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Functional Properties of the H1-Neurone in the Third Optic Ganglion of the Blowfly, *Phaenicia*

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Summary. Response properties of the identified H1-neurone upon monocular stimulation were investigated by means of extracellular recordings. Comparison with optomotor torque responses under the same or similar stimulus conditions demonstrated:

1. The neurone is excited by regressive pattern motion and inhibited by progressive pattern motion. Vertical motion and stationary patterns induce only weak excitatory responses (Fig. 3, 8).

2. If the spatial wavelength (λ) of the pattern is smaller than twice the interommatidial angle $\Delta\varphi$, i.e. $\Delta\varphi < \lambda < 2\Delta\varphi$, the response properties with regard to the direction of pattern movement are reversed: regressive motion causes an *inhibition* and progressive motion an *excitation* (Fig. 8A). This finding accords with the concept of geometrical interference between the array of receptors and the moving striped pattern causing a reversal of the direction of movement of the interference pattern by 180 deg. As in the optomotor torque response, the geometrical interference is related to the interommatidial angle.

3. The response versus pattern velocity functions possess a spatial wavelength (λ) dependent maximum as do optomotor torque responses (Fig. 8).

4. The response versus pattern velocity curves share a common peak if the λ-dependence is eliminated by plotting the response versus the contrast frequency (Fig. 9). The maximum of the dependence lies at $w/\lambda = 1.4$ Hz and thus agrees well with that of the optomotor torque response at 1–3 Hz (Fig. 10).

5. The size and sensitivity profile of the receptive field is similar to that obtained by evaluation of the torque response.

6. Statistical properties of the response under steady-state conditions show that the most frequent spike interval deviates from that corresponding to the average frequency: the lower the average frequency the larger the deviation. This finding is due to the asymmetrical distribution of the spike intervals. Of the two measures, the spike frequency corresponding to the most frequently occurring spike interval gives a better fit to the optomotor torque response.

I. Introduction

A moving surrounding elicits turning reactions in insects, the 'optomotor reactions'. These reactions have been studied extensively by means of behavioural experiments yielding insights into the mechanisms of movement perception underlying these reactions (Hassenstein and Reichardt, 1956; review Reichardt and Poggio, 1976).

Electrophysiological studies revealed the existence of *D*irectionally *S*elective *M*otion *D*etecting neurones (DSMD). Such motion sensitive neurones were first reported in flies by Bishop and Keehn (1966) to occur in the third optic neuropil and central protocerebrum, and have since been studied extensively by means of extracellular (e.g., Bishop and Keehn, 1966; Bishop et al., 1968; McCann and Dill, 1969; McCann and Foster, 1971; McCann, 1973; Mastebroek et al., 1977; Zaagman et al., 1977) as well as intracellular recordings (Dvorak et al., 1975; Eckert, 1976; Hausen, 1976a, b; Eckert, 1977; Hengstenberg, 1977; Eckert, 1978; Eckert and Bishop, 1978).

These DSMDs are of particular interest in relation to optomotor responses since they may be an integral part of the neuronal system controlling such behavioural reactions. In this communication I report on the functional properties of the 'contralateral horizontal inward fibre' (Bishop et al., 1968) in relation to optomotor responses. This neurone has been

Abbreviations: *DSMD*, directionally selective motion detecting neurone; *imp/s*, impulses/s (=i/s); *PSTH*, peristimulus time histogram

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identified anatomically by means of intracellular dye injections (Hausen, 1976a, b; Dvorak and Eckert, in preparation), and was provisionally named the 'H1-neurone' (Hausen, 1976a).

II. Materials and Methods

A. Experimental Preparation

Female specimens of the blowfly *Phaenicia* (=*Lucilia*) *sericata* were the principle species used in this study. Some experiments were also performed on the blowfly, *Calliphora erythrocephala*. The experimental animals were taken from cultures bred in the institute.

The animals were prepared for the experiments according to the procedure described previously (Dvorak et al., 1975; Eckert and Bishop, 1978). In addition the head was fixed to the thorax via a wax bridge in order to reduce head movements. The posterior part of the head was cut open and some of the air sacs removed to permit access to the brain tissue. A tungsten electrode was placed on the exposed posterior part of the third optic ganglion. The indifferent electrode consisted of an Ag-AgCl wire which was inserted into a small opening cut into the back of the head capsule. Subsequently the opening was sealed with wax in order to prevent dehydration. Frequent checks with standard stimulus conditions showed that stable recordings could be obtained lasting for several hours. In order to ensure the same conditions of adaptation, the animals were kept in the dark for 20 min after completing the experimental preparation. After placement of the electrode the animal was allowed to adapt to the pattern luminance for 5 min.

B. Stimulus Equipment

The experimental apparatus is shown schematically in Fig. 1. Moving stimulus patterns were presented by a pattern projector. The spatial wavelength (angular width of a dark and a light stripe) of the pattern, λ [deg], could be varied between 2 and 40 deg by using different cylinders and/or different distances (Q) between the pattern cylinder (PC) and the screen (S). The mask (M) was used for changing the size of the stimulus field. Spatial distortions of the projected pattern have a strong effect on the response of these neurones, therefore the pattern projector was constructed so that the light source was always in the centre of the metal cylinders. The distortions of the pattern on the circular milky glass screen could be compensated by keeping the distance D between the lamp (L) and the screen (S) equal to the distance D′ between the animal and the screen.

The pattern cylinders were mounted on a gearbox (Minarik Co.) which was driven by a DC-controlled motor. Pattern velocities, w, could be varied between 0.16 and 160 deg/s. The intensity of the quartz iodine lamp (L) was controlled by a DC power supply. The luminance of the pattern was measured with a compensated thermopile (Kipp and Zonen, The Netherlands) and a Luxmeter (Gossen), respectively.

The average irradiance $\bar{I}$ and the contrast m are given by

$$\bar{I}=\tfrac{1}{2}(I_{max}+I_{min}) \quad \text{and} \quad m=\frac{I_{max}-I_{min}}{I_{max}+I_{min}},$$

where I_{max} and I_{min} denote the maximal and minimal irradiance, respectively.

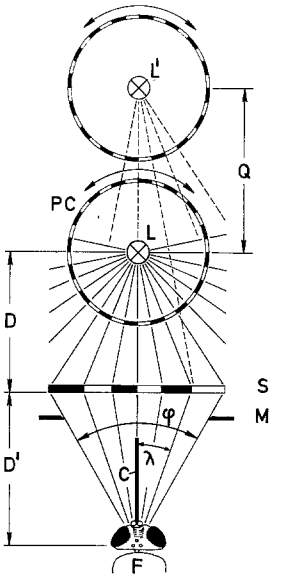

Fig. 1. Semi-schematic drawing of the pattern projector used for stimulus presentations. The rays of a *DC*-operated quartz iodine lamp (*L*) located in the axis of a metal pattern cylinder (*PC*) project onto a milky glass screen (*S*). The pattern cylinder is mounted on a *DC*-driven motor via a gear box. The pattern cylinder together with the light bulb can be moved continuously over a distance *Q*, as indicated by the light bulb position *L'*, enabling a continuous change in spatial wavelength. Furthermore, different pattern cylinders could be used. A piece of charcoal blackened cardboard (*C*) was attached to the animal preventing binocular vision. *F*, fly; *M*, mask

C. Data Collection and Analysis

After breaking the tip insulation of the coated tungsten electrode with a brief current pulse, the electrode was lowered onto the third optic ganglion. Usually, spikes of the motion sensitive neurones, the "contralateral horizontal inward fibres" (Bishop et al., 1968), were obtained immediately after penetration of the neurolemma covering the optic ganglia. The signals were amplified and filtered (frequency bandwidth of 0.4 to 3 kHz). The filtered signal was then fed into a window discriminator of our own construction allowing separation of spikes of different amplitudes.

Data were continuously recorded on magnetic tape (Ampex, model 1300; Hewlett Packard, model 3960, Bell&Howell, model CPR 4010B). A frequency-to-voltage converter (FVC), also of our own construction, was employed to obtain the instantaneous frequency. The time constant of the FVC could be varied (0.02 to 1 s) in order to obtain average frequency responses. Some of the data were analyzed with a didac 800 computer (Intertechnique).

Data points in this communication were obtained from 6–14 animals. Average values $\bar{x}$ of single experimental data points x_i of total number N and their standard errors are shown.

The slope of the continuous curve of Fig. 10 was evaluated by means of a linear regression curve.

D. Definitions

The direction of horizontal pattern movement stimulating ommatidia from the anterior to the posterior regions of the eye is called *progressive*; reversal of this direction of motion is called *regressive* (Götz, 1968).

The ratio of angular velocity w[deg/s] and spatial wavelength λ [deg] is called the *contrast frequency* w/λ [s^{-1} = Hz].

The direction of motion eliciting a maximal response is called *preferred direction*, the reverse direction of motion *antipreferred* (null direction of Bishop et al., 1968).

Peristimulus time histogram will be abbreviated PSTH.

III. Results

A. Neuron Identity

Extracellular recordings could be obtained easily in the dorsal part of the lobula plate and the dorsolateral protocerebrum upon stimulation of the contralateral eye (relative to the position of the electrode). Regularly, spikes of a second motion sensitive neurone were encountered possessing the same directional sensitivity. However, this latter neurone responded to stimulation of the ipsilateral eye and, furthermore, its spike amplitude was usually smaller than that of the neurone responding to stimulation of the contralateral eye. Upon stimulation of both eyes, both spike potentials were recorded simultaneously (compare also Bishop et al., 1968; McCann and Dill, 1969, 1969) as has been found in *Calliphora,* though infrequently (Hausen, 1976b).

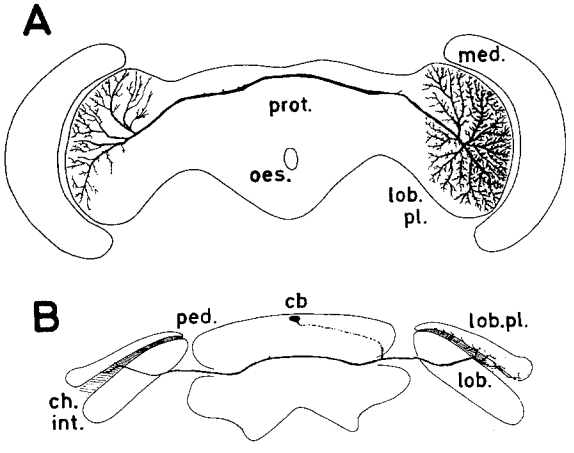

Fig. 2A and B. Graphical reconstruction of an H1-neurone after fluorescence microphotographs of serial frontal (**A**) and horizontal (**B**) sections. The cells were stained by intracellular iontophoretic injection of Procion Yellow. The dendrite is shown on the right side and the telodendron on the left side, respectively. The dendritic arborisations penetrate deeply into the lobula plate (*lob. pl.*), the caudal part of the third visual neuropile. The axon traverses the rostral part of this neuropile, i.e. the lobula (*lob.*), ascends and crosses along the dorsal surface of the central protocerebrum to the contralateral side, traverses the contralateral lobula, branches in inner optic chiasma (*ch. int.*) and penetrates into the contralateral lobula plate. The cell body fiber originates close to the dendritic arborisation. It traverses, descending, to the median plane, terminating in a cell body (*cb*) which lies dorsal to the frontal orifice of the oesophageal canal. The direction of signal transmission is from right to left. *med.*, medulla; *oes.*, oesophagus; *ped.*, optic peduncle. *Phaenicia* ♀

By applying extra-/intracellular double recording and dye injection techniques it was possible to identify these neurones: Fig. 2 shows such a neurone which was identified anatomically by intracellular injection of Procion Yellow. The neurone has been described for *Calliphora* too, and was named provisionally H1-neurone (Hausen, 1976b). These findings will be dealt with elsewhere (Dvorak and Eckert, in preparation).

Since we know the anatomy of the cell and its direction of signal propagation, the terms *ipsi-* and *contralateral* will hence forward be used with respect to the input region of the cell, i.e. the dendrite shown on the right side of Fig. 2 (dendritic arborisation = ipsilateral).

B. General Properties of the Response

The effects of stationary and horizontally moving patterns on the spike frequency of the H1-neurone are shown in Fig. 3. In the presence of a stationary, illuminated pattern the resting activity varied from 2–25 impulses/s (imp/s) (Fig. 3A) depending on mean irradiance (see also Fig. 5 and 8). Regressive pattern movement (i.e. from posterior to anterior of the eye) strongly increased the spike activity to levels approaching 200 imp/s (Fig. 3B). Progressive movement, on the other hand, usually caused complete inhibition of spiking (Fig. 3C).

Figure 4 shows a peristimulus time histogram (PSTH) for an H1-neurone depicting transient and

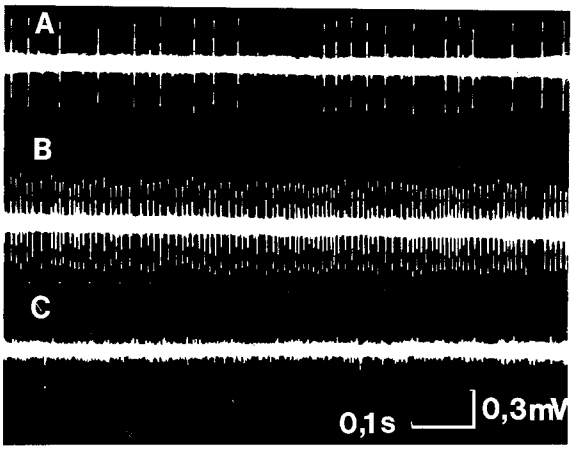

Fig. 3A–C. Response of the H1-neurone to a moving grated pattern 3 s after the onset of the stimulus. The more intensely reproduced part of the spike corresponds to a second peak of the action potential. The stimulus was presented to the contralateral eye. **A** Stationary pattern. **B** Pattern movement in the preferred direction, i.e. regressive. **C** Pattern movement in the anti-preferred direction (null direction), i.e. progressive. Pattern wavelength $\lambda = 21.5$ deg; contrast $m = 0.68$; angular velocity $w = 11$ deg/s; average pattern irradiance 0.08 mW/cm^2. *Phaenicia* ♀

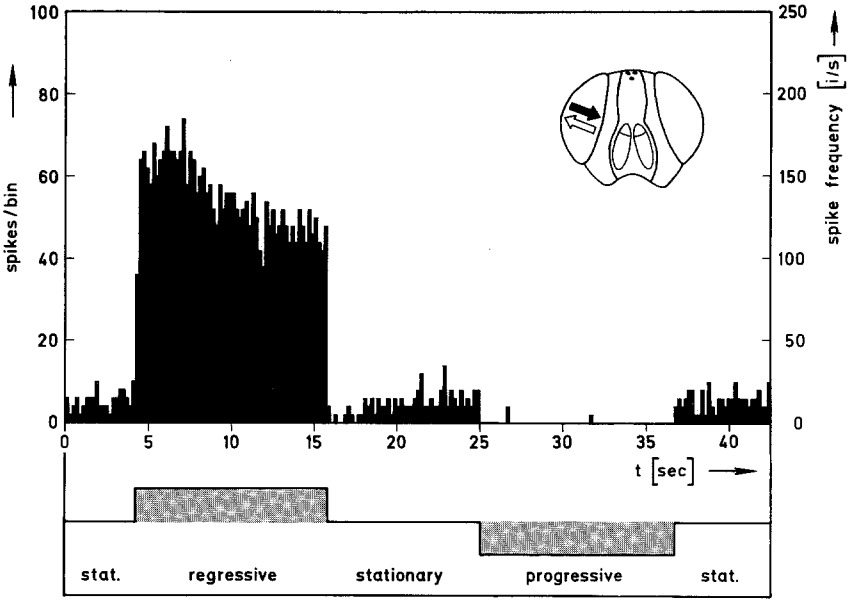

Fig. 4. Peristimulus time histogram (*PSTH*) of the H1-neurone to stationary and horizontally moving patterns. The left ordinate is given in spikes per bin and the right ordinate in imp/s (i/s), respectively. The lower trace in the figure indicates the stimulus. Regressive pattern motion results in a strong excitation, whereas progressive pattern motion results in strong inhibition, almost completely abolishing spike activity. The corresponding directional sensitivity of the neurone is shown in the inset in which the solid black arrow signifies excitation and the outlined inhibition. Spatial pattern wavelength $\lambda = 21.5$ deg; pattern velocity $w = 35$ deg/s; average pattern irradiance $\bar{I} = 0.08$ mW/cm^2; bin width 200 ms. *Phaenicia* ♀

steady-state response characteristics. The PSTH shows the number of spikes occurring in consecutive time intervals of 200 ms duration during various stimulus presentations. The resting activity in this case was approximately 13 imp/s. As shown in Fig. 4 the onset of regressive movement caused the spike frequency to increase transiently to 65 imp/s and then decrease subsequently to a steady-state value of 50 imp/s. Cessation of regressive movement was followed by post-excitatory inhibition lasting for one to two s after which time spike activity returned to the previous resting level. Progressive movement either reduced the spike activity or, depending on the strength of the stimulus, suppressed it completely. Upon cessation of the inhibitory stimulus, spike activity immediately returned to the resting level. Occasionally, a transient increase in spike frequency above the resting level was observed, indicating a post-inhibitory excitation.

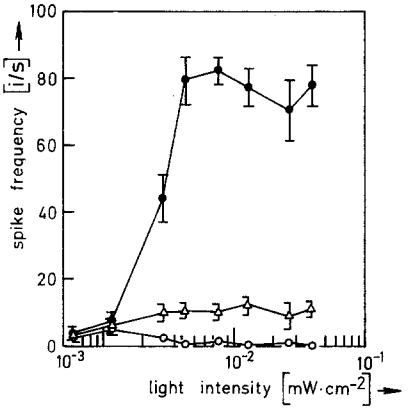

Fig. 5. The average response and associated standard error of the H1-neurone are shown as a function of the average pattern irradiance. Filled circles (●) show response to regressive pattern motion and open circles (○) the response to progressive pattern motion. The corresponding response values for stationary patterns, taken between measurements of the responses to moving patterns, are shown by open triangles (△). Pattern wavelength $\lambda = 11.4$ deg; pattern velocity $w = 10$ deg/s. *Phaenicia* ♀

C. Intensity Dependence

The response to stationary and moving patterns as a function of mean irradiance is shown in Fig. 5. In a fully dark adapted cell spontaneous dark activity was 1–4 imp/s. Upon illumination, resting activity was elevated to 10–16 imp/s; occasionally, a higher resting activity (20–25 imp/s) was observed. The threshold irradiance for directional responses was 1.2×10^{-3} mW/cm^2. At intensities above this threshold the excitatory and inhibitory effects of regressive and progressive movement, respectively, sharply increase and then plateau at mean irradiances higher than 4×10^{-3} mW/cm^2.

D. The Extent of the Receptive Field

Although the general response properties are invariant within the receptive field of the H1-neurone, a constant stimulus presented to separate parts of the field results in different absolute spike frequencies. In order to determine the variation in movement sensi-

tivity within the respective field a different type of stimulus was used, which is described in detail elsewhere (Eckert and Bishop, 1978). Briefly, 16 sequentially flashing light bulbs were mounted on a semicircular bar which was part of a gimbal system. If the phase difference in the flashes from successive lights is suitably adjusted, such a stimulus induces apparent ("phi") movement evoking clearly directional responses in the H1-neurones. With the animal positioned in the centre of the light carrying bar the response to apparent motion in the vertical and horizontal direction was determined for different positions within the receptive fields of both eyes (Fig. 6).

Figure 6 shows that under these stimulus conditions the neurone responded to monocular stimulation of the ipsilateral eye. Stimulation of the contralateral eye was essentially ineffective, apart from a small effect attributable to ommatidia 'looking' across the midline (binocular region of the eye). Horizontal apparent motion elicited a strong response in the ventral part of the receptive field. The peak was found approximately 20 deg ventral to the equator of the eye. In the dorsal part of the eye the response still differed from the resting level by a factor of 1.7, but the difference was much less pronounced than in the equatorial and ventral parts of the eye.

Vertical apparent motion elicited a response which was much smaller than its horizontal counterpart. A peak was found at approximately 20 deg lateral of the longitudinal axis of the animal. The response amplitude ceased gradually towards the lateral region of the eye. Responses to vertical apparent motion were very small in the posterior region of the eye (110–160 deg; not shown in Fig. 6). But stimulation of this eye region by horizontal object motion still elicited a response.

Thus, the receptive field of this cell corresponds to that of the whole eye. Its centre is approximately 20 degrees lateral of the longitudinal axis, and 20 degrees ventral of the equator of the eye, i.e. in the anterior, equatorial eye region. In the experiments described below, the stimulus pattern was positioned in this most sensitive part of the receptive field.

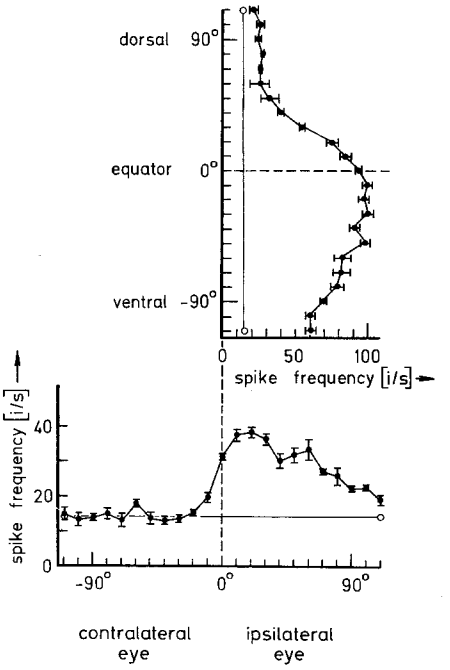

Fig. 6. Extent of the receptive field as measured by the response to sequentially flashing light bulbs spaced 12.5 deg apart. The upper graph shows the response to horizontal 'apparent motion' and the lower graph illustrates the response to vertical 'apparent motion'. Thus, the upper graph represents a vertical cross section and the lower graph a horizontal cross section through the receptive field of the neurone, respectively. Note the different scales for the spike frequency in both graphs: in the upper graph we find that the response in the dorsal part of the receptive field is still clearly higher than the resting activity (14.2 i/s), whereas in the lower graph, the response to stimulation of the right (i.e. the ipsilateral) eye corresponds to the resting activity (indicated by open circles connected by a straight line)

E. Statistical Properties of the Response

The response to regressive movement of different angular velocities is given in Fig. 7. PSTH's are shown on the left side (Fig. 7A–F); on the right side are the corresponding spike interval histograms (Fig. 7G–M). The excitatory response was barely above the background level at low pattern velocities; towards intermediate velocities the response increased rapidly and reached a maximum (compare with Fig. 8) and decreased towards high pattern velocities. Within an intermediate range of pattern velocities and especially at high pattern velocities, the transient response already described could by observed (Fig. 7B) following the onset of the stimulus.

As is evident from Fig. 8, a certain spike frequency could be elicited by two different pattern velocities (which were slower and faster, respectively, than the pattern velocity eliciting a maximal response). Since no differences were found in the stochastic properties of the response to these different stimulus conditions provided the *average* spike frequency was the same, the PSTH and spike interval histograms corresponding to a given *average spike frequency* are shown in Fig. 7. Figure 7L presents an example of this observation: both spike intervals shown were derived from responses in which the average frequencies were 70 imp/s and 81 imp/s, respectively. The corresponding pattern velocities for both spike interval histograms were 8.4 deg/s (black histogram) and 124 deg/s

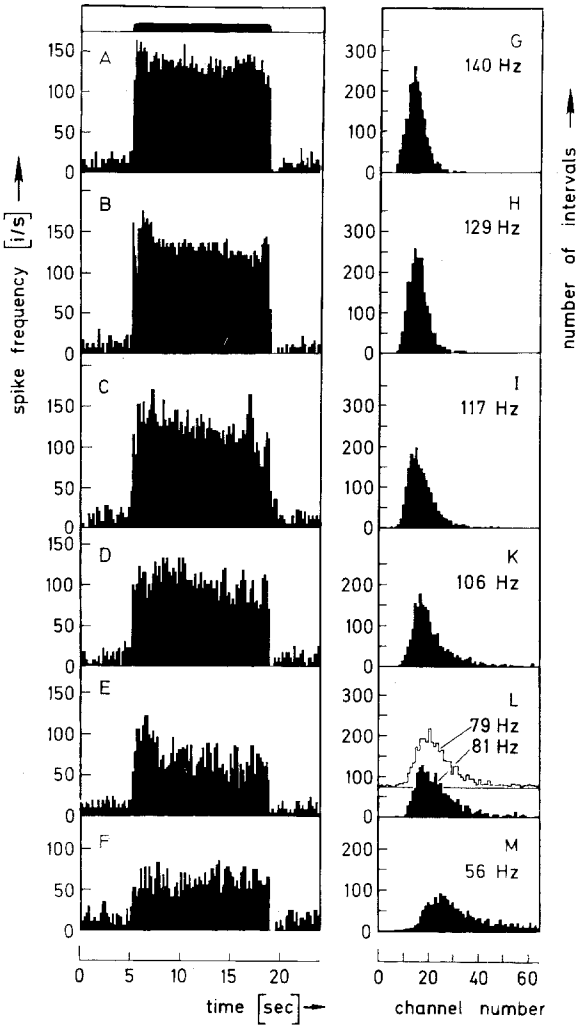

Fig. 7A–M. PSTHs of the response to different pattern velocities (**A–F**) and their corresponding spike interval histograms (**G–M**). The latter were obtained from responses which had already reached the steady-state value (i.e. approximately 3 s after the onset of the excitatory stimulus). The average spike frequency elicited by each pattern velocity is given on the right part of the figure. The bin widths of the PSTHs correspond to 200 ms; the channel widths of the spike interval histograms correspond to 0.5 ms. Each spike interval histogram was obtained from a total of 2000 intervals. **A, G**: 35 deg/s; **B, H**: 23 deg/s; **C, I**: 13 deg/s; **D, K**: 11 deg/s; **E, L**: 8.4 deg/s and 124 deg/s respectively; **F, M**: 4 deg/s. Pattern wavelength $\lambda=21.5$ deg; average pattern irradiance: $\bar{I}=1.2$ mW/cm^2. *Phaenicia* ♀. For details see text

(outlined histogram). Neither histogram exhibits any statistically significant differences.

The interval histograms show a peak whose position depends on the average spike frequency of the neurone. At low average frequencies the peak occurs at later times (Fig. 7M) than at high average frequencies (Fig. 7G). Because of the asymmetrical distribution of the spike intervals, the most frequent interval does not necessarily coincide with the corresponding average frequency. For example, the average frequency of curve D in Fig. 7 is 106 imp/s, whereas the peak value of the corresponding interval histogram lies at 16×0.5 ms$=8.0$ ms, which corresponds to 125 imp/s. Thus, the *most frequent* spike interval corresponds to a higher spike frequency than the observed *average* spike frequency.

The asymmetry of the spike interval histograms was investigated by statistical means applying the sign test (Zeichentest) to the interval histograms shown in Fig. 7G and L. Denoting:

D = most frequently observed value;
$\tilde{x}$ = central value, i.e. the value at which the cumulative distribution of spike intervals reaches 50% of the end value;
$\bar{x}$ = average value of spike intervals;

we find for the spike interval histogram shown in Fig. 7G that $D\cong\tilde{x}\cong\bar{x}$, i.e., the distribution is symmetrical; whereas for the spike intervals shown in Fig. 7L we find that $D<\tilde{x}<\bar{x}$, i.e., the distribution is asymmetrical possessing a long tail towards longer spike intervals. A further quantitative measure of the asymmetry is given by the skewness, γ, defined as

$$\gamma=\frac{\mu_3}{\sigma^3}$$

with

$$\mu_3=\frac{\Sigma(x_i-x)^2}{n-1} \quad \text{and} \quad \sigma=\sqrt{\frac{\Sigma(x_i-x)^2}{n-1}}.$$

For a symmetrical distribution we expect $\gamma=0$, whereas an asymmetrical distribution of spike intervals causes a value $\gamma=0$. For the spike interval histograms shown in Fig. 7G we find $\gamma=0.267$, i.e., the distribution is almost symmetrical; whereas for the spike interval histograms shown in Fig. 7L we obtain $\gamma=1.842$, i.e., $\gamma>0$, and thus, these spike intervals are distributed asymmetrically around the mean.

F. Dependence of the Response on the Pattern Velocity

The velocity dependence measured at several spatial wavelengths is shown in Fig. 8. For regressive movement, spike frequency increases as pattern velocity increases, reaches a maximum, then decreases at high velocities. The curves illustrate that, for regressive movement:

(1) the peak response is shifted to higher velocities at longer spatial wavelengths, and

(2) peak spike frequencies are spatial wavelength dependent.

Also, with increasing spike frequencies in response to regressive movement, the corresponding progressive movement exerts an increasingly strong inhibitory influence (e.g. Fig. 8D). Of particular interest is the response measured at $\lambda=2.0$ deg (Fig. 8A). Here, regressive and progressive movement produced effects exactly opposite to those observed for longer spatial wavelengths. This reversal in the response

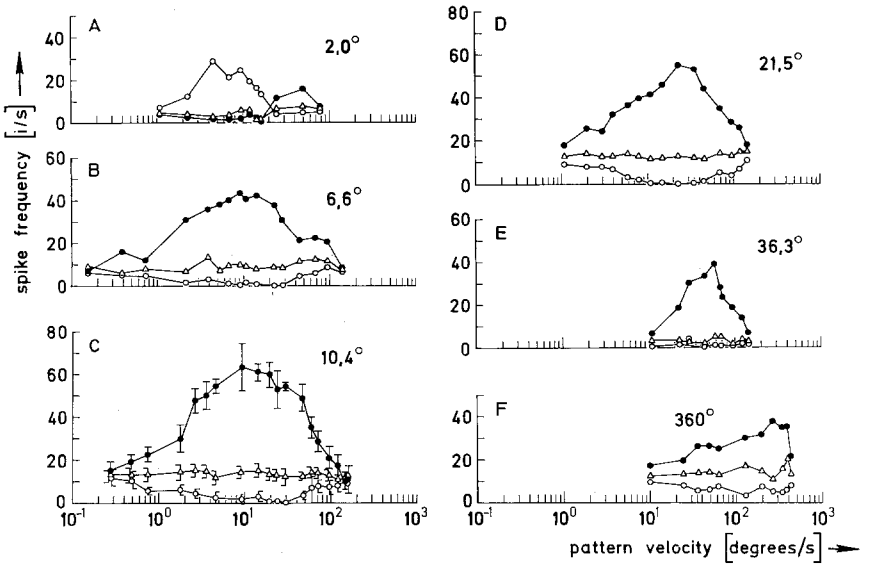

Fig. 8A–F. Response of an H1-neurone to stationary and horizontally moving patterns as a function of the pattern velocity. The pattern wavelengths are given in the upper right hand corner of each graph. Figures A–E give examples of the response characteristics obtained from one animal. The stimulus pattern was provided by the pattern projector described in Sect. II.B; the response to a 360 deg pattern was obtained from a different animal which was positioned inside a rotating drum described elsewhere (Bishop et al. 1968). Each data point was obtained by averaging the spike frequency over 45 s. The standard error for such measurements is exampled in curve C. Filled (●) and open circles (○) show the response to regressive and progressive pattern movement, respectively; the open triangles (△) depict the corresponding response to a stationary pattern, taken between the measurements of the response to moving patterns. *Phaenicia* ♀

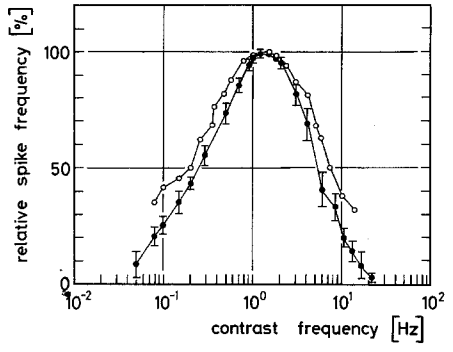

Fig. 9. The normalised spike frequency of the H1-neurone is shown against the ratio of pattern velocity and pattern wavelength, i.e., the contrast frequency. The response is taken as the difference in spike frequency elicited by regressive pattern motion and a stationary pattern and is normalised with respect to the peak amplitudes. Filled circles (●) correspond to averages of data points obtained from curves like those shown in Fig. 8. Open circles (○) give the spike frequency corresponding to the interspike interval occurring most frequently. Bars indicate standard error. Details see text. *Phaenicia* ♀

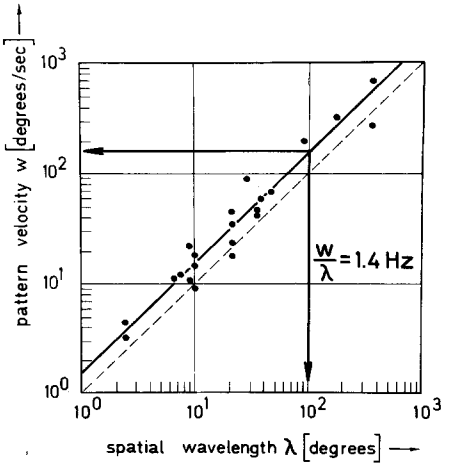

Fig. 10. Peak values of the spike frequency versus pattern velocity curves obtained for different pattern wavelengths are shown in a w/λ-diagram. A regression line (thick line) through the data points indicates that a response maximum occurs if the pattern moves with a contrast frequency of w/λ = 1.4 Hz (see arrows). *Phaenicia* ♀. Values for 180 deg and 7.3 deg obtained from *Calliphora* ♀. The dashed line shows the regression line obtained from optomotor experiments on *Musca* (Eckert, 1973)

characteristics is due to the well known phenomenon of geometrical interference (e.g. Götz, 1964; Buchner, 1976). Figure 8A shows in addition that at velocities higher than 10 deg/s the 'normal' response is again observed. This small effect is probably a stimulus artefact: a slightly incorrectly milled pattern cylinder possesses an additional 360 deg harmonic component which would induce a 'normal' response at higher pattern velocities.

G. Dependence of the Response on the Contrast Frequency

In the preceding section it was shown that, for regressive movement, the peak response shifts to higher velocities as the spatial wavelength is increased (Fig. 8). To clarify this relationship the curves given in Fig. 8 were normalized with respect to their peak response values and the averaged results plotted as

a function of contrast frequency (w/λ). If normalized with respect to spatial wavelength, all velocity dependence curves share approximately the same maximum (Fig. 9): in other words, the response of these neurones does not depend on pattern velocity, but rather on *contrast frequency*. In Fig. 10 the peak values of the curves shown in Fig. 8 are plotted in a velocity vs. spatial wavelength diagram. The regression line through these data points gives the maximum for the average curve of Fig. 8 as $w/\lambda = 1.4$ Hz.

IV. Discussion

Insect optomotor reactions, such as the well studied yaw torque, and thrust responses are based on directional motion perception (e.g., Hassenstein and Reichardt, 1956; Reichardt and Varjú, 1959; Götz, 1964; Kirschfeld, 1972; Reichardt and Poggio, 1976). From behavioural experiments on *Drosophila*, two independent movement detector systems with orthogonal directions of maximum sensitivity were postulated (Götz, 1968): one system, sensitive to horizontal movement, controls torque responses, whereas the second system, sensitive to vertical movement, controls thrust responses. Subsequently, these directions of maximum sensitivity were related to the photoreceptor array (e.g., Kirschfeld, 1972; Buchner, 1976).

Electrophysiological experiments have shown that there are two groups of neurones in the optic lobes of flies with a directional preference for horizontal and vertical movement, respectively (Bishop and Keehn, 1966). It has been repeatedly suggested that these neurons are intimately involved with the control of the above-mentioned optomotor responses (e.g., Bishop and Keehn, 1966; Bishop et al., 1968; McCann and Dill, 1969; McCann and Foster, 1971; Zaagman et al., 1977).

The H1-neurones possess directional sensitivity with respect to moving stimulus patterns: horizontal, regressive movement evokes a strong increase in spike frequency, whereas movement in the opposite direction (i.e. progressive movement) typically inhibits spiking (Figs. 3 and 4). Vertical movement, however, is a relatively ineffective stimulus (Fig. 6; see also Bishop et al., 1968; Zaagman et al., 1977). Optomotor torque responses also exhibit a marked directional sensitivity to horizontal movement. Hence, in order to obtain clues about the possible rôle of the H1-neurones in the optomotor system, we shall compare their response properties to those obtained for torque responses under comparable stimulus conditions.

The general response properties (as shown by Fig. 3–5, and 8) regarding the dependence of the spike frequency on the direction of pattern movement accord with measurements of *Calliphora* (Hausen, 1976b; Zaagman et al., 1977). Hausen (1976b) reports a similar transient increase in the response elicited by regressive pattern movement which slowly decreases to a stationary value above the background spike frequency. A comparison of the response characteristics of the H1-neurone with those of the class II a1 units (e.g., Bishop et al., 1968; McCann and Dill, 1969) shows them to be identical. The extra/intracellular double recording resulting in the stained cell shown in Fig. 2 proves the identity of class II a1 unit and H1-neurone.

An interesting feature of the response of this neurone is shown in Fig. 8A. Upon regressive pattern motion an inhibitory response is elicited, whereas progressive pattern movement evokes an excitatory response. That is, response properties are *reversed* with respect to the directional sensitivity of the neurone since the preferred direction, i.e. the direction of pattern movement eliciting a maximal response, now *inhibits* spiking. Such a finding was also reported for *Calliphora* (Zaagman et al., 1977; Fig. 8 of their report).

This response behaviour, induced by small pattern wavelengths, is to be expected from geometrical interference between the striped pattern and the array of receptors, resulting in Moiré patterns and obeying the relation $\Delta\varphi_h < \lambda < 2\Delta\varphi_h$ (Hertz, 1934; Hassenstein and Reichardt, 1956; Götz, 1964; Eckert, 1973; Buchner, 1976). In this equation, $\Delta\varphi_h$ denotes the effective divergence angle between neighbouring receptors interacting for the perception of movement. In *Phaenicia*, the divergence angle $\Delta\varphi$ along a horizontal axis corresponds to $\Delta\varphi = 2.2$ deg in the anterior part of the eye and increases to $\Delta\varphi = 3.0$ deg within the stimulated area (i.e. approximately 60–70 deg lateral to the midline; Eckert and Franceschini, unpublished results[1]). As an average divergence angle over the whole stimulated eye region (anterior equatorial) we obtain $\overline{\Delta\varphi} = 2.6$ deg. According to the relation given above, this value corresponds to $2\overline{\Delta\varphi_h}$, since we can elicit a reverse reaction by stimulating with a pattern wavelength of $\lambda = 2.0$ deg. The optical measurements thus yield an effective divergence angle of $\Delta\varphi_h = 1.3$ deg and reverse reactions occur at $1.3° < \lambda < 2.6°$. The response of the H1-neurone to a pattern wavelength $\lambda = 2.0$ deg confirms this expectation and shows that its response properties can be correlated directly to the mosaic structure of the eye at the input level of the receptors. (A similar result is obtained by considering the divergence angle of neighbouring ommatidia along oblique axes of the eye deviating from

[1] The divergence angles $\Delta\varphi$ were determined in live, intact animals by evaluation of the deep pseudopupil according to the method described by Franceschini and Kirschfeld (1971, Sect. 6.3.2)

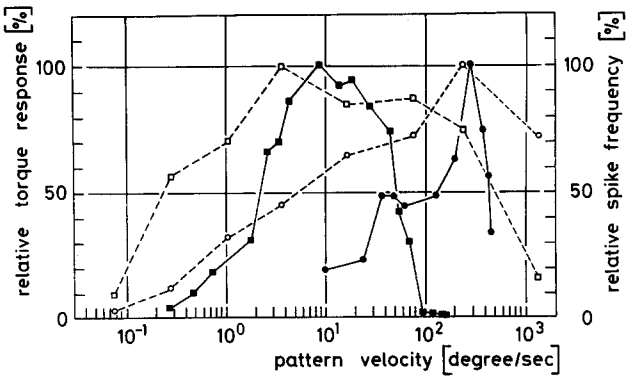

Fig. 11. Response versus pattern velocity curves obtained from electrophysiological responses (●, ■; continuous curves) of the H1-neurone in *Phaenicia* ♀ and optomotor responses (○, □; dashed curves) in *Musca*. Responses are scaled to the same peak amplitudes (■): λ=10.4 deg; (□): λ=11 deg; (●, ○): λ=360 deg

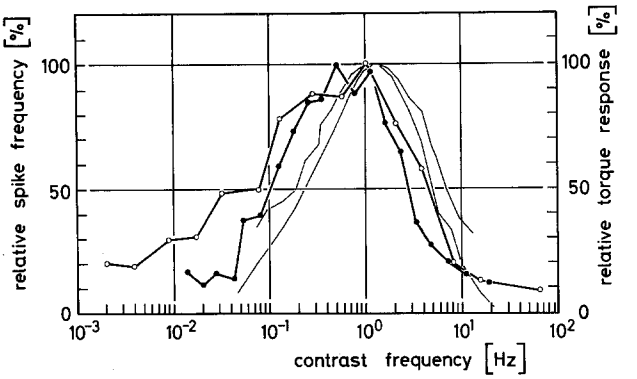

Fig. 12. Dependence of the optomotor response (●, ○; thick lines) and the response of the H1-neurone (thin lines) upon the contrast frequency. (●): *Chlorophanus* (from Hassenstein 1951); (○) *Musca* ♀ (from Reichardt 1965); Electrophysiological data (thin lines) obtained from *Phaenicia* ♀ (Fig. 9). For details see text

the horizontal axis by +30 deg and −30 deg, respectively). These findings confirm experimental results on *Calliphora* (Zaagman et al., 1977) and accord with optomotor measurements of the torque response for which reverse reactions were observed obeying the relationship given above (Hassenstein and Reichardt, 1956; Götz, 1964; Eckert, 1973; review Reichardt and Poggio, 1976; Buchner, 1976).

The similarity between the general response characteristics of the optomotor responses and those of the H1-neurone extends beyond the general features discussed above. Both the neurone and the torque response are elicited at very low light levels: in the almost completely dark laboratory, illuminated only very weakly by the control lights of the instruments, one invariably elicits responses by moving an object in the receptive field of these cells or by just moving around. Recently, it has been shown that, actually, illumination levels corresponding to light fluxes of one photon/s·receptor already elicit responses in the H1-neurone (Dvorak and Lillywhite, in prep.). This light sensitivity is comparable to the threshold light intensity at which optomotor torque responses have been elicited in the fly *Musca* (Eckert, 1973), i.e. 10^{-4} asb corresponding to approximately 0.5 photons/s·receptor.

Another striking similarity is observed in the response versus pattern velocity functions of the optomotor torque response and the output of the H1-neurone: the position of the maximum depends on the pattern wavelength (e.g., Hassenstein and Reichardt, 1956; Reichardt and Varjú, 1959; Götz, 1964; McCann and McGinitie, 1965; Eckert, 1973; Buchner, 1976). Such functions from both experimental approaches are illustrated in Fig. 11 for two pattern wavelengths. The two curves on the left side of the Figure give the response to very similar patterns of 10.4 deg and 11 deg, respectively. Both curves possess a similar maximum: however, the velocity dependence of the turning response is much broader than that of the response of the lobula plate H1-neurone. Comparable characteristics (position of maximum, half-width) are also found in the respective responses to a pattern with a spatial wavelength of 360 deg (Fig. 11). However, since both responses, the torque and the neurone's response, do not depend on the pattern velocity alone but rather on the ratio between pattern velocity and pattern wavelength (i.e., the contrast frequency), the experimental data resulting from both experimental approaches are summarized in Fig. 12 in which the normalized responses are given as a function of the contrast frequency. The close fit between electrophysiological and optomotor data is apparent especially if one takes the frequency corresponding to the *most frequently observed spike interval* in the response (the uppermost thin curve), rather than the average spike frequency of the H1-neurone.

It cannot be decided at the moment which parameter is the more relevant, the spike interval corresponding to the average spike frequency, or the spike interval occurring most frequently. In principle, either parameter may be more efficient in eliciting the response of the postsynaptic neurone. However, this question could only be answered if the response properties of the postsynaptic neurone were known. It is suggestive, however, that the curve obtained from the most frequently occurring spike interval gives a better fit to the optomotor data than the 'average frequency' curve; this may provide a hint that this parameter may be the more relevant one. However, other mechanisms appear possible such as a diminishing nonlinear relationship between H1-spike rate and

torque which would also tend to broaden the normalised response curve.

One has to keep in mind that the optomotor experiments were carried out with the housefly *Musca*, whereas the response of the H1-neurone was obtained from *Phaenicia*. This restriction is not very severe, since preliminary studies on the optomotor responses of *Phaenicia* and *Calliphora* have revealed no differences regarding the shape and peak of such response versus pattern velocity curves. Reverse reactions could be elicited, too, by the use of a pattern wavelength of 2 deg. The same stimulus was used for these optomotor experiments and the electrophysiological experiments, respectively. In the optomotor experiments, the turning tendencies of the animals walking on a Y-maze globe were evaluated (Eckert, unpublished results).

As seen from the comparison made between the responses of the H1-neurone and the optomotor torque responses, there is evidence supporting the 'working hypothesis' that this neurone is part of the neuronal network controlling the animal's torque response. Further support arises from the position of the peak (Figs. 9 and 10) found for a contrast frequency of approximately 1.4 Hz which coincides approximately with the corresponding peak response of the optomotor torque response. The latter was evaluated from the regression line shown in Fig. 10 and lies at 1 Hz (*Musca*, Eckert, 1973). In fact, for all torque responses as well as lift responses so far investigated in different insect species, values of 1–3 Hz were found (Hassenstein and Reichardt, 1956; Reichardt, 1965; review Reichardt and Poggio, 1976; Wehrhahn, 1978).

As a last point we may briefly consider whether the H1-neurone could be involved in the control of more than one behavioural response. It is unlikely that it takes part in the control of another visually controlled, behavioural response – the landing response – a response which is also elicited most effectively by horizontally moving stimuli. This view is based on two experimental findings; firstly, that the landing response shows a maximal reaction strength at a contrast frequency of 6–7 Hz (Fligge, 1978; Eckert, 1979) and secondly, that the preferred direction of the H1-neurone corresponds to regressive pattern motion, whereas the landing response is most easily elicited by progressive stimulus movements.

The results presented in this communication have indicated that the H1-neurone in the lobula plate may be an integral part of the neuronal network controlling the torque responses of flying flies.

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