

ADAPTATION AND OTHER PHENOMENA IN THE  
OPTOKINETIC RESPONSE OF THE CRAB,  
*CARCINUS*

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(Received 21 September 1965)

During the course of the experiments which have contributed to the previous papers there appeared a number of new observations which did not fit readily into those topics. Although each is a qualitative new finding which seems at first sight to refer to only one aspect of the optokinetic response, taken together they shed further light on the type of system we are dealing with. All of these new observations could be quantified in detail, but it appears that a highly accurate set of measurements which are intended to measure the parameters of one simple system are out of place until a wide variety of qualitative experiments, with suitable controls, have narrowed down the choice of alternative models.

METHODS

The eye movements of the crab *Carcinus* have been recorded by the methods outlined in Fig. 1 of the first paper (Horridge, 1966*a*). Drum movements and eye movements are recorded directly with photocells. The single light, when used as stimulus, moves on an arm which is mounted on the solenoid of a pen-recorder. The drum of equally wide black and white stripes has a repeat period of 30°. Most of the observations reported here were made on the same preparations that have provided material for the previous papers but have been reserved for a later place in the argument.

RESULTS

*Adaptation*

When an oscillatory drum movement suddenly starts at a frequency which is lower than about 1/sec., the eye follows without a decline at successive oscillations so long as maximum angular velocities of about 2°/sec. are not exceeded, although the initial movement may not be typical when the movement has a sudden onset. At higher frequencies the difference between the response to the first and later oscillations is accentuated as in B and C of Fig. 1. This type of response is found whether or not the movement is suddenly switched on in the middle of a cycle. If, on the other hand, the oscillations slowly increase in amplitude during the course of a few cycles, one may never see the initial sharp response, as at (5) in Fig. 1 D. After numerous oscillations the response wanes, but even with a stimulus of amplitude 1° at 3/sec. (max. angular velocity 10°/sec.) a small response persists after hundreds of oscillations, at 1 in Fig. 1 D.

The question now arises whether a system for detection of slow movements remains unadapted after the response to fast oscillations has fallen to negligible proportions. This is related, in systems analysis, to the question of whether we are dealing with a single transmission line or to many in parallel and whether stimulation influences the time-constants. The topic is relevant to the electrophysiological finding that of the numerous movement-receptor axons of the crustacean optic tract, some respond to rapid movement, others to movement of intermediate velocity and others only to slow movement in the visual field (Waterman, Wiersma & Bush, 1964).

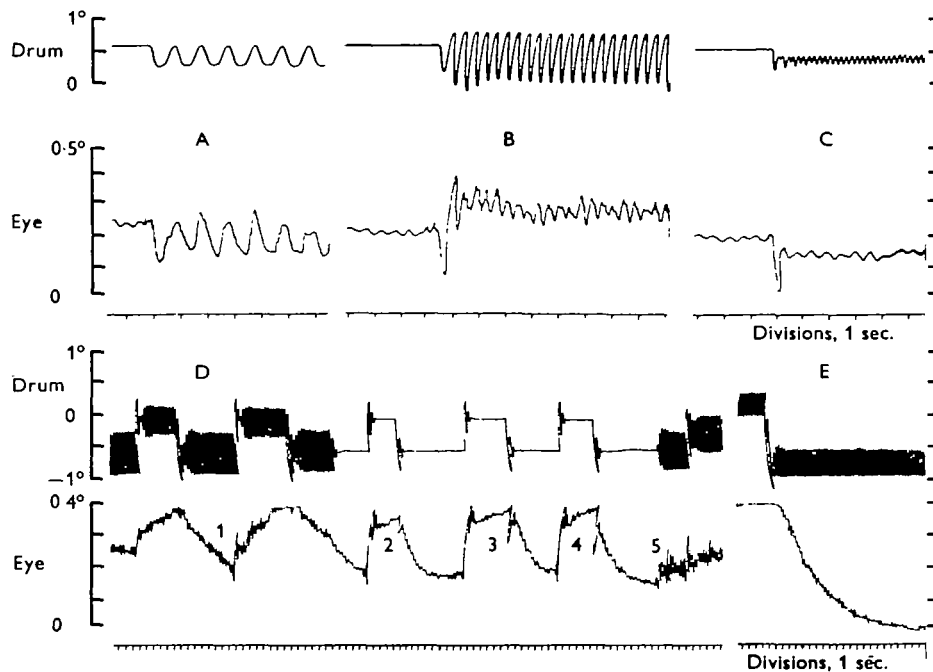


Fig. 1. Features related to adaptation. A, Drum oscillations at 1/sec. together with a net displacement, are followed at about 20% of the stimulus amplitude. B, At 2/sec. there is a large initial response lasting one cycle, followed by a small maintained oscillatory response. C, At 5/sec. there is a large initial response but nothing at the stimulus frequency. D, The animal has been stimulated by angular movements of  $0.5^\circ$  at 3/sec. for a long period until there is little response at this frequency. Steps of  $0.5^\circ$  lasting 7-8 sec. are now superimposed on this oscillation. The responses to the steps have slow rising and falling phases as at (1). The drum oscillation at 3/sec. is now stopped and the rising phase at once becomes steep. The falling phase also steepens but (in this crab) only progressively as at (2), (3) and (4). When the oscillation is restored, together with the step, the response to the latter is again slowed, as at (5). E, The same failure of the rapid phase for a  $1^\circ$  step.

The response to a step-function during a period of oscillations is quite different from the response to a step-function alone. The contrast is shown in Fig. 1 D. This particular crab was giving faster responses to a step in one direction than in the other. The drum could not be moved instantaneously and performed a damped oscillation, but this is a constant feature throughout the experiment, and in fact adds its own point of interest, in that the response to it progressively increases as the adaptation to the rapid oscillation wears off, as at (2), (3) and (4) in Fig. 1 D.

A step movement of the drum causes the same amplitude of response whether.

not accompanied by rapid oscillations, but with them present there is no initial fast phase. With a step-function superimposed on an oscillation the eye creeps towards its new equilibrium position. During this time the net movement of the drum is in the opposite direction to that of the eye. The situation resembles that in an optokinetic memory experiment when the subsequent recovery movement of the eye loses fast components as the previous period of darkness is lengthened, but comes to the same final equilibrium by a movement which is against the apparent movement of the surroundings. It is a testable prediction that the same rapid components are lost in each case.

With Fig. 1D in view it is possible to interpret the difference in the response to the step in the two directions in the middle section of the record by suggesting that only the fast component is weaker in the downward direction. In fact at (3) and (4) in Fig. 1D the downward fast component is beginning to return.

In adaptation to an oscillatory stimulus each part of the eye acts independently. This is most readily shown by covering a part of the eye with a temporary blinker, then allowing the response to wane with repetition. On removing the blinker while the stimulus continues the percentage following suddenly increases but then wanes again to a new level which is greater than before. Similar effects can be obtained from wide-field interneurons of the insect optic lobe (Horridge, Scholes, Shaw & Tunstall, 1965). This result suggests that the adaptation occurs at the input to the movement receptor units in the crab.

#### *Change in gain*

Two measures of responsiveness have been used in these papers. One measure, the velocity gain, was defined as the ratio of the response, the eye velocity, to the true stimulus, the slip speed (Horridge & Sandeman, 1964). This is applicable to all later experiments, and needs to be modified in only two ways: (a) it is an average figure after tremor and eye flicks are smoothed out, and (b) the response does not coincide with, but in part follows, the period over which the stimulus acts. The second measure of responsiveness is the percentage following, defined as the amplitude of the peak response expressed as a percentage of the stimulus amplitude. This is more useful in memory experiments and for oscillatory stimuli.

Factors which modify the responsiveness have already been encountered. The velocity gain varies with the velocity of the stimulus, which is inconvenient because analysis cannot be made linear by use of small amplitudes. At velocities greater than about  $1^\circ/\text{sec}$ . the velocity gain falls off by adaptation. In optokinetic memory, and in apparent movement, the percentage following towards a single light falls off rapidly with stimulus amplitude for angular movements of more than about  $1^\circ$  (Horridge, 1966c). The percentage following to small oscillatory movements at  $1^\circ/\text{sec}$ . is independent of simultaneous other movements at a tenth of this speed, as illustrated in Fig. 1D.

Changes in responsiveness can also arise internally, and when they increase spontaneously they show that not all the reduction in a previously adapted response represents a loss of the stimulus such as a loss by sensory adaptation. During a period of leg waving the gain commonly increases violently as in Fig. 2. This shows that a part of the loss of the response can be compared with the closing of a gate which is

at times reopened. A similar change is found during 'arousal', to be treated below (Fig. 7).

A steady decline in gain during the course of a response is a constant feature when the stimulus is a continuous large movement in the vertical plane.

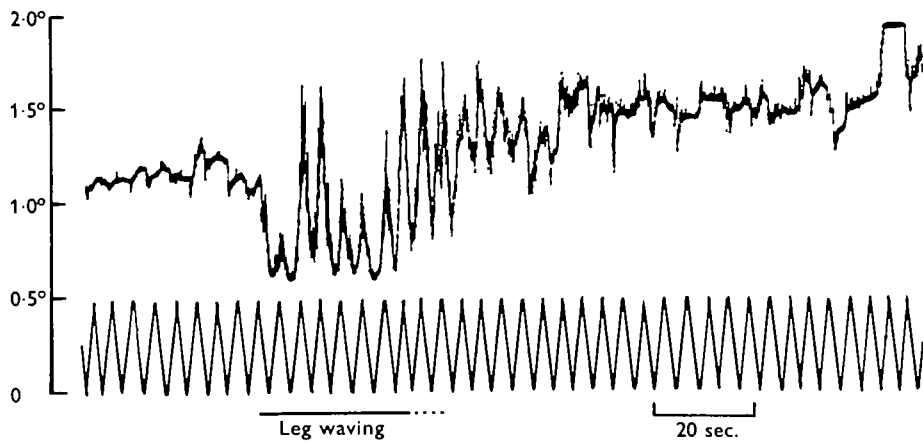


Fig. 2. Change in gain as correlated with leg waving in *Carcinus*. A continuous drum oscillation of triangular wave form, of amplitude  $0.5^\circ$  and half-period 2 sec., was present all the time. Waving of the legs occurred during the period shown by the horizontal line. Except at moments of reversal the drum was moving with a constant velocity of  $0.25^\circ/\text{sec}$ . This is from an open-loop preparation in which responses exceed the stimulus amplitude.

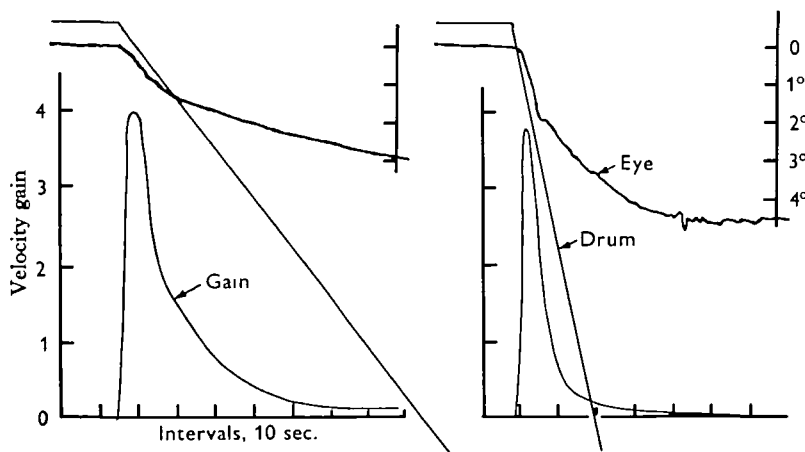


Fig. 3. Vertical responses to rotation of a drum which has a horizontal axis along the line between the crab's two eyes. Movements are upwards in front of the crab. The response of the eye is at first quite large, as for horizontal movements, but rapidly falls off to  $4^\circ$ .

#### *Eye movements in the vertical plane*

In a black/white striped drum illuminated with a 60 W. bulb, the eye shows vertical spontaneous movements as follows: (a) a background high-frequency tremor of  $0.05^\circ$  up to 5/sec.; (b) rapid flicks of up to  $0.2^\circ$  with rapid return to almost the same base line; (c) slow oscillations down to a rate of  $0.1-1^\circ$  in 100 sec., much increased in the dark.

This is similar to the situation in the horizontal plane and in fact these small movements are all two-dimensional, and they can be so plotted.

The vertical response of the eye to drum rotations about a horizontal axis shows that the eye is fully sensitive to movement in this plane. With a brightly illuminated striped drum a velocity gain of 10 can be achieved in the range  $0.01-0.25^\circ/\text{sec.}$ , especially with vertical movements which are *rising* in front of the animal. However, this response is maintained only for a few degrees and the velocity gain rapidly declines until the eye eventually comes to rest, Fig. 3. If at this point movement is stopped the eye drifts back at a rate of  $0.1-1.0^\circ/\text{min.}$  in the light (and much faster in the dark). As in the horizontal plane, there is no exact position of rest, but the resting position is controlled in this plane to an accuracy of  $1-2^\circ$  by the statocysts (Horridge, 1966*d*). If the movement of the drum is continued about its horizontal axis, the eye never makes a nystagmus movement (or fast recovery phase) in either direction, but the gain drops until it comes to rest, as described above, and there it stays. The fall in gain brings the slip speed of the stimulus past the eye to the value of the drum speed. In the horizontal plane the same effect occurs only when the drum is moving faster than about  $5^\circ/\text{sec.}$  in healthy *Carcinus*. Normally, continued slow drum movement on a vertical axis causes the regularly repeated slow forward and fast return phases of optokinetic nystagmus.

After a flick in the vertical plane the eye returns with a characteristic smooth curve (with a time-constant of 1-5 sec.) almost to the point from which the flick occurred. Despite the statocyst control, exact positional control in the vertical plane is lost in the dark and it seems reasonable to assume that, in the vertical as in the horizontal plane, there is no proprioceptive control of the eye position. Therefore the ability of the eye to return after a flick is probably related to the visual memory, which is certainly excellent in this plane. To test the latter, the light was turned out, the drum was moved on its horizontal axis through  $1^\circ$  during a dark period of 10 sec. On re-illumination the eye followed by 50-85% of the change in angle.

So far as they have been investigated the eye responses in a vertical direction do not differ from those in the horizontal plane except for the lack of the fast phase of nystagmus and the lower gains in the former.

#### *Drift and eye tremor*

In a previous paper, three types of eye movement were briefly described (Horridge & Sandeman, 1964). (a) Tremor has an amplitude of about  $0.05^\circ$  and a frequency in the range 2-5/sec. (b) Irregular wandering movements, as mentioned in that paper, are now seen as part of the frequency spectrum ranging from tremor to low frequency drift. (c) Deliberate scanning movements which can be elicited when contrasting objects are suddenly presented to the crab. (d) A new category, saccades or flicks (see below), are defined as rapid spontaneous jumps of  $0.05-0.2^\circ$  with a slow return phase.

The eye is stabilized by contrasting objects in the visual field. A figure previously published (Horridge & Sandeman, 1964, fig. 18) shows a reduction in the medium-frequency components of the eye movement when more contrast is introduced into the visual field. A more vivid example can be produced in experiments where the stimulus is a single small light. One tiny light (producing an illumination at the eye down to  $0.0003$  lux) equivalent to 1 candle at 57 m. is adequate to stabilize the eye

position. An eye flick followed by recovery back to the same resting position is shown in Fig. 4A. In the dark, as in Fig. 4B, there is more low-frequency oscillation and it is difficult to keep the trace on the paper. The change that occurs when the light goes out, as in Fig. 4, is primarily the introduction of a drift at about  $0.01^\circ/\text{sec}$ . (in this instance) together with more obvious oscillations with periods of 1–10 sec. A spectral analysis of the frequency components is required, but it is possible to point out at

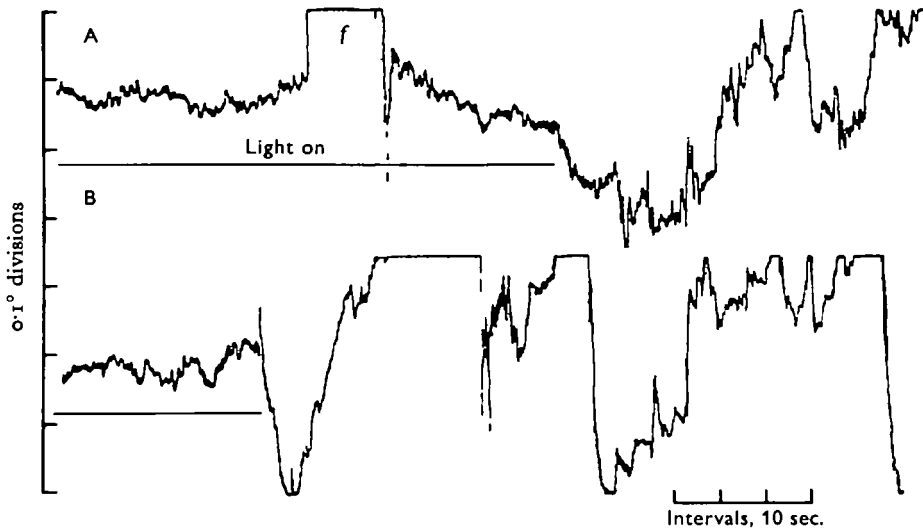


Fig. 4. Vertical movements of the eye; upward movement of the eye is downward on the trace. A, Steady position of the eye, with tremor, when seeing a single light of  $0.05$  lux. There is an eye flick at  $f$ , followed by a return to the former position. The light is on for the period shown by the horizontal straight line. B, As in A, with greater drift at about  $0.01^\circ/\text{sec}$ ., and increased tremor.

this stage that the highest frequency of tremor is little influenced by contrasts in the visual field (although it is modified by tensions in the eyestalk muscles). It is the low-frequency components which change. The relative movement which is caused by the high-frequency tremor is below the amplitude threshold and above the velocity threshold of the optomotor response.

The importance of a small relative movement in the enhancement of edges as against areas has already been demonstrated by a modification of the optokinetic memory experiment (Horridge, 1966*b*). The technique used there, of artificially applying a controlled tremor by oscillating an object in front of a clamped eye, can be adapted in the following way to show that a stationary contrasting object is seen less well than a slightly moving one, as follows.

A crab with both eyes seeing has the left eye clamped to its carapace while the movements of the right eye are recorded. A set of stationary stripes stand before the left eye. The right eye will now follow the movements of a separate set of stripes in its field of view with a velocity gain which is not much less than that of the normal optokinetic response, Fig. 5B. This it would not do if the left eye had been free to move in front of the stationary stripes, because the left eye would then stabilize itself by the stripes and inhibit any movement of the right eye. When clamped, the left

eye is not so effective in inhibiting the response of the right eye. The topic has been previously discussed as relevant to the perception of stationary objects and the inference has already been made that small movements of a free eye make possible the perception of stationary objects (Horridge & Sandeman, 1964). The additional point, illustrated in Fig. 5C, is that when the previously stationary stripes are made to oscillate a little before the clamped left eye they at once become effective in suppressing the movement of the right eye. For stripe oscillations to be effective the

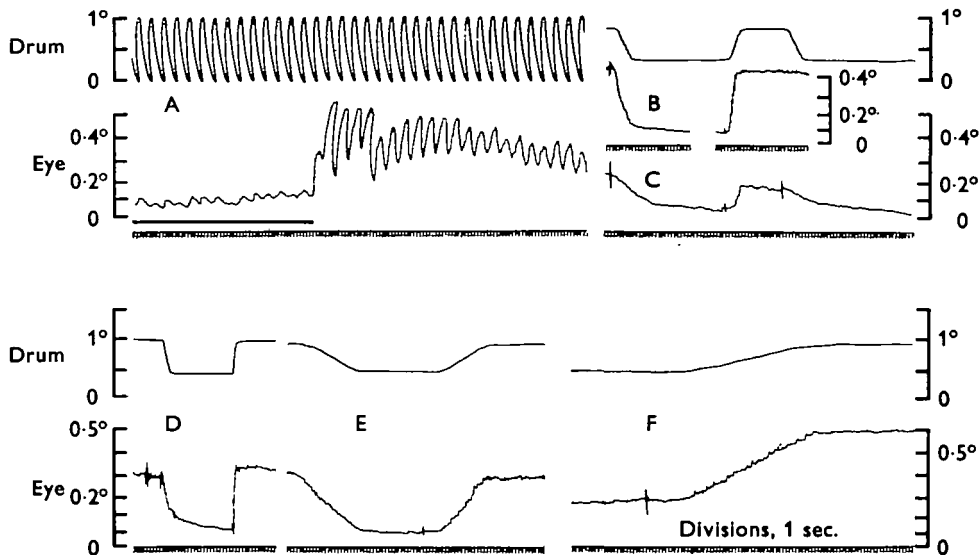


Fig. 5. Crab eye responses, with movement of the striped drum on the upper line and simultaneous movements of the eye on the lower trace. A, Increase in the response, with adaptation, following the removal of a blinker from part of the eye, showing that adaptation does not spread to the whole eye. B, Response of a right seeing eye to a ramp of  $\frac{1}{3}$  in 5 sec.: (i) with stationary stripes in front of the left clamped eye, (ii) as in (i) but the stripes are now oscillated through  $1^\circ$  at  $\frac{1}{3}$  sec. The lower set of traces show tremor which develops during ramps of  $0.5^\circ$  in 2 sec. (C),  $0.5^\circ$  in 20 sec. (D),  $0.5^\circ$  in 50 sec. (E).

amplitude should be from  $0.2^\circ$  to  $2^\circ$  and the period from 1 to 10 sec. The success of the experiment, and the required values, vary greatly from crab to crab, just as with the accentuation of edges by eye tremor (Horridge, 1966*b*). The conclusion is that crabs really differ in the effectiveness of imposed tremor.

Tremor can be increased by eye movement, as seen in Fig. 5F, where, as the eye movement follows the ramp-function, there are irregular small jumps. This phenomenon has several traceable causes, probably none of which is fundamental. The eye tends to move in small jumps, frequently with overshoot. The numerous muscles involved have not settled to a new equilibrium. During stimulation, but not at rest, there can be a conflict between the two eyes. With the exception of incipient movements, and overshoots which correct themselves by evoking a relative movement of the visual field in the opposite direction, there is as yet no evidence that small eye movements in the range defined as tremor are ever enhanced by stimulation. In the light they are cut down, presumably by optokinetic stabilization, caused by increase in the forward gain.

*Saccadic flicks*

Among the details of the eye movements are small excursions of recognizable appearance which often are characteristic for the individual. They are quite distinct from the irregular eye movements which accompany all leg waving or attempted locomotion. The best examples have turned up in the locust, Figs. 6 and 7, where

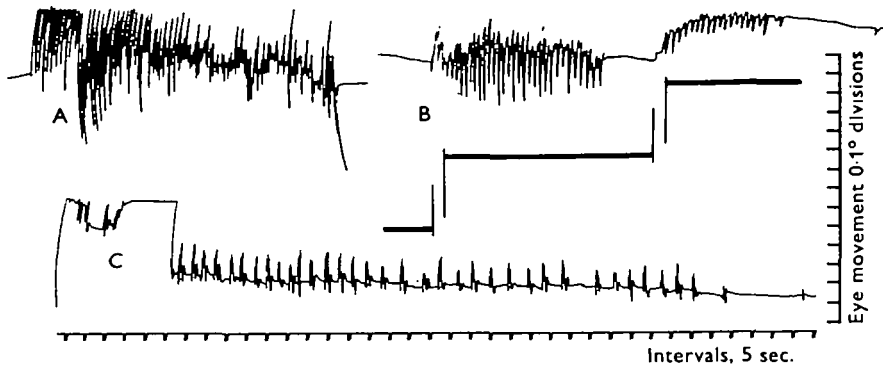


Fig. 6. Spontaneous side-to-side head movements of a locust with prothorax rigidly held. A, Movements which occur during a period of antenna flicking. B, The animal was aroused by a drum movement of  $0.5^\circ$  in a dark period of 3 sec. There was no maintained head-turning response to this movement but regular head movements started. At the second similar stimulus the head moved through  $0.2^\circ$  and at the same time waved less strongly. C, Regularly repeated flicks after a large head movement.

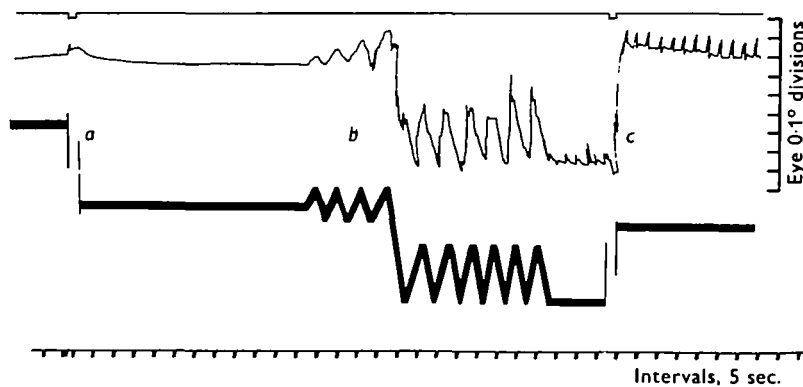


Fig. 7. Arousal by a visual stimulus. Head movements of the locust in response to the shift of a stationary drum by  $2.6^\circ$  during a dark period of 2 sec. At *a* the movement causes a response of only  $0.05^\circ$  in the appropriate direction. Then follow ten small manually operated oscillations of the drum at *b*. The animal now starts to flick its head rhythmically and continues to do so while at *c* it makes a response of  $0.65^\circ$  to the same drum movement as before.

they can be more regular than in *Carcinus*, Fig. 8. A movement in the visual field, or switching off the light as in a memory experiment, can set off a train of flicks, as in Fig. 6B and C. This is sometimes a sign that the animal is waking up and will thereafter co-operate in the experiment, as in Figs. 6B and 7. The act of 'arousal' is measured as no more than a change in the percentage following or velocity gain.



The flick and subsequent return to equilibrium are not features which necessarily depend on the closed visual feedback loop. They can also appear in open-loop systems, and during the course of a movement which is disengaged from the stimulus, as in



Fig. 8. Eye flicks in *Carcinus* during the course of a response to a slow movement of a single light as shown on the same scale. Note that recovery from flicks is in either direction.

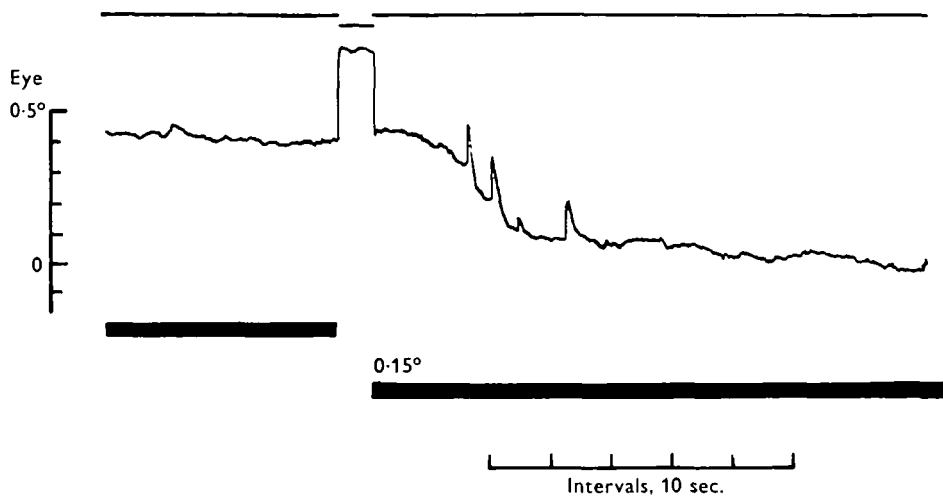


Fig. 9. Flicks of a blinded eye during the course of a movement in a memory experiment with a drum movement of  $0.15^\circ$  during a 5 sec. dark period. These movements cannot be visually controlled.

a memory experiment, Fig. 9. With visual feedback the optokinetic memory accounts for recovery, and percentage recoveries are very high, but it is not easy to understand why this should be so in the open-loop condition. One conclusion is that in these instances the flick is a predetermined movement which is imposed independently by a distinct neuron bearing an occasional burst of impulses, either centrally or peripherally.

#### DISCUSSION

This being the final of a short series on varied but related topics, I feel free to range over several aspects of the control of eye movements in Crustacea and to relate them to wider aspects of vision and movement.

On the input side it is most likely that movement-receptor interneurons of the optic tract are the pathway of the optokinetic responses, even in the optokinetic memory. This conclusion is embodied in Fig. 9 of the first paper (Horridge, 1966*a*), where the velocity amplifier inferred from optokinetic experiments is transposed

into the memory situation. We may now modify this by having two pathways, one for fast and one for slow movements, of which one can remain functional while the other is eliminated by adaptation. It is a testable hypothesis that classes of movement-receptor interneurons form these separable pathways, but it is also possible that the time constants of single system change during adaptation. The projection of retinal fibres on the lamina (Pedler & Goodland, 1965) in the fly fits in with the finding that in *Chlorophanus* movement is abstracted by adjacent or subadjacent ommatidia (Reichardt, 1961). The dependence of arthropod vision upon movement is also explained by the inference that movement is abstracted by the lamina. On this view, the long time constants required for optokinetic memory will be found in the lamina ganglionaris.

The acuity on the input side remains astounding. The structural units of the optic lamina, the first neuropile, are the optic cartridges which contain the first-order synapses (Hámori & Horridge, 1966). They are equal in number to the ommatidia and there is an interweaving of primary fibres between here and the retina. Therefore even in the first neuropile the spatial representation of ommatidia is poorer than the inter-ommatidial angle which is about  $2.0^\circ$  for *Carcinus*. The representation must be more smeared in more proximal neuropiles. Yet this mechanism is able to detect a stimulus angle of  $0.1^\circ$  in an isolated shift, and an angle of  $0.03^\circ$  in a steady movement, to amplify this signal, and to register a response in the form of a movement.

The former conclusion that the eye primarily sees movements, and sharpened contrasts with the help of its own eye movement, must be slightly modified. The crab sees stationary areas as contrasting areas (and remembers them while the light is out) though not necessarily so distinctly when eye movements are completely prevented.

Many of the experiments presented in this and the previous papers show that it is a great simplification to regard the optokinetic response as a system of movement perception (having one set of fixed time-constants) from which the output is taken directly as the response of the whole animal. The celebrated model for movement perception, worked out in detail by Reichardt (1961) and others, is still, however, a possible model of the input system into a unidirectional movement-receptor interneuron. It remains to be seen to what extent the outputs from numerous rather inaccurate movement-receptor neurons is smoothed in the brain.

The retention times for a visual stimulus show that time-constants for movement perception can be extraordinarily long. A similar retention cannot be separated from other experiments on the optomotor response. For example a beetle, *Chlorophanus*, in a Y-maze globe is stimulated more or less continuously but only has the opportunity to reveal its turning tendency each time that it arrives at a fork in its path. When an insect walks along a bend on a narrow constricting causeway and then along a straight stretch of path, it will thereafter tend to turn in the opposite direction when given a choice (Dingle, 1965). This reveals a memory of a previous motion, and the stimulus has been demonstrated as being in part visual, and therefore relevant to almost all optokinetic phenomena. By contrast, in the optokinetic memory experiments, we have the retention of a stationary position which is later shown to be a persistent cause of a movement response.

In conclusion, the functions of the stalked eye are numerous. Small eye movements in all planes are effective in modifying the visual input, as in the perception of edges, and possibly in depth perception. The eye is stabilized in the horizontal and vertical

planes by the optokinetic response, and evidence of a positional control by proprioceptors is still lacking. The statocyst responses stabilize the eye approximately with reference to the vertical, irrespective of body movements so long as these are small. All optokinetic responses to drums, or to lights in a dark room, are a by-product of the eye stabilization; it is only the much-less sensitive optomotor responses of the appendages which stabilize the body position in freely walking or swimming animals. The primary effect of the optokinetic response is in modifying the visual input, and in most of the above experiments it has been used only as an indicator of movement perception.

## SUMMARY

1. Adaptation to oscillatory stimuli is significant in the range 1–10/sec., for angular amplitudes of about 1°. The mechanism for perception of slow components remains unchanged when that to fast components is eliminated by adaptation.
2. Spontaneous leg movements are accompanied by a temporary increase in gain, showing a central control of the gain.
3. All eye movements are in two dimensions and components in the vertical plane appear similar to those in the horizontal plane, except that in the vertical plane the maximum range is over about 5° and there is no fast return phase.
4. The eye position is less stable in the dark. A single small light giving 0.0003 lux is sufficient to remove low-frequency components from the spontaneous eye movements.
5. An imposed tremor of amplitude 0.2–2.0° and period 1–10 sec. is sufficient to make stationary stripes, which would otherwise be ineffective, have an inhibitory effect on movements of the other eye.
6. A new form of arthropod eye movement, saccadic flicks, can be a sign of arousal and attention.
7. Optokinetic responses are a consequence of the visual stabilization of the eye.

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