Some Spatial and Temporal Properties of Movement Fibres in the Optic Tract of the Crayfish

By

Tsuneo Yamaguchi[1], Teruya Ohtsuka[2], Yasuo Katagiri[3] and Tateo Shimozawa

Zoological Institute, Hokkaido University

(With 11 Text-figures)

Recent studies on visual information processing in various animals have shown that a basic rule governing the handling of visual inputs is that those modalities which contribute important information to the animal are abstracted immediately into a variety of parallel channels, each carrying signals related to particular parameter of the total visual input.

One example of such parallel transmission is the presence of movement sensitive units in the retina or optic tract (e.g. Bishop *et al.*, 1968; Lettvin *et al.*, 1959, 1961; Horridge *et al.*, 1965; McCann and Dill, 1969; Swihart, 1968; Northrop and Guignon, 1970). These units must be the main channel transmitting to the brain important information about objects moving the receptive field. The brain then decides, for instance, on following a prey or escaping from an enemy.

In the crab and the lobster, the most regularly responding type of fibre has been named the "medium movement" fibre (Waterman and Wiersma, 1963; Waterman *et al.*, 1964; Wiersma *et al.*, 1964; Wiersma and Yamaguchi, 1967a; Wiersma, 1970). All of the fibres in this group have exactly similar properties; with increase of speed above a certain value, the frequency of spikes increases and stimulus repetition does not give a conspicuous habituation. Therefore, these fibres will respond for an indefinite time to objects like stripes on a moving drum or a swinging pendulum. In addition to these fibres the crab and the lobster have "slow movement" fibres and "fast movement" ones. These fibres are remarkable in that they react with a high frequency discharge to very slow or fast movement of objects respectively.

In the crayfish, however, the most commonly found movement fibres react

Present addresses

1): Department of Biology, Faculty of Science, Okayama University.

2): Department of Physiology, School of Medicine, Keio University.

3): Department of Physiology, Tokyo Women's Medical College.

Jour. Fac. Sci. Hokkaido Univ., Ser. VI, Zool. 19 (1), 1973.

to a much wider range of speeds, but in a noticeably different manner (Wiersma and Yamaguchi, 1966, 1967b). In practice it is impossible to make these fibres give a constant frequency output because their responses habituate quickly, especially to a stimulus moving through the ommatidia located along the same row in the eye. For instance, if a shadow is cast on a homogeneous white background a vigorous response occurs when the field is entered but the number of spikes very quickly diminishes and firing may stop altogether, even though the shadow has not yet reached the middle of the receptive field at that time, whereas any movement in the ommatidia located along the row which has not been exposed will cause a response. In this connection, this common type of movement fibre has been named the "jittery movement" fibre and includes 11 different kinds of unit which are able to be distinguished by their receptive fields in much the same way as for the sustaining fibres (Wiersma and Yamaguchi, 1966).

We now describe further analysis of some spatial and temporal properties of such jittery movement fibres in the crayfish optic tract. This paper is the first in which the results of investigations of 1) the stimulus area-response relationship and 2) the reactivity of the movement fibre to change in temporal pattern of the background illumination with or without moving stimulus will be presented.

Materials and Methods

All experiments were conducted with adult specimens of the crayfish, *Procambarus clarki* (Girard). The technique for insertion of metal electrodes into the optic nerve and for recording from single units was as described elsewhere (Yamaguchi and Ohtsuka, 1973).

Three kinds of the visual stimulus were employed.

(1) For experiments in which the diameter of the stimulus was to be varied, a piece of diffusing material directly illuminated with a 3 volts tungsten filament lamp from the rear and bordered by an iris diaphragm provided a light spot whose diameter could conveniently be changed; the maximum intensity was about 10 lux. The operation of such a light spot was controlled electrically by a pulse generator (MSE-3, Nihon Kohden).

(2) The effect of various stimulus parameters on the activation of the movement fibre was investigated with a specially constructed stimulator. The set-up consisted of two concentric cylinders. During the experiments the crayfish with a recording electrode on the movement fibre in the optic tract was set in the centre of the cylinders. The inner cylinder (24 cm in diameter, 30 cm in height) painted completely black was fixed and had a square window (15 cm × 15 cm) covered with a diffusing screen. The outer cylinder (30 cm in diameter), made of transparent plastic sheet, could be rotated; its angular velocity could be changed in six steps between 9 and 450 degrees/sec by changing the gear ratio of the driving motor, and the angular velocity was registered on one beam of the oscilloscope. Higher or slower angular velocities could be obtained by manual movement of the outer cylinder. On the surface of the outer cylinder, black tape in various figures could be stuck. The light spot provided by a diaphragm, lenses and light source (a tungsten filament lamp; maximum intensity, 4515 lux) and controlled by the pulse generator was shone perpendicularly on the window of the inner cylinder, so the various figures of the black tape were projected on the diffusing screen of the inner cylinder. For those experiments requiring movements of a white object, a mask with an opening in various

patterns was stuck on the surface of the outer cylinder, and through the opening the window of the inner cylinder was illuminated by the light source from the front. Therefore, looking from the crayfish's position, on a bright or a dark background of a certain diameter, a black or a white object moved horizontally to and fro.

(3) In order to investigate the reactivity of the movement fibre to changes in the temporal pattern of the background illumination with or without moving stimuli, a flickering light source was used. A light source with a flash frequency between 0.5 and 30 Hz was provided by a stroboscope (SS4B, Toshiba; flash half-width, below 30 μsec) or a glow modulator tube (Sylvania 1B59/R1130B; maximum intensity, 32 lux).

Flashes from these light sources could be delivered to a semitransparent screen in front of the eye or directly to the eye. Flash duration and frequency were controlled by a pulse generator. In the case of the experiments of flickering light with paired flashes, the paired flashes were produced by a single glow modulator tube which was triggered by output from two separate pulse generators with independent duration, intensity and delay time. In some cases, the 3 volts tungsten filament lamp controlled by the pulse generator and a switch was employed as a light source providing flickering light with a frequency of less than 10 Hz to define the general nature of the response, although it did not allow studies with any precision.

Results

I. *Effect of stimulus area*

The movement fibres react as well to moving objects which are lighter than the background as to ones that are darker, provided they are relatively small (Wiersma and Yamaguchi, 1966, 1967b). In the series of experiments in which the angular size was varied by round or rectangular stimuli moving with constant angular velocity and constant stimulus background, the maximal response was obtained with a stimulus size of 10–30 degrees (Fig. 1). The influence of the angular size of stimulus could then be analysed by changing some factors of a square stimulus, such as height or length. Data obtained in an experiment with a black rectangular object as the stimulus are shown in Figure 2. The response of this movement fibre (O7) was affected by the angular size of both the height and length of object; when the height or length was extended while the other factors were held constant, the response increased as the former or the latter approached the size of 30 or 20 degrees respectively, but then decreased when the former or the latter was further extended. Thus, these results may be taken to indicate that concerning the excitation of movement fibres, the spatial summation could not be described by a simple linear relationship.

For the further quantitative analysis of the stimulus area-response relationship, a stationary spot light was projected on the eye surface and then the latency and number of spikes elicited by turning it off were measured. As shown in Figures 3, 4, and 5, it is evident that with an increase of the spot size to about 10–30 degrees in diameter the response increases; with further increase of the spot size the response decreases again. And it is also apparent that the latency of the response decreases markedly with increasing size, independently of the change

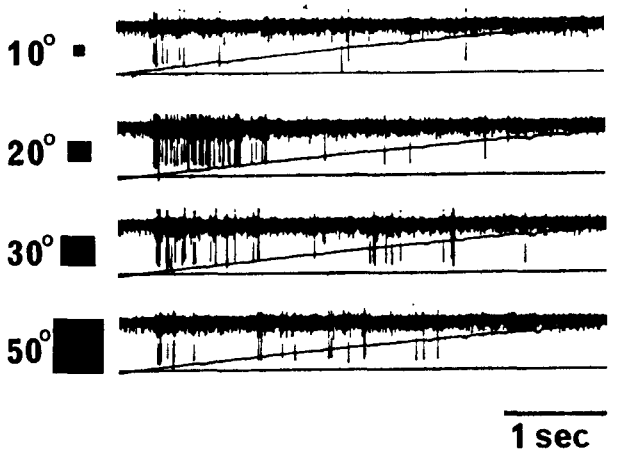

Fig. 1 Response of a movement fibre (O6) to dark squares of different angular size moved at 9 degrees/sec through the receptive field. The position of the stimulus is marked by the middle beam: its deflection was adjusted so that a crossing of this beam and the upper beam corresponded to the position in which the leading edge of stimulus entered just into the window (see *Methods*), while a crossing of this beam and the lower beam corresponded to the position in which the same edge moved just out of the window. With increasing angular size the response increases up to an angular size of about 20 degrees: then the response decreases with further increase of the angular size.

in magnitude of the response. The position of the spot light in the receptive field made no difference. However, the optimal spot size, i.e. that which gave a maximal response, was dependent on the size of the receptive field; it was about 10 degrees in diameter for small field fibres, such as O6 (Fig. 3), but about 30 degrees in diameter for large field fibres, such as O7 (Fig. 4). When the intensity of the spot light was weaker, the optimal spot size increased and the latency became longer (Fig. 3). Under the steady illumination from another light source, the optimal spot size decreased and the latency became longer (Fig. 5).

At this point, we would like to note that a suppressive effect of increased stimulus area has been reported in the retinal ganglion cells of several vertebrates (in the frog, Hartline, 1940; Barlow, 1953; Schipperheyn, 1965; Grüsser *et al.*, 1967; Butenandt and Grüsser, 1968: in the toad, Ewert and Hock, 1972; in the cat, Kuffler, 1953: in the rabbit, Barlow *et al.*, 1964). In all these cases, the organization of the receptive field of the cell into a central excitatory receptive field and a peripheral inhibitory receptive field has been demonstrated, and the decrease in response depends on the spatial summation in both the receptive fields. Contrary to this, evidence of inhibitory action by a moving stimulus in retinal areas surrounding the excitatory receptive field of a crayfish movement fibre has not been obtained, and we may suppose that the area effect has a different organization basis.

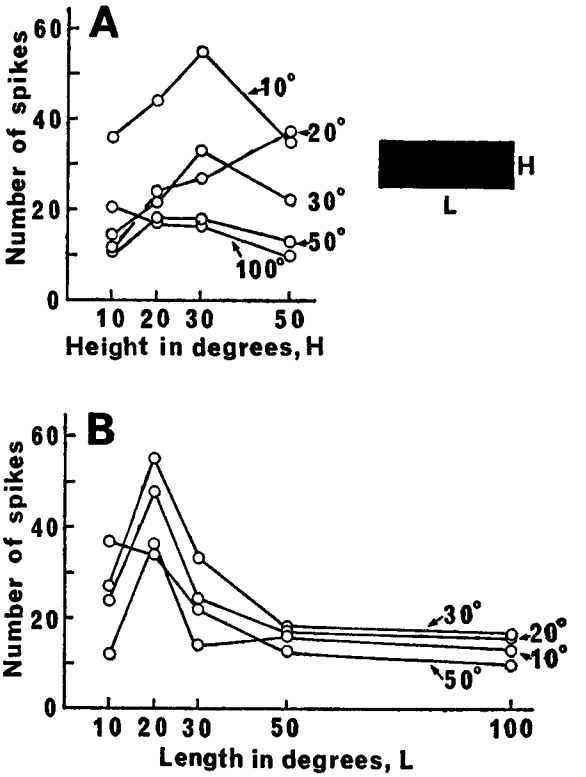

Fig. 2 The effect of stimulus area on the response of movement fibre (O6) when dark rectangular objects were moved with an angular velocity at 9 degrees/sec through the receptive field. In A, the height, H, of the object was extended in the direction of movement, while the length, L of object noted near each the graph, was held constant. On the contrary, in B, the length of object was extended in the direction perpendicular to that of object movement, while the height of the object which is noted near each the graph, was held constant. On the ordinate the frequency of spikes during the traverse of the object through the window is plotted.

II. *Response of the movement fibre to a moving object on a background of intermittent illumination.*

Figures 6A and 7A, B give typical examples of the responses of space constant movement fibres[1] (O65 and O67) and jittery movement fibres (O6 and O35) to a

1) Two space constant movement fibres whose receptive fields change markedly in size with body position have been established by Wiersma and Yamaguchi (1966). They differ from each other in that one (O65, fast space constant movement fibre) is only slightly stimulated by an object with jittery motion in the plane of the eye, but gives a burst when a fast-moving object approaches, whereas the other (O67, jittery space constant movement fibre) reacts best to the same type of jittery moving object as the jittery movement fibre.

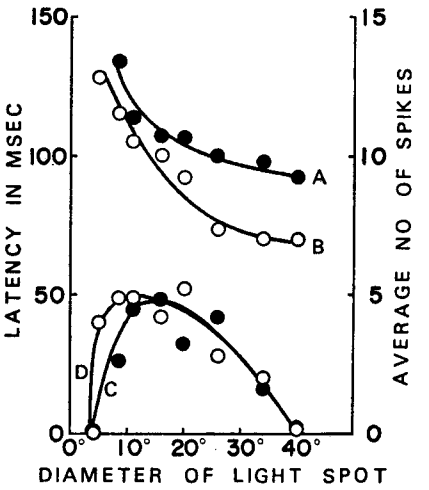

Fig. 3

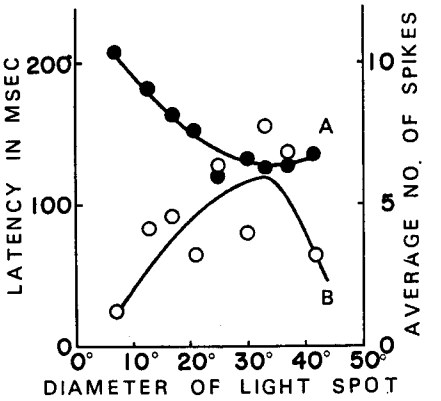

Fig. 4

Fig. 3 Stimulus area — response relationship of a movement fibre (O6). Stationary light spots of two different intensities (open circles, 8.4 lux; solid ones, 1.0 lux), whose diameters could be varied, were used as stimuli and the responses were evoked by turning them off. The average number of spikes was obtained from the data on 5 successive trials with intervals of 10 seconds. A and B represent the relationship between the diameter of light spot and the latency, and C and D represent the relationship between the diameter of light spot and the average number of spikes.

Fig. 4 Stimulus area — response relationship of a movement fibre (O7). Open circles represent the relationship between the diameter of light spot and average number of spikes, and solid ones the relationship between the diameter of light spot and the latency. The intensity of the spots was 8.4 lux. See Fig. 3 for other explanations.

smooth movement or stepwise movement of the black object under steady illumination. The moving shadow caused distinct discharges when it entered the receptive fields but, in general, there were no subsequent discharges, unless motion was temporarily stopped (see Fig. 7B; where the signal trace is horizontal, the shadow was stationary in the receptive field), after which renewed movement caused a short burst. On its return trip fewer spikes were elcited, as would be expected since many "sampling" stations would be now refractory.

On the other hand, when, instead of the steady illumination, intermittent illumination of different frequencies was used, the results were typically as shown in Figures 6B-E and 7C, D, G and H. There was no response to the intermittent stimulation if the object was moved outside of the receptive field. However, when the object was kept moving through the receptive field with flash frequencies between 1 and 10 Hz, a rhythmical discharge corresponding to flash frequency was evoked (Fig. 6B-D). These discharges did not show "habituation". On its return trip, only a few spikes corresponding to flash frequency were elicited, as

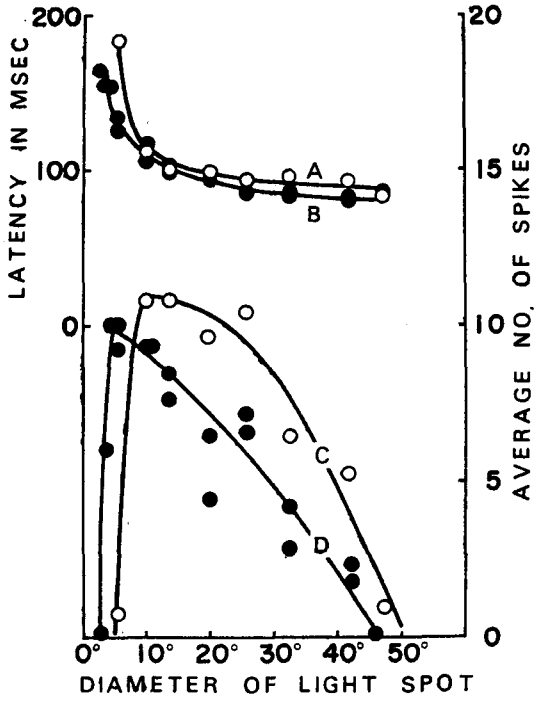

Fig. 5 Stimulus area—response relationship of a movement fibre (035). A and B represent the relationship between the diameter of the light spot and the latency, and C and D the relationship between the diameter of the light spot and the average number of spikes. In A and C, the light spots (light intensity, 8.4 lux) were turned off in the presence of steady background illumination (light intensity, 7.8 lux), but in B and D, they were turned off without any background illumination. See Fig. 3 for other explanations.

would be expected since the habituation would be set up at that time. This type of discharge of the movement fibre corresponds to "apparent motion" in psychophysical experiments. With intermittent illumination of more than 10 flashes per second, however, depending on the flash intensity, a rhythmical discharge could not be observed during the movement of an object across the receptive field (Fig. 6E). From these facts it may be considered that regardless of the nature of the background illumination, the movement fibre can react well to a moving object and to changes in the position of an object during a temporary dark period, and the c.f.f. (critical fusion frequency) of the movement fibre appears to be about 10 Hz.

To test the possibility that, not movement itself, but successive changes in position of object stimulate the movement fibres, the intermittent illumination with short flashes of 6 μsec was used as the only background illumination. Such the brief duration guaranteed that with due regard to the ommatidial angle (3–5°), practically no image movement occured during illumination of the moving object at slow speed (e.g., 9°/sec.). With low flash frequency the movement of the object could be completed during the interval between two flashes. Even under these circumstances, the movement fibre did show a rhythmical discharge corresponding to flash frequency if a moving object entered its receptive field. Therefore, this

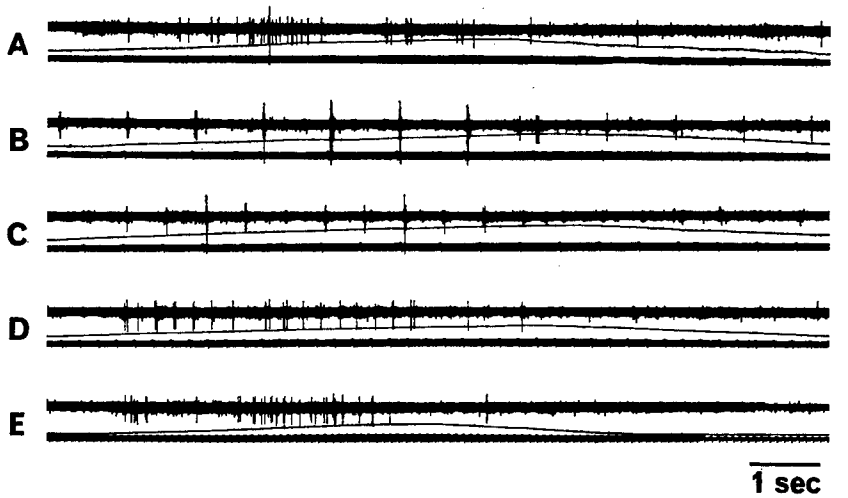

Fig. 6 Simultaneous recording of the responses of two different space constant movement fibres, O65 (large spikes) and O67 (small spikes) to a moving dark object under different kinds of illumination. Background light spot (43.5° in diameter) was projected on the screen in front of the eye, and it was interrupted by a moving rectangular object (17.4° in width and 43.5° in length) which was moving continuously from upper to lower and back at the constant angular velocity of 3°/sec. In each record, at the beginning of recording the object was completely outside of the background light spot. A; response with a steadily illuminated background. Note the marked habituation of O65. B-E; responses with a background of flickering illumination with the frequency of 1 Hz in B, 1.7 Hz in C, 4 Hz in D and 10 Hz in E. These records indicate that the discharges of both the fibres synchronized well with each light flash and their habituation was less than in the case of A.

apparently indicates that change in absolute position within the receptive field is the true stimulus, identical with movement within the receptive field and the change in position to cause the response can be said not to require the successive stimulation of neighbouring ommatidia.

Concerning this feature of the movement fibre in the crayfish, another interesting point is that the class 2, movement-detecting neurones in the frog's retina respond little or not at all to illumination without movement, respond well to change in position under intermittent illumination even when relatively large jumps in the visual field occur during a dark pause between two flashes (Grüsser *et al.*, 1963; Grüsser *et al.*, 1968).

On the other hand, movement fibres in the crayfish react about as well to moving objects which are brighter than the background as to ones that are darker, provided they are relatively small. For objects brighter than the background the response is caused by the trailing edge, whereas it is leading edge for objects darker than the background (Wiersma and Yamaguchi, 1966, 1967b, see Fig. 7A,

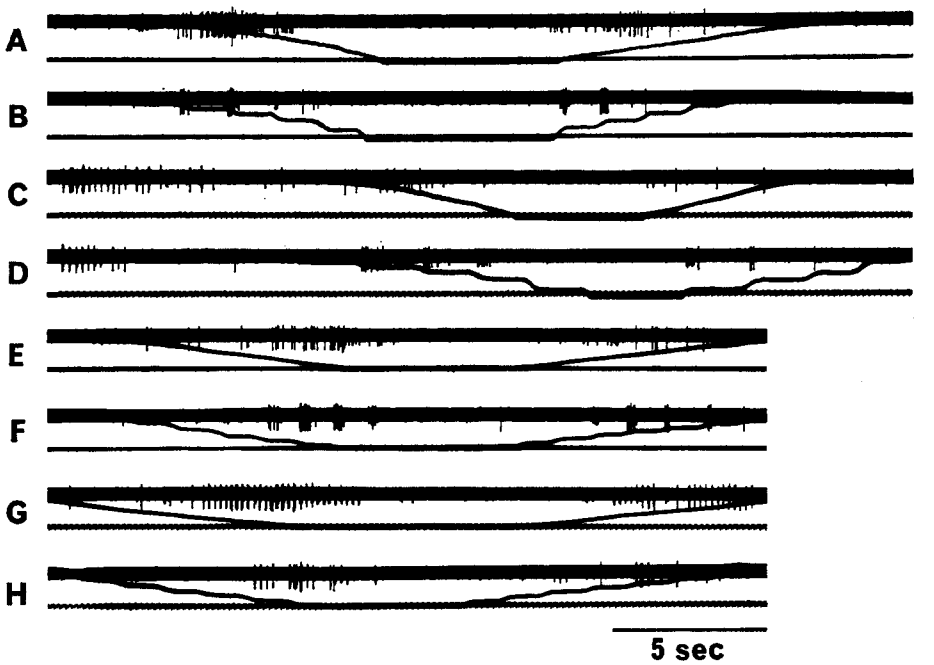

Fig. 7 Responses to horizontal movement of a rectangular, dark or bright object, of two jittery movement fibres. One, O6, for the dorsoposterior field (large spikes) and one, O35, for the dorsoanterior field of the eye (small spikes). The object (18.5° in width, 52.7° in length) was moved manually on the surface of the diffusing screen. In each record, the middle beam of the oscilloscope indicates the movement of the object; its deflection was adjusted so that a crossing of this beam and the upper beam corresponded to the position in which the leading edge of object entered just into the window, while a crossing of this beam and lower beam corresponded to the position in which the same edge moved just out of the window. Downward deflection represents forward movement relative to the eye. A and E; continuous movement of a dark A or bright E object under steady illumination. B and F; stepwise movement of a dark B or Bright F object under the steady illumination. C and G; continuous movement of a dark C or bright G object under the intermittent illumination with frequency of 5.5 Hz. D and H; stepwise movement of a dark D or bright H object under the intermittent illumination with frequency of 5.5 Hz.

B, G, H). These response characteristics of the movement fibre were not affected by the intermittent illumination. That is, when the dark or bright object was moved continuously or stepwise through the receptive field, the discharges synchronized with each the flash were caused by its leading edge for the former, but by its trailing edge for the latter, as shown in Figure 7C, D, G, and H.

III. *The response to intermittent illumination without moving stimuli.*

According to Wiersma and Yamaguchi (1967b), the movement fibres react to sudden darkening with a very short "off" burst, provided that their receptive fields have been illuminated for some considerable time previously. When a light is flickered on and off several times per minute the "off" discharges shorten and soon disappear altogether. Therefore, it would be expected that the movement fibre does not respond to flickering flashes with a frequency of, for example, over 10 Hz, except with a transient burst evoked immediately after the onset of the flash train. In fact, as shown in Figures 6 B, C, D, E and 7D, G, H, the movement fibre responds little or not at all to regular flashes without a moving stimulus. However, during the intermittent illumination the response of the movement fibre could be brought about by change in any one of the parameters of the flashes, such as the flash frequency, the flash duration or the flash intensity.

In each record of Figure 8, the unusual recording system is explained in the Legend, dots represent the occurrence of spikes and each sweep of the oscilloscope

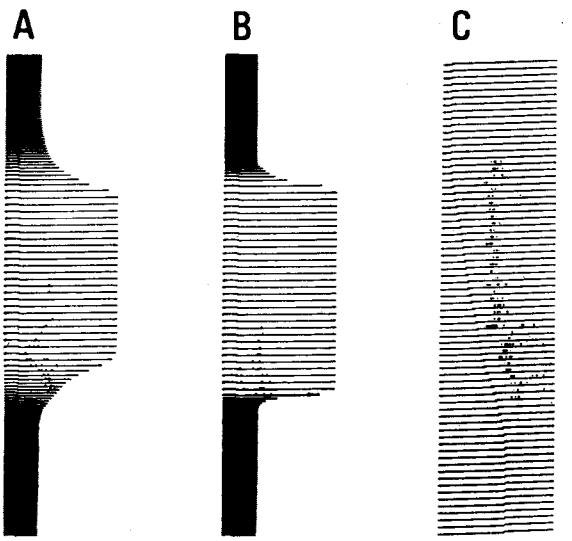

Fig. 8 Response of a movement fibre (O7) to changes in flickering light. In the recordings, the oscilloscope sweeps were triggered by the stimulator at the beginning of each stimulus sequence, dots represent the occurence of spikes and each sweep of the oscilloscope at a constant velocity triggered one flash. Record is read from bottom to top, left to right. A; response to gradual change in frequency from 30 Hz to 8 Hz and *vice versa*. Each flash duration is 100 msec. Note the response with marked facilitation and following habituation. B; response to quick change in frequency from 30 Hz to 8 Hz and *vice versa*. Each flash duration, 100 msec. The response is less and habituates more quickly. C; response to decrease in flash duration from 500 msec. The flash frequency was kept at 8 Hz.

with constant velocity triggered one flash. Hence, each line of the record indicates the interval between two successive flashes. This recording method afforded great facility for analysing the time course of the response under the flickering flashes. In record A, a decrease in the flash frequency induced a response with a rhythmic discharges corresponding to the flash frequency followed by habituation, provided that the retina had been stimulated for some considerable time. When the frequency of the flickering flashes (each flash duration, 100 msec) was changed gradually from 30 Hz to 8 Hz and *vice versa*, the response induced by decreasing the frequency was first facilitated and then habituated, although a gradual increase in the frequency had no effect on the fibre. The record B shows that the response to a quick decrease in the frequency was less, but it more quickly habituated than the response to gradual decrease. The record C indicates that a decrease in flash duration from 500 msec to 50 msec (the frequency, kept in 8 Hz) induced also a facilitated response followed by habituation.

Therefore, these experiments reinforce the conclusion that the response of the movement fibre is triggered by the magnitude of the decrease in the total light energy of the background illumination.

Above mentioned experiments were made with flickering flashes of equal duration repeated serially. Such flickering flashes are simply described in terms of their frequency. In the next place, we have studied the reactivity of the movement fibre to change in any one of the parameters of flickering flashes of unequal periods (refer to Fig. 11B-E). These flickering flashes, in other words, were made up of paired flashes. Note that the train of flashes shown in Figure 11 does not represent the mixing of two independent frequencies. Figure 9 shows that during such flickering flashes, responses of the movement fibre were brought about by decreasing the inter-flash interval between the paired flashes or, the flash duration or the flash intensity in either member of the pair, but they were locked in their occurences to the unchanged flash in each pair. Another point of interest is that as shown in record C, when the paired flashes were not equal in their light intensity or duration, the responses evoked by, for example, decreasing light intensity were invariably locked in their occurences to the flash of higher light energy in each pair. Therefore, it is clear that the synchronization of the responses with flickering flash cannot be explained solely in terms of change in the parameters of the flickering flash. Synchronization or "locking" is rather a complex function of the temporal pattern of successive stimuli and light energy.

Most of the movement fibres always habituated to some extent on repetition of the stimulus, but some movement fibres responded with more spikes to flashes at certain intervals, as illustrated in Figure 10B. There was a wide range of habituation characteristics as measured by the rate of the decline in the response with flashes repeated at different intervals, and in the recovery curve during a period of rest. Some recovered within a minute, others required up to several minutes. This range demonstrates that most of the habituation effects are of central origin and do not depend on sensory adaptation. Concerning this, a

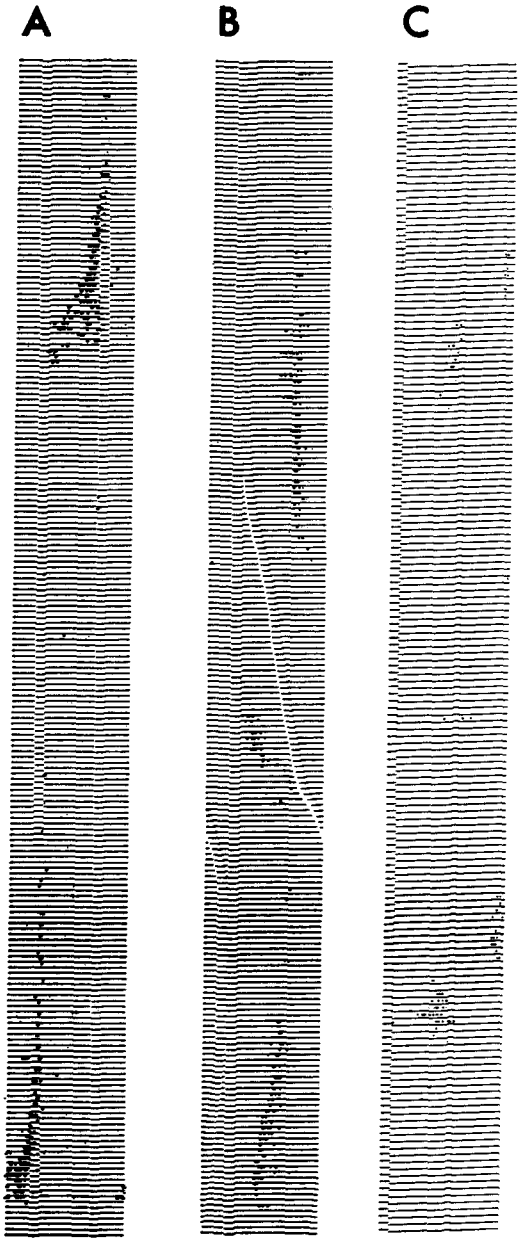

Fig. 9 Responses of a movement fibre (O7) to flickering light composed of paired flashes. In the recordings, dots represent the occurence of spikes and each sweep of the oscilloscope beam triggered a pair of flashes (sweep frequency, 10 Hz). Records are read from left to right, from bottom to top. A; changes in light intensity of one flash of the paired flashes. Flash duration, 10 msec. Inter-flash interval between paired flashes, 43 msec. It should be noted that the responses were caused only by decreasing the light intensity of one flash of the pair, but they were locked in their occurrences to the unchanged flash in each pair. B; change in the interval between the flashes in the pair. Flash duration, 10 msec. The responses occured only when the intervals were shortened. C; change in light intensity of one flash of the pair. In this recording, the duration of the first flash and the second one were 10 msec and 5 msec respectively. Note that the responses were evoked by decreasing light intensity, but they were locked in their occurrences to the flash of higher light energy in each pair.

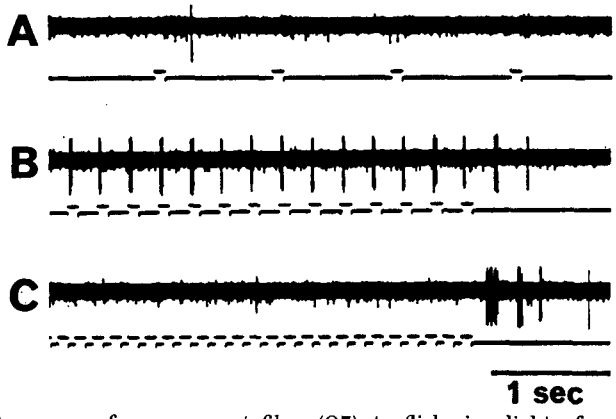

Fig. 10 Responses of a movement fibre (O7) to flickering light of various temporal patterns. 100 msec light flash flickered on the total eye with various frequencies. A; the response to flickering light with a low frequency, 1 Hz. Latency, 250 msec. B; the extra discharge was caused by cessation of flickering light with a frequency of 4 Hz, during which every flash was followed by grouped discharge. Latency, 250 msec. C; a discharge in bursts was evoked by cessation of flickering light.

peculiar phenomenon in Figure 10 is that with the frequency about 4 Hz each flash evoked the spikes without habituation, while with a frequency below or above 4 Hz each flash did not evoke spikes. This type of response was rarely encountered and was not typical of the movement fibres. Another interesting finding is that after rather long illumination with flickering flashes with a frequency of less 10 Hz, an abrupt cessation of illumination produced a cluster of spikes with a period corresponding to the flash interval, the firing lasting for 1–3 cycles (Fig. 10B, C). When the stimulus frequency was above 10 Hz, the response was of a rather ordinary type.

Discussion

The stimulus area-response relationship

In the present experiment it was found that the activation of the jittery or space constant type of movement fibres was maximal if a dark or bright object moving through the receptive field had about the size of 10–30 degrees. This area dependency of the response of movement fibres seems to be caused by factors similar to those responsible for the area-response relationship obtained with a non-moving light spot projected on the eye surface. In the retinal ganglion cells of several vertebrates, a suppressive effect of increased area of stimulus can be explained by spatial summation in the excitatory and inhibitory receptive field of these cells (Hartline, 1940; Kuffler, 1953; Barlow, 1953; Barlow *et al.*, 1964; Schipperheyn, 1965; Grüsser *et al.*, 1967; Butenandt and Grüsser, 1968; Ewert and

Hock, 1972). However, any evidence of regional differentiation of the receptive field of the crayfish's movement fibres has not been obtained though the possibility still remains. It is therefore impossible to describe the data obtained for the crayfish's movement fibres by the same neural function due to receptive field organization which was deduced for the vertebrate's retinal ganglion cells.

In the crayfish, the chracteristic effects of increased area were (1) independence of stimulus location over the receptive field, (2) an effectiveness proportional to number of ommatidia stimulated, and to (3) intensity of stimulation. Similar suppressive effect of increased stimulus has been also found for the visual unit of the locust ventral nerve cord (Palka, 1967). Considering these characteristics, this type of suppression may be at present accounted for on the neural basis of excitation-dependent inhibition (Tauc, 1960), by which an excitatory input simultaneously produces a pronounced inhibition: the inhibition must be able to override simultaneous excitation and it must be relatively more effective with larger than with smaller areas.

Reactivity of the movement fibre and intermittent illumination

By the optokinetic analysis of movement perception in the beetle, *Chlorophanus*, Reichardt and his colleagues were led to the conclusion that the minimum peripheral requirement for movement perception involves the spatial transfer of stimulation from one visual receptor to its neighbour (Hassenstein, 1951, 1961; Reichardt, 1957, 1961, 1962; Reichardt and Varjú, 1959). Hence, the effective stimulus will have the form $d\theta/dt$, where θ is the angular direction of the object perceived to move.

On the other hand, another type of perception is possible: through uneven excitation of the same ommatidia at different times. This mechanism would work when an object traverses the eye or the background light flicks, but only if the eye possess some kind of "memory" and can compare a previous retinal excitation with a subsequent one. In the present experiment, obviously both spatial and temporal factors are crucial.

In fact the existence of the temporal factor in movement perception of the crayfish is emphasized by the fact that under the intermittent illumination the movement fibres respond to a change in the temporal pattern of the background illumination, such as a decreased flash intensity, shortened flash duration or decreasing frequency, without any moving object. In this case, the movement fibres respond with spikes only to an adequate dI/dt, where I is the light intensity of the background. However, the movement fibres react very little or not at all to an increase in steady illumination. To sudden darkening they may respond with a very short "off" burst. Even under flickering flashes with the frequency less than about 10 Hz, the movement fibres respond only to decreases in total light energy of the background. It is, therefore, obvious that it is the reduction of light energy from the background with adequate dI/dt that is important in evoking the

response. This is further supported by the fact that under steady or flickering illumination, for objects lighter than the background the response is caused by the trailing edge, whereas it is the leading edge for objects darker than the background.

Concerning the problems of the temporal factor, it is quite interesting that in the newt, the land salamander (Himstedt, 1969), the dragonfly larva (Etinne, 1968) and the water strider (Meyer, 1971), feeding behaviour is released not only by a moving light spot, but also by a stationary light spot when it is flickering rhythmically. In these animals, the releasing value of flickering stimuli depends on flicker frequency and most feeding reactions appear between 2 and 10 Hz for the newt and the land salamander, 10 and 20 Hz for the dragonfly larva, and 1.6 and 8 Hz for the water strider.

Another interesting result is that with intermittent illumination of less than 10 flashes per second, depending on the flash intensity, a rhythmical discharge of the movement fibre was obtained during the movement of object across the receptive field. This result indicates that a change from one position to another anywhere within the receptive field is the true stimulus, and has an effect identical with movement within the receptive field; the change in position necessary to cause the response does require the successive stimulation of adjacent or neighbouring receptors. This type of firing of the movement fibre corresponds to "apparent motion" in psychological experiments with intermittent illumination. Concerning this matter, Grüsser *et al.* (1963) and Grüsser *et al.* (1968) have found that movement-detecting units in the frog's retina respond well to change in position under intermittent illumination even when relatively large jumps in the visual field occur during the dark pause between two flashes. From an optokinetic experiment on the beetle, it was concluded that a series of successive stimuli impinging on different parts create an illusion of movement, and when successive light stimuli are presented to the beetle eye, an optomotor response is evoked if the ommatidia so stimulated are more than two ommatidia apart (Hassenstein, 1961; Reichardt, 1961). It seems to be that the successive activation of the adjacent –but– one ommatidium is not required for spatial factor of movement perception.

The most remarkable property of the movement fibre is the synchronization of the response with the flickering flash which was evoked by decrease in light energy of the intermittent illumination. Although our knowledge about this problem is still very fragmentary, the flash may possess not only a stimulating effect, but also a inhibiting effect on the movement fibres, that is, it may be able to give a response with synchronization its occurrence with the flash frequency, and both the effects may be proportional to light intensity. If we accept this assumption, it becomes considerably easier to understand the peculiar phenomena observed in the flickering flashes of unequal periods, duration or light intensity (Figs. 9C, and 11D, E).

When the eye was subjected to repetitive stimulus (light flash or moving object), there was usually a progressive reduction in the response of the move-

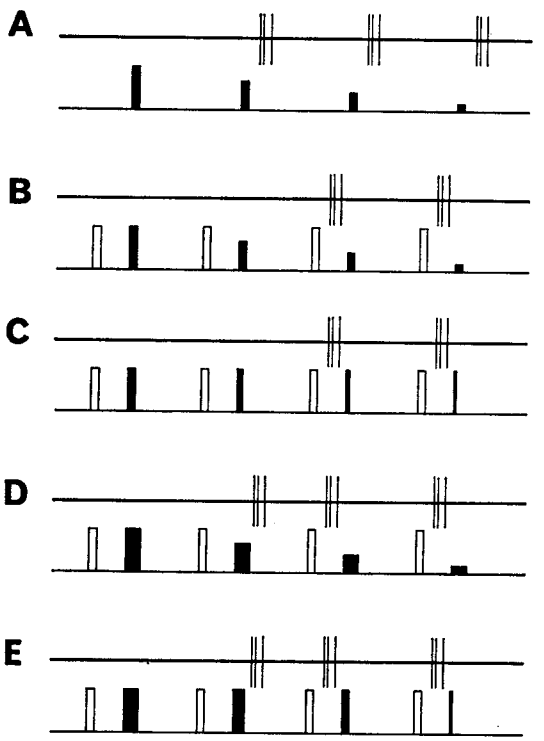

Fig. 11 Schematic illustration of reactivity of the movement fibre to change in parameters of the flicker light composed of single flashes in A or of paired flashes in B-E.

ment fibre, but the response was evoked immediately when the stimulus shifted to different part of the visual field or when any one of the parameters of the stimulus changed. Therefore, the failure of the response (habituation) may be not due to fatigue at the primary level or to an intrinsic property of the ommatidium which responds to the intensity of the light that falls upon it, although complications may arise from the past history of the receptor and interactions with its neighbours, but it seems to depend upon the integrity of rather complex functions at the higher level of optic ganglia. And it should not be confused with adaptation, which is another inherent property of the receptors: it is rather a dynamic process of control of selective blocking from the nervous system outwards. This type of habituating property of the movement-sensitive neurone has been also found in other animals, such as the "newness' neurone in the frog (Lettvin *et al.*, 1961) and movement sensitive neurone in the locust (Horridge *et al.*, 1965). Further investigation of the underlying mechanism of habituation of the movement sensitive neurone might give some important clues to solve the neural mechanism of the movement perception.

Acknowledgement: The authors express their deep gratitude to Prof. Mituo Tamasige for his helpful suggestions and criticisms. We also thank Dr. J.A. Coles for his assistance in preparing the manuscript.

Summary

1. Spike discharges of single movement fibre were recorded in the optic nerve of the crayfish, *Procambarus clarki* (Girard) with steel needle electrodes.

2. The effect of stimulus area on the responses was examined. The fibres could be classified into two types according to the angle subtended by the stimulus area which produced the maximal response: for the large field type this was about 30° and for the small field type this was about 10°.

3. When the object was kept in moving through the receptive field under intermittent illumination with flash frequencies between 1 and 10 flashes per second, a rhythmical discharge at the flash frequency was evoked.

4. Under steady or intermittent illumination, for objects lighter than the background the response was caused by the trailing edge, whereas it was the leading edge for objects darker than the background.

5. The movement fibres reacted very little or not at all to an increase in steady illumination. To sudden darkening they responded with a very short "off" burst, provided that their receptive field had been illuminated for some considerable time. However, when the background illumination was intermittent, the response was facilitated and then habituated. When the illumination ceased, 2 or 3 bursts were produced at the frequency of the preceding flashes.

6. Most of the movement fibres always habituated to some extent on repetition of the stimulus, but some movement fibres did not habituate to flashes in a certain band of frequencies, usually centred at 4 Hz.

7. The effect of intermittent illumination composed of paired flashes was also studied. When the durations of the flashes in the pair were not equal, a decrease in flash frequency produced a response which was locked to the flash of longer duration.

8. With paired flashes, decrease in the light intensity of either member of each pair produced a response which facilitated and then habituated. The occurence of response was locked to the unchanged flash.

9. If the interval between the flashes in the pair was progressively reduced at a constant frequency, spikes were induced and their occurences were locked to either the first or second flash of the pair.

10. When the light intensities of the flashes in the pair were not equal, the occurence of the response to decrease in light intensity of either the first flash or the second flash was locked to the flash of higher intensity.

References

Barlow, H. B. 1953. Summation and inhibition in the frog's retina. J. Physiol. **119**: 69–88.

————, Hill, R. M. and W. R. Levick 1964. Retinal ganglion cells responding selectively to direction and speed of image motion in the rabbit. Ibid. **175**: 377–407.

Bishop, L. G., Keehn, D. G. and G. D. McCann 1968. Motion detection by interneurons of optic lobes and brain of the flies *Calliphora phaenicia* and *Musca domestica*. J. Neurophysiol. **31**: 509–525.

Buttenandt, E. and O.-J. Grüsser 1968. The effect of stimulus area on the response of movement detecting neurons in the frog's retina. Pflügers Archiv **298**: 283–293.

Etinne, A. S. 1968. Die Beantwortung vom Flimmerfrequenzen durch die Lebellenlarve *Aeschna cyanea* M. Z. vergl. Physiol. **61**: 34–40.

Ewert, J.-P. and F. Hock 1972. Movement-sensitive neurones in the toad's retina. Exp. Brain Res. **16**: 41–59.

Grüsser, O.-J., Grüsser-Cornehis, U., Finkelstein, D., Henn, V., Patutschnik, M. and E. Buttenandt 1967. A quantitative analysis of movement detecting neurons in the frog's retina. Pflügers Archiv **293**: 100–106.

————, ———— and M. D. Licker 1968. Further studies on the velocity function of movement detecting class-2 neurons in the frog retina. Vision Res. **8**: 1173–1185.

Grüsser-Cornehis, U., Grüsser, O.-J. and T. H. Bullock 1963. Unit response in the frog's tectum to moving and nonmoving visual stimuli. Science **141**: 820–822.

Hartline, H. K. 1940. The effects of spatial summation in the retina on the excitation of the fibres of the optic nerve. Amer. J. Physiol. **130**: 700–711.

Hassenstein, B. 1951. Ommatidenraster und afferente Bewegungsinteration. Z. vergl. Physiol. **33**: 301–326.

———— 1961. Wie sehen Insekten Bewegungen. Naturwiss. **48**: 207–214.

Himstedt, W. 1969. Zur Funktion eines Reizfiltermechanismus im visuellen System von Urodelen. Z. vergl. Physiol. **62**: 197–204.

Horridge, G. A., Scholes, J. H., Shaw, S. and J. Tunstall 1965. Extracellular recordings from single neurones in the optic lobe and brain of the locust. In "The physiology of the insect central nervous system", Ed. by J.E. Treherne and J.W.L. Beament, Academic Press, New York.

Kuffler, S. W. 1953. Discharge patterns and functional organization of the mammalian retina. J. Neurophysiol. **16**: 37–68.

Lettvin, J. Y., Maturana, H. R., McCulloch, W. S. and W. H. Pitts 1959. What the frog's eye tells the frog's brain. Proc. I.R.E. **47**: 1940–1959.

————, ————, ———— and ———— 1961. Two remarks on the visual system of the frog. In "Sensory Communication", Ed. by W.A. Rosenblith, The M.I.T. Press, Cambridge.

McCann, G. D. and J. C. Dill 1969. Fundamental properties of intensity, form and motion perception in the visual nervous systems of *Calliphora phaenisis* and *Musca domestica*. J. gen. Physiol. **53**: 385–413.

Meyer, H. W. 1971. Visuelle Schlüsselreize für die Auslösung der Beutefanghandlung beim Bachwasserläufer *Velia caprai* (Hemiptera, Heteroptera). 2. Untersuchung der Wirkung zeitlicher Reizmunster mit Flimmerlicht. Z. vergl. Physiol. **72**: 298–342.

Northrop, R. B. and E. F. Guignon 1970. Information processing in the optic lobes of the rubber grasshopper. J. Insect Physiol. **16**: 691–713.

Palka, J. 1967. An inhibitory process influencing visual responses in a fibre of the ventral nerve cord of locusts. Ibid. **13**: 235–248.

Reichardt, W. 1957. Autokorrelationsauswertung als Funktionsprinzip des Zentralnervensystems. Z. Naturforsch. **12b**: 447–457.

———— 1961. Autocorrelation, a principle for the evaluation of sensory information by the central nervous system. In "Sensory Communication", Ed. by Rosenblith, W.A., The M.I.T. Press, Cambridge.

———— 1962. Nervous integration in the facet eye. Biophys. J. **2**: 121–143.

———— and D. Varujú 1959. Übertragungseigenschaften im Auswertesystem für das Bewegungssehen. Z. Naturforsch. **14b**: 674–689.

Schipperheyn, J. J. 1965. Contrast detection in frog's retina. Acta physiol. pharmacol. neerl. **13**: 231–277.

Swihart, S. L. 1968. Single unit activity in the visual pathway of the butterfly *Heliconius erato*. J. Insect Physiol. **14**: 1598–1601.

Tauc, L. 1960. Evidence of synaptic inhibitory actions not conveyed by inhibitory postsynaptic potentials. In "Inhibition in the nervous system and Gamma-aminobutyric acid", Ed. by Roberts, E., Pergamon Press, Oxford.

Waterman, T. H. and C. A. G. Wiersma 1963. Electrical responses in decapod crustacean visual systems. J. cell. comp. Physiol. **61**: 1–16.

————, ———— and B. M. H. Bush 1964. Afferent visual responses in the optic nerve of crab, *Podophthalmus*. Ibid. **63**: 135–155.

Wiersma, C. A. G., 1970. Neural components of the optic nerve of the crab, *Carcinus maenas*. Proc. Kon. Ned. Akad. Wet. **C73**: 25–34.

————, Bush, B. M. H. and T. H. Waterman 1964. Efferent visual response of contralateral origin in the optic nerve of the crab, *Podophthalmus*. J. cell. comp. Physiol. **64**: 309–326.

———— and T. Yamaguchi 1966. The neuronal components of the optic nerve of the crayfish as studied by single unit analysis. J. comp. Neurol. **128**: 333–358.

———— and ———— 1967a. The integration of visual stimuli in the rock lobster. Vision Res. **7**: 197–204.

———— and ———— 1967b. Integration of visual stimuli by the crayfish central nervous system. J. exp. Biol. **47**: 409–431.

Yamaguchi, T. and T. Ohtsuka 1973. Dual channeling mechanism of brightness and dimness information in the crayfish visual system. J. Fac. Sci. Hokkaido Univ. Ser. VI, Zool. **19**: 15–30.