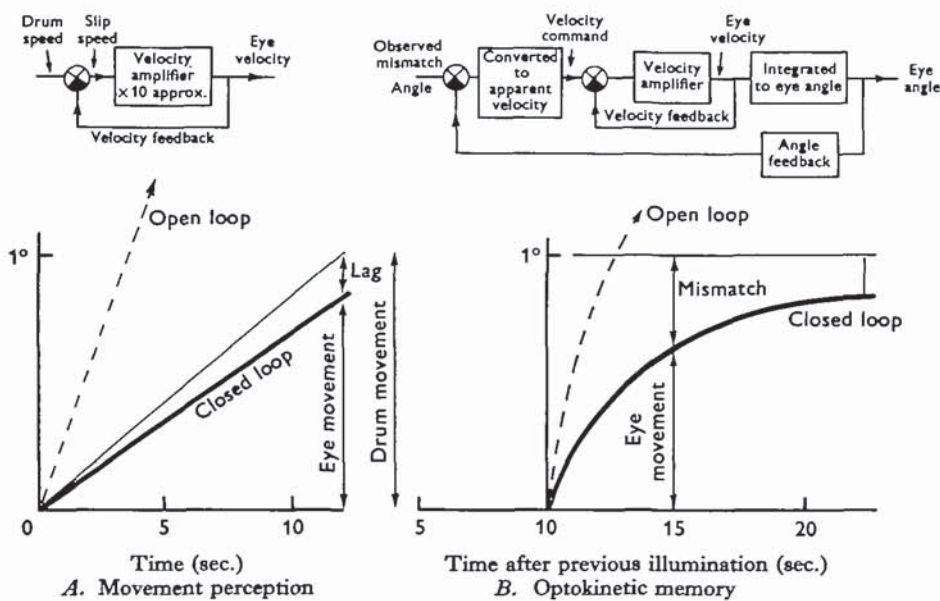


Fig. 9. The optokinetic response to movement (left) compared to optokinetic memory (right). On the left the eye movement lags behind the drum movement by an amount which measures the forward gain. On the right the movement of the eye has the effect of reducing the mismatch in the memory experiment. In the block diagram for the memory experiment the velocity amplifier from the left has been incorporated. An apparent memory of position is therefore explained by the mechanism for perception of movement, rather than the reverse.

loop is closed. When the gain A is large, say > 5 , a large change in gain makes almost no difference to the closed-loop response. In Fig. 8 the range shown by v on the open-loop curve gives, on calculation, the range shown by w on the closed-loop curve. A feature of this system is that the forward gains are surprisingly high for input angles which are near the interommatidial angle.

The two optokinetic systems, for movement perception and for the memory experiment, are shown side by side in Fig. 9, in which the system for responses to movement is incorporated into that for memory, not vice versa.

Correlation by the crab of the new drum position with its memory of the former position evidently takes place simultaneously both to the left and to the right within each eye. This inference follows from the observation that the response to a movement

of $\frac{3}{8}$ stripe period (Fig. 4*d*) is less than that to $\frac{1}{2}$ stripe period ($4e$) and that to $\frac{1}{2}$ period is near zero rather than being a large movement in one direction or the other. The responses agree with the supposition that the crab takes the difference between the leftwards and rightwards correlations. A well-known model for the perception of movement (Reichardt, 1961) contains this principle also, but for the optokinetic memory it is not possible without further information to decide how many periods of stripes take part, i.e. how many ommatidial fields contribute to the correlation for each point.

DISCUSSION

The results of these experiments would be expected if the crab had a central representation of a stationary visual world. Whether its significance lies here or not, the optokinetic memory is revealed as one mechanism which stabilizes the freely moving eyestalk despite deviations such as tremor, eye flicks and protective retraction.

Instead of interpreting the response to very slow movements in terms of a comparison between two positions of the objects in the visual field, which are suddenly seen as having moved, the analysis in this paper has tended to justify the opposite approach. The system for movement perception is accepted as a mechanism which correlates ommatidia which are stimulated at one time, before the dark period, with their neighbouring ommatidia which are stimulated after the dark period. This correlation mechanism lies within the system which is here called the velocity amplifier, with forward gain A . To interpret the memory experiments, the system for velocity detection has been incorporated and extended, as in Fig. 9*B*. The comparison of a mismatch between two positions is still, however, an essential element in the perception of movement, although it does not appear explicitly in the system for the control of the responses.

SUMMARY

1. A crab is held at the centre of an illuminated stationary striped drum or any visual field with strong contrasts. After a time all lights are turned off and the drum is moved in the dark. The light is restored when the drum is stationary in its new position. The animal responds by a movement of the eyes.
2. Stimuli of 0.5° over a dark period of 2 min. or 1° over 15 min. give a response. The response depends on the angle of the drum movement, and is slower in performance and less in total amount for longer periods of darkness.
3. On re-illumination the movement of the eye relative to the stationary drum is such that the visual field moves across the eye in the opposite direction to the eye's movement, but nevertheless the perception of small drum oscillations is not impaired.
4. When the visual feedback loop is opened by clamping the seeing eye and painting over the moving one, eye movements can be greater than drum movements, as in movement perception. Comparison of calculated with experimental closed-loop conditions shows that in the memory experiment there is no attenuation or amplification in the visual feedback loop.
5. Perception of very slow movements and stabilization of eye position could, but do not necessarily, depend on this accurate but short-lived directional memory.

I am indebted to my students for lively discussions on the issues raised here, and to P. R. B. Shepherd for part of figure 2.

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