J. Exp. Biol. (1966), 44, 255–261
With 5 *text-figures*
Printed in Great Britain

OPTOKINETIC MEMORY IN THE LOCUST

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(*Received* 21 *September* 1965)

Having established that a crab can retain a visual impression of the positions of contrasting stripes in its visual field for a period of many minutes in the dark with an accuracy of about $\frac{1}{10}^\circ$ over short periods, it became of immediate interest to know whether other arthropods can do the same. The same technique as in the previous papers (Horridge, 1966*a*) was therefore applied to the locust as a convenient large insect. The locust is especially appropriate in that we have information on the electrophysiology of the visual system (Horridge, Scholes, Shaw & Tunstall, 1965) and on the optomotor response to moving striped drums (Thorson, 1965). The question is of interest not only for comparative purposes but because for further analysis of some aspects of optokinetic memory an insect is more likely to be of value than a crab as an experimental animal.

A tendency to avoid change in the visual pattern recurs commonly in the behaviour of insects. The technique used in this paper provides one means of experimental analysis, and, as shown in the succeeding paper, the memory of the position of a single light shows that the ability is distributed over the eye.

METHODS

The same experimental arrangement as before was used, with the following modifications. A locust (*Locusta migratoria* bred from original stock from the A.L. Research Centre, London) was attached by modelling clay to a piece of wood so that its thorax, abdomen, legs and wings were firmly held, but the head projected over the end of the wood and was free to move on the neck in all directions. The flag for recording movements was attached with insect wax to the top of the head and projected back over the wings so that the recording photocell was out of sight of all but a few posterior ommatidia. The drum was moved by hand so that a steel pin at its rim travelled from one fixed magnet to the other during the dark period. Illumination of the drum was by a 60 W. pearl bulb at a distance of about 1 m.

RESULTS

Types of record. In a series of experiments with dozens of locusts there have been two main types of record, those without obvious saccadic or flicking movements of the head and those with them. Further, it has become clear that some animals which are normally without special head movements may develop them when aroused by provocative movements in the visual field. In Fig. 1 a locust without spontaneous head flicks is stimulated at A by a movement of the drum first one way, then the other. This is a typical method of testing whether animals are responsive to drum movements.

As the record shows, in this case a rather regular series of flicks soon appears, with a frequency of one in 3 or 4 sec. At B the light is turned out and the head fails to recover from the next flick until the light is restored. At C the drum is moved while the light is out, and the flick frequency falls as the head moves over a period of about 20 sec. to its new position. At D the head movement is in the opposite direction to the drum movement because the latter exceeds a half stripe period (Horridge, 1966*a*); the flicking continues during the course of the response. A new feature shown by this response,

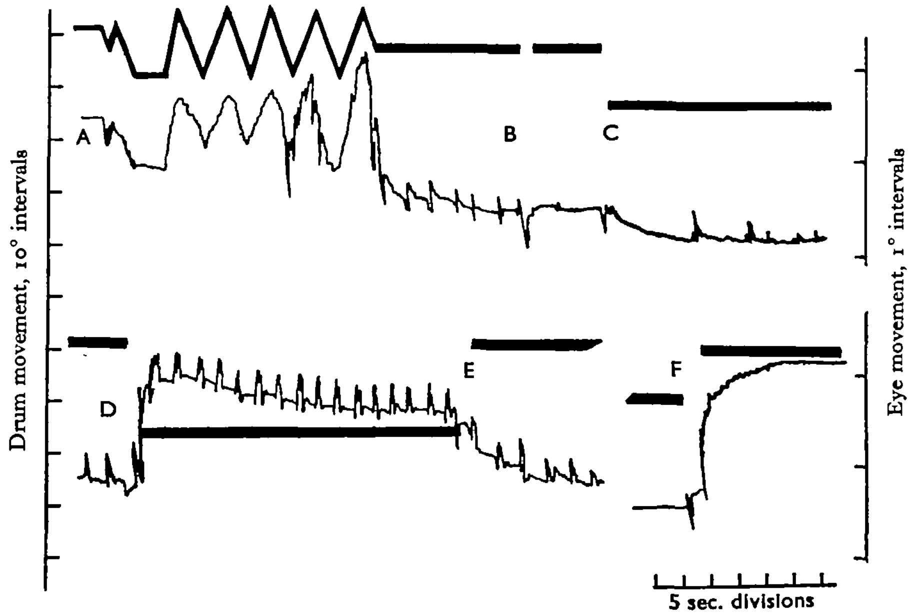

Fig. 1. Records of head movements of the locust in response to drum movements as shown. A, Motion of the drum to and fro initiates regular flicks. B, Drift in the dark when the light goes out, followed by recovery on re-illumination. C, Response of 0·34° to movement of 11° in a dark period of 2 sec. D, Response (with flicks) against the direction of drum movement. E, The return movement gives a slower response. F, Response without flicks but with increased tremor as the eye approaches the new position. The stripe period is 28·4°.

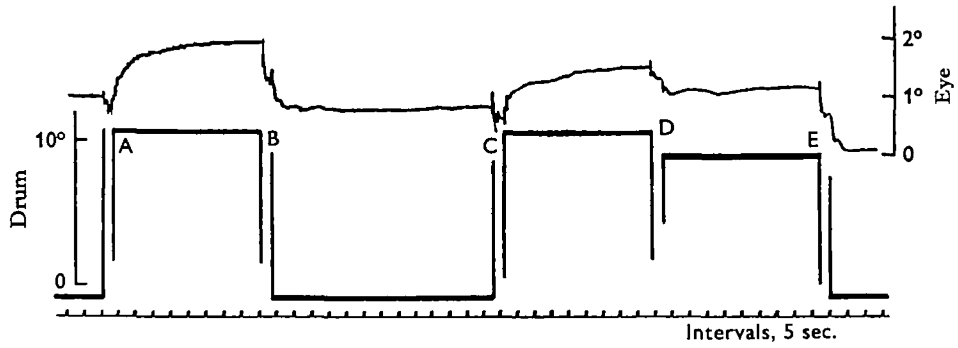

Fig. 2. Typical head movements without flicks in response to drum movements of 11° (A), 11° (B), 11° (C), 1·4° (D), 9·6° (E) during dark periods of 4 sec. The stripe period is 28·4°; results are plotted in Fig. 5.

and quite different from the responses of the crab, is the overshoot and subsequent recovery over a period up to 1 min. We must bear in mind that in the locust there are an unknown number of proprioceptors including chordotonal organs and hair plates, which, in addition to the eyes, may influence head position. At F the response to a smaller drum movement is in the same direction as the drum, and a tremor which is larger than normal develops during the course of the response. Similar enhancement of tremor is found in the eye movements of crabs in conditions which can be interpreted as exacting for the crab.

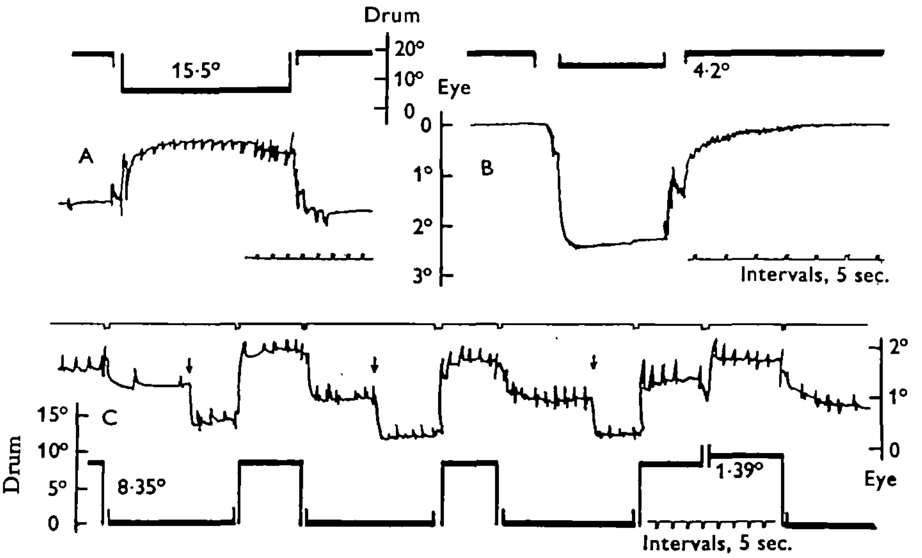

Fig. 3. Typical responses showing head flicks and tremor. A, Response against the direction of a drum movement of 15·5°, with a stripe period of 28·4°. Note how the head flicks are restricted to the duration of the response. B, Large response of 2·5° (and back again) to a drum movement of 4·2° during dark periods of 3 sec. Note how the drift in the dark is cut short as the eye begins to respond in each case. C, A series of responses as obtained for Fig. 5, showing responses to the left and to the right. All the stimuli were 8·35° except the one marked 1·39°. A consistent difference in size of upward and downward responses was corrected at each point shown by an arrow.

Typical responses, without head flicks, to different drum movements are shown in Fig. 2, where drift is rather low. This record shows that responses in one direction can be more rapid than in the other, as found also in the crab, and like all records it illustrates how the head movements take place in the light *with the drum stationary* so that the head is actually moving against the direction of the stimulus which it perceives as a consequence of its movement.

Further aspects of the response are illustrated in Fig. 3. Drum movement, or sharp changes in illumination without movement, can arouse the periodic flicking of the head, as in Fig. 3A; drift in the dark can be in either direction and enhanced tremor is a feature of the later part of the response when it is flattening out, as in Fig. 3B; head flicks, memory responses and a steady drift in one direction can proceed independently of each other as in Fig. 3C, where the drift is corrected three times at points marked by arrows.

In any one animal the head flicks are rather consistent in appearance. The initial rapid phase contains high-frequency components up to 20/sec. and its form suggests that antagonistic neck muscles are excited simultaneously. This is followed by a return to the previous position more slowly but each flick occupies only about 1 sec. The subsequent damped oscillation shown in Fig. 4 originates in the stem of the recording flag.

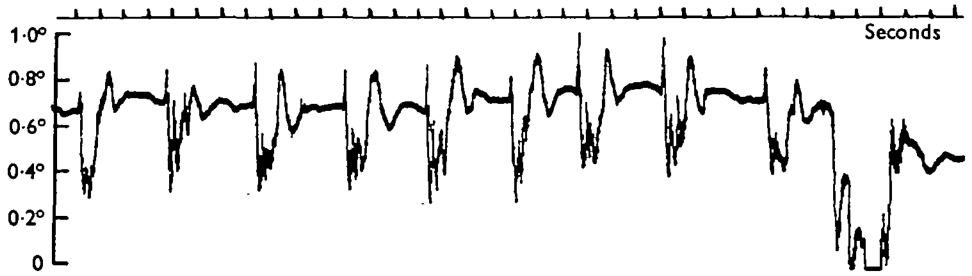

Fig. 4. The output from the photocell at higher amplification showing the head flicks. The frequency response of the electrical recording equipment exceeded 100 cyc./sec. but damped low-frequency oscillations are introduced by the shaft of the flag which moves over the photocell.

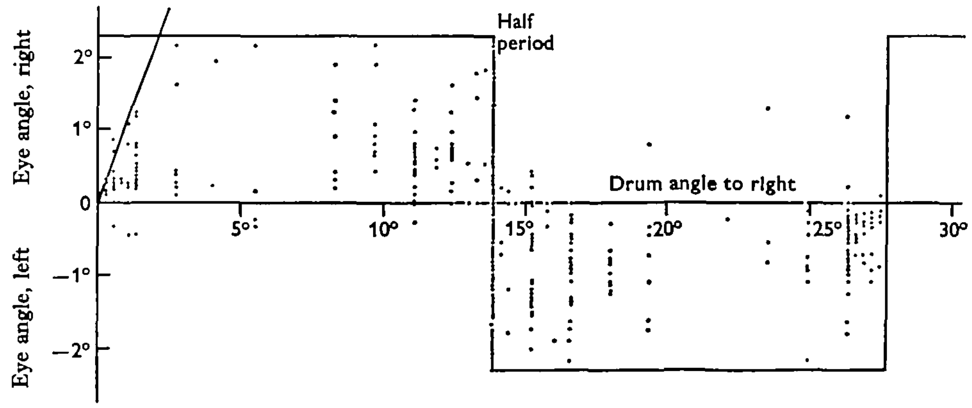

Fig. 5. Head movements of the locust for various drum movements which were made during a dark period of 10 sec. Over the range 0–½ stripe period the responses are in the same direction as the drum movement and over the range ½ to 1 stripe period they are in the opposite direction, showing that the animal is responding mainly to areas of black and white. Both eyes could see and the head was free to make tremor or other movements. At the left the sloping line shows when eye angle equals drum angle.

Head movements, after the new equilibrium has been reached, are plotted for various drum movements in Fig. 5, in which results from several animals are combined. Responses have the same periodicity as the stripes of the drum, showing that black and white stripes are seen as such, with little emphasis upon edges (Horridge, 1966*b*). It is relevant to say here that the general illumination was high and intervals between tests were not deliberately long, being usually 0·5–1·0 min. as in Fig. 3C.

The scatter in the results at first sight looks serious but indifferent responses can be obtained very easily, and all measurable results have been included. Although necessary to demonstrate the optokinetic memory, the repeated switching on and off of the light cannot fail but be a serious disturbance. A noticeable feature of the results is the much larger scatter around movements of ½ stripe period than around movement of one or zero stripe period. For drum movements of ± 5° around zero a reasonable optimum response can be abstracted by drawing an envelope round the points; this cannot be done at ± 5° around ½ stripe period. For a drum movement of exactly ½ stripe period (measured with an accuracy of 0·1°) the responses range across the whole scale. Evidently the locust sometimes infers here a movement to the left and sometimes to the right, unlike the crab, which gives eye responses passing through zero with a smaller scatter. It must be remembered that in the locust two eyes are involved and perhaps two centres for the decision of the net direction of movement.

Head flicks of the gross type illustrated in Fig. 3 seem to make no difference to the responses with reference to memory or to perception of edges. Since all the experiments have been made with a freely moving head and a closed visual feedback loop, little can be said about conditions which govern perception by a head which is held rigid with reference to the stripes for all the time that they are illuminated. It seems reasonable to predict, however, that tremor will have little effect on the perception of edges at the light intensities used here because the closed-loop curve for a freely moving head with tremor has the same periodicity as the stripes. However, under conditions where inter-receptor contrast is low, as at low light intensities, or with finer stripe patterns, tremor may prove to be a factor in the enhancement of vision in the locust.

DISCUSSION

These results raise more questions than can be immediately answered. Since it is now found in the first crustacean and the first insect tested, the optokinetic memory is probably a general phenomenon in arthropods, and perhaps in all animals with optomotor responses. If the optokinetic memory is a by-product of the mechanism for detection of movement, then the time-constants in that system must be long, and the mechanism is strongly protected from large changes in overall illumination. If on the other hand the optokinetic memory is a sign of a spatial representation of the environment which has evolved as part of the stabilization of the visual impression of the outside world in a freely moving animal, it is reasonable to inquire where it resides—in the lamina, the corpora pedunculata, or somewhere between.

The results from the locust almost all fall in the upper left and lower right quadrants of Fig. 5. In contrast to the situation in the crab, discussed in the previous paper, edges are therefore not accentuated relative to areas. The experimental conditions were favourable for the latter, with reasonably bright illumination giving a large contrast between black and white, a short interval between tests and therefore little adaptation, and opportunity for large head movements which could scan a large fraction of a stripe period. But the crux of the matter is whether the animal has directional information of its own scanning or tremor movements. If it has this information and can distinguish a white–black edge from a black–white edge, then accentuation of edges by small eye movements is still consistent with a periodicity of response curve equal to the stripe period. The argument developed for the crab assumed that the edges are accentuated while their black–white or white–black nature is lost. The results for the crab are consistent with the view that the crab makes no use of possible information of the direction the eye is travelling as it passes across a contrasting edge during a flick.

In discussing 'peering' movements made by locust nymphs, both Kennedy (1945) and Ellis (1953) suggest that they 'sharpen' vision, presumably by enhancing the contrast at edges, but were unable to test this suggestion. Following a different suggestion, Wallace (1959) showed that the regular slow peering movements, which measure 1–12° with an average of about 6°, enable the animal to estimate distance without binocular vision. Locusts were observed making peering movements when about to jump and, to confuse the estimation of the range, the object to be jumped at was moved in time with the peering movement. Movement of the object in the opposite direction to the peering caused the locust to jump short; whereas moving it with the direction caused it to overshoot. Clearly the locust remembers the position of a single object in the visual field and correlates this over the extreme positions of its peering movement. There may be some connexion with the present work on optokinetic memory. However, peering movements consist of a swaying by the whole body on the legs. They are 10–100 times as great as tremor movements and in peering the animal must know in which direction it is making a movement. In mentioning Wallace's experimental result it must be pointed out that he assumed that the locust estimates the distance of the object by its movement across the retina during peering, but if he had measured head movements as well as body movements an effect of the optomotor regulation of head position would no doubt have been found. If so, it can be said that both optokinetic memory and the optomotor response play a part in the estimation of distance by a jumping locust.

There are numerous examples of insect behaviour showing a stabilization of the body axes with reference to objects seen. The origin of the visual component found by Dingle (1965) to cause the alternation of turns by the bug *Dysdercus* is one example of this type. In this case a delayed compensatory turning response is made some time after the completion of a turn in the opposite direction by freely moving animals, but a parallel could be drawn with the tendency to turn shown by the beetle *Chlorophanus* on a Y-maze globe. In both cases the effects of a visual stimulus are stored up until the animal has the opportunity to turn. Whether phenomena of this kind are related to the optokinetic memory or not, it is evident that the simplest responses to visual stimuli contain a strong memory component.

SUMMARY

1. A migratory locust is held relative to a stationary contrasting visual field and all lights are then turned off while the visual field is moved in the dark. On re-illumination the locust turns its head as in an optomotor response.

2. The response shows that the locust can retain the former position of the visual field to 0·1° over many seconds in the dark.

3. No preference for edges, as opposed to areas, appeared when a drum of equal black and white stripes was used as stimulus. In this respect the locust differs from the crab.

4. As in the crab, the optokinetic memory is interpreted to be a part of the visual stabilization mechanism.

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