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On spiking units in the first optic chiasm of the blowfly

III. The sustaining unit

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Abstract. We recorded from the spiking sustaining unit in the optic chiasm between lamina and medulla in the brain of the blowfly *Calliphora vicina*, and investigated both temporal and spatial properties of the light-adapted cell. The sustaining unit fails to follow the highest temporal frequencies followed by the photoreceptor, but its temporal resolution is substantially better than that of the on-off unit. The sustaining unit does not display the fast temporal adaptation as previously described in the on-off unit. As compared with the on-off unit, the sustaining unit has a high sensitivity to small contrasts. Although the sustaining unit continues spiking as long as the light is on, its response is also transient as it adapts rapidly after a change of intensity. The receptive field and the line spread function of the sustaining unit have a similar size and profile: a central lobe with a half-width of approximately 2° surrounded by a circular inhibitory zone located at about 3° off-axis.

Key words: Blowfly – Sustaining unit – Lamina – Spatio-temporal processing – On-off unit

Introduction

Over 20 years ago Arnett (1971, 1972) discovered spiking units in the optic chiasm between lamina and medulla in the brain of the fly *Phaenicia sericata*. On the basis of their response to illumination, Arnett classified these units as either on-off or sustaining. The on-off unit produced a transient response to both the onset and the cessation of light, whereas the sustaining unit responded with a steady spike train to a steady light. Neither of them spiked in darkness. Arnett analysed the spatial properties of these units in the dark-adapted eye. The receptive field of the on-off unit extended beyond that of a single neuro-ommatidium and had an elliptical shape with its major axis horizontally. The receptive field of the sustaining unit showed three roughly circular regions arranged adjacently along a horizontal line. Stimulation of the central region elicited the sustaining response, whereas the adjacent regions only responded with a transient spike train to the cessation of illumination. Both the sustaining and the on-off unit exhibited the same spectral sensitivity as the photoreceptors R1-6 (McCann and Arnett 1972). On the basis of lesion experiments, Arnett (1972) found both units to transmit spikes centripetally (from lamina to medulla).

Recently, we recorded from these units in the blowfly *Calliphora vicina*, and we studied in particular the properties of the on-off unit (Jansonius and van Hateren 1991, 1993). On-off units have a much lower temporal resolution than blowfly photoreceptors. Related to this, the on-off unit adapts quickly to trains of short light pulses, a phenomenon we called fast temporal adaptation. This fast temporal adaptation is independent for on- and off-pulses, and takes place independently in different areas of the receptive field. The receptive field of the on-off unit measures about 7 (horizontally) by 5 interommatidial angles. The half-width of the line spread function (calculated from the response to moving sinusoidal gratings) is, however, only slightly broader than that of the photoreceptor, suggesting that the receptive field consists of a number of more or less independent subunits. Lateral inhibition occurs when two different areas of the receptive field are stimulated simultaneously. The on-off unit does not respond to contrasts of less than 10%.

Although we are at present able to record almost routinely from the on-off unit, the sustaining unit has proven to be much more difficult to record from. Nevertheless, as a result of continuous experiments on the on-off unit, we collected an appreciable amount of data on the sustaining unit. In this article we present data on the temporal and spatial properties of the sustaining unit, collected with stimuli that were similar to those used for the on-off unit. We relate our findings to the anatomical circuitry shaping the responses of both the on-off and the sustaining unit, and we discuss possible

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functions for the sustaining unit in coding visual information.

Materials and methods

For all experiments, we used female blowflies *Calliphora vicina* (*Calliphora erythrocephala M.*), taken from a laboratory culture (F1 to F3, parents caught outside, raised on a vitamin A rich diet). Experiments were performed on unanaesthetised animals after removing a small piece of cuticle from the posterior side of the head, exposing the first optic chiasm between the retina-lamina on the one side and the medulla-lobula complex on the other side. We made extracellular recordings from neurons in this chiasm with tungsten microelectrodes (A-M Systems, type 5760). The recordings from the sustaining unit were either single unit recordings or recordings simultaneously from one on-off unit and one sustaining unit. In the latter case, spikes from the on-off unit were always considerably larger than spikes from the sustaining unit. The recorded signal was amplified, band-pass filtered (1-3 kHz), and sampled at 5 kHz by an ADC (CED1401, Cambridge Electronic Design). From this sampled signal spikes were discriminated on line by an IBM PC/XT-compatible computer at two levels, enabling discrimination of the two types of units in the simultaneous recording. Also on line a post stimulus time histogram with a bin-width of 1 ms was compiled from 40 to 200 stimulus presentations, and stored on disk. Further analysis of the data was performed off line. This article is based on recordings from 10 sustaining units: 5 single unit recordings and 5 together with an on-off unit. In addition, for Fig. 2C measurements were performed on photoreceptors using standard methods for intracellular recording (Jansonius 1990).

All temporal experiments were performed by illuminating the ipsilateral (right) eye with a wide-field stimulus (extent about 45°), consisting of a LED (Siemens LD57C, peak wavelength 560 nm, half-width 25 nm). The spatial experiments (moving edges and gratings) were done by exposing units in the frontal part of the eye, close to the equator, to patterns generated on a CRT (Tektronix 608). This stimulus had a spatial extent of 30°, and a frame rate of 240 Hz. For these experiments we took great care to align the horizontal and vertical axes of the fly's eye with the corresponding axes of the stimulus. All experiments (except the experiment of Fig. 1 A) were performed from a light-adapted state, with a mean luminance of $I=20$ cd/m^2. We measured in the photoreceptor at this stimulus intensity a plateau depolarization of (12 ± 1)mV ($n=10$).

Results

Figure 1 A shows the response of a dark-adapted sustaining unit to a 500 ms light flash (starting at time 200 ms) of intensity I from darkness. The neuron responds with a train of spikes to the onset of the flash, and adapts rapidly to a lower spike rate. After the cessation of the flash, the spike train stops: the sustaining unit does not spike in darkness. During steady illumination of intensity I (prolonging the flash of Fig. 1 A indefinitely), the average spike rate of the sustaining unit finally drops to approximately 9 spikes/s ($\sigma=4$ spikes/s, $n=6$). Figure 1 B shows the response of the same unit, light-adapted to intensity I, to a 20% increase in intensity (duration 500 ms, starting at time 200 ms).

In the remainder of this article, we concentrate on the light-adapted sustaining unit. First we describe the temporal and then the spatial properties.

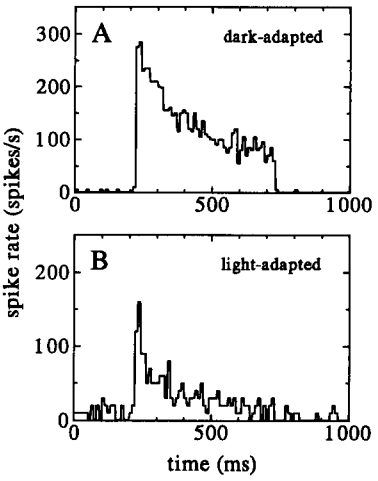

Fig. 1. **A** Response to a 500 ms light flash of intensity I on a constant intensity 0 (darkness). Average of 100 stimulus presentations, repetition time 5 s, bin-width 10 ms. Flash starts at $t=200$ ms. **B** Response to a 500 ms light flash of intensity 1.2 I during a constant intensity I (contrast 20%). Same cell as in **A**. Average of 10 stimulus presentations, repetition time 5 s, bin-width 10 ms. Flash starts at $t=200$ ms

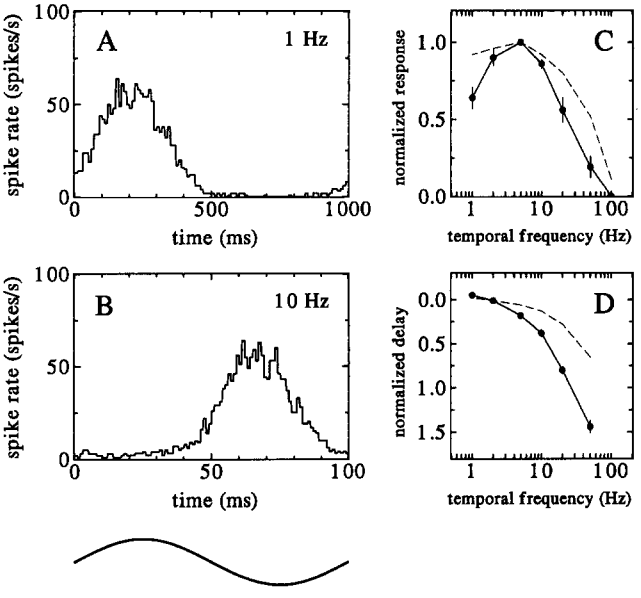

Fig. 2A–D. Response of the sustaining unit to wide-field stimuli modulated sinusoidally in time. **A** Response to a sinusoid (see *bottom trace*) of frequency 1 Hz and modulation 10% (i.e., varying between 0.9 I and 1.1 I with a mean value of I). Average of 100 cycles, bin-width 10 ms. **B** Response to a 10 Hz sinusoid, modulation 10%, average of 1000 cycles, bin-width 1 ms. **C** *Continuous line:* response (peak to peak spike rate) as a function of frequency. Average of 4 units after normalization. *Error bars* represent the standard deviation of the mean (also in the next figures). *Dashed line:* normalized response of a photoreceptor to the same stimulus. **D** Delay (normalized to the stimulus period) of the peak spike rate relative to the positive peak of the sinusoidal stimulus (see *bottom trace* to the left). Average of the same 4 units

Temporal properties

We investigated the temporal frequency response of the sustaining unit by exposing the unit to a wide-field stimulus with an intensity sinusoidally modulated in time,

using frequencies between 1 and 100 Hz and a modulation of 10%. Figure 2A presents the response of a unit to 1 Hz stimulation. At this frequency, the spike rate closely follows the stimulus (bottom trace on the left). Figure 2B shows the response to 10 Hz stimulation. Again, response follows stimulus, but now the phase difference caused by the response delay (see below) becomes visible. Figure 2C gives the response (difference between the maximum and minimum spike rate) as a function of frequency, averaged over 4 units after normalization. None of the units responded to 100 Hz stimulation. As compared to the photoreceptor at this background intensity (dashed line in Fig. 2C), the high-frequency roll off of the sustaining unit is shifted to lower frequencies. The sensitivity gradually decreases towards the lower frequencies (1–2 Hz), more strongly than a similar decrease of sensitivity in the photoreceptor. This is consistent with the fact that the spike rate of the sustaining unit adapts (decreases) after the onset of a prolonged illumination (see Fig. 1B), whereas the photoreceptor does not noticeably adapt at this intensity. Figure 2D shows the delay of the maximum in the spike rate relative to the positive peak of the sinusoidal stimulus, normalized to the stimulus period (continuous line: sustaining unit; dashed line: photoreceptor). In a linear system, this corresponds to the phase; a normalized delay of 0.5 is equivalent to a phase of $-180°$, i.e., the response lags the stimulus 180°. The (normalized) delay is related to the time to peak of the step response, approximately 30 ms in the sustaining unit (see Fig. 1) which is substantially longer than the corresponding 15 ms in the photoreceptor at this intensity. The (normalized) delay is composed of a pure delay (latency) between stimulus and response [approximately 20 ms in the sustaining unit (see Fig. 1), cf. 7 ms in the photoreceptor] and an additional lag due to the low-pass filtering.

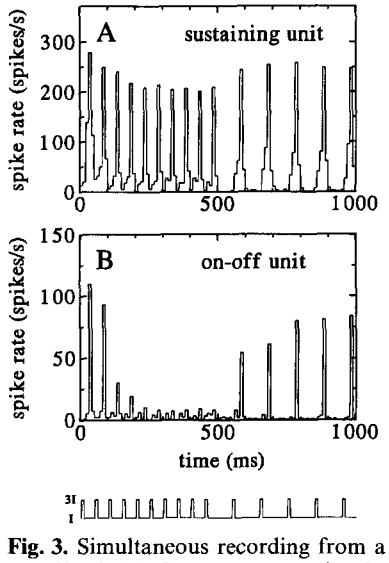

Fig. 3. Simultaneous recording from a sustaining unit (**A**) and an on-off unit (**B**). Response to a train of 10 ms light pulses of intensity 3 *I* during a constant intensity *I*, 10 pulses with interval 50 ms followed by 5 pulses of 100 ms interval (see *bottom trace*). Average of 100 stimulus presentations, repetition time 5 s, bin-width 10 ms

Although the sustaining unit fails to follow the highest temporal frequencies followed by the photoreceptor, its temporal resolution is still substantially better than that of the on-off unit (Jansonius and van Hateren 1991). An allied question is whether the sustaining unit displays fast temporal adaptation, a striking property of the on-off unit which is related to its poor temporal resolution. We explored this by repeating the experiment of Fig. 4 in Jansonius and van Hateren (1991), now in a simultaneous recording from a sustaining and an on-off unit. We stimulated the eye with a short train of light pulses, pulses of 10 ms of intensity 3 *I* during a constant intensity *I*. Every 5 s, 10 pulses with interval 50 ms were followed by 5 pulses of 100 ms interval. Figure 3A presents the response of the sustaining unit: the sustaining unit readily responds to both the 50 ms and the 100 ms pulse train. We found this consistently in all 3 sustaining units where we did this experiment. The on-off unit, on the other hand, fails to respond to the 50 ms pulse train from the second pulse onwards (Fig. 3B, and also Jansonius and van Hateren 1991), which is the fast temporal adaptation.

Spatial properties

We estimated the size and the profile of the receptive field with an edge of 50% contrast, moving at a speed of 30°/s. Figure 4A shows the results for a horizontally

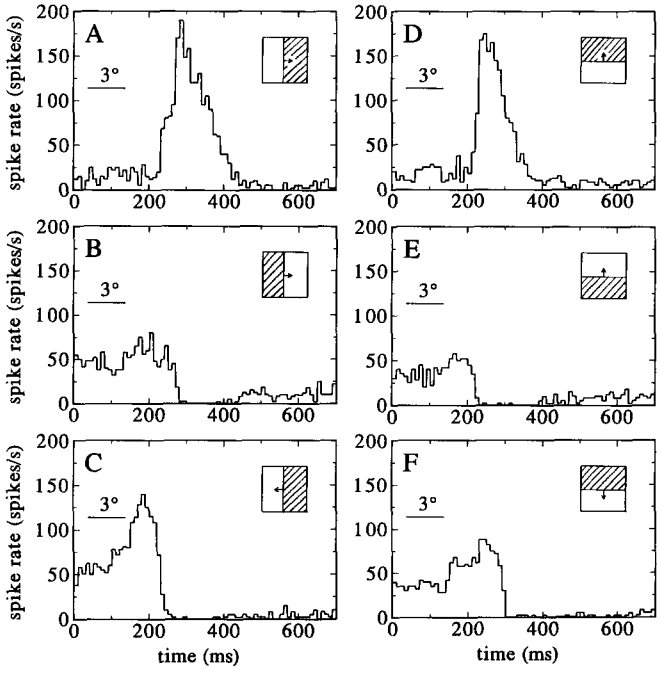

Fig. 4A–F. Responses to edges of 50% contrast (intensity on the one side 0.5 *I*, on the other side 1.5 *I*) moving at a speed of 30°/s. **A** Response to a horizontally moving bright edge (dark side leading). **B** Response to a dark edge moving in the same direction. **C** Response to a dark edge moving in the opposite direction. **D**, **E** and **F** are the vertical counterparts of **A**, **B** and **C** respectively. Average of 100 stimulus presentations, repetition time 1 s, bin-width 10 ms

moving bright edge. The half-width of the response is about 100 ms, which corresponds to a spatial extent of 3°. Figure 4B gives the response to a dark edge moving in the same direction. The slight increase of the spike rate at time 200 ms, prior to the response in Fig. 4A, indicates an inhibitory zone adjacent to the central lobe. The distance between main lobe and negative sideband corresponds to about 3°. In Fig. 4C the dark edge moves in the opposite direction. This response suggests another inhibitory zone at the other side of the central lobe. We observed this consistently in the 3 units investigated. Figure 4D, E and F present the corresponding results for vertically moving edges. The vertical extent of the receptive field is approximately the same as the horizontal one. Moreover, the responses of Fig. 4E and F indicate that there are also negative sidebands in the vertical direction.

The on-off unit has, despite its large receptive field of approximately 10°, a relatively high spatial resolution when tested with moving sinusoidal gratings (Jansonius and van Hateren 1993). Although the receptive field of the sustaining unit is much smaller than that of the on-off unit, it seems still larger than that of the photoreceptor (approximately 1.4°, Smakman et al. 1984). Therefore, it is interesting to measure the spatial resolution of the sustaining unit as well. We measured the response to moving sinusoidal gratings with spatial frequencies between 1 and 16 cycles/30°, a contrast of 25%, and a temporal frequency (contrast frequency) of 5 Hz (the sustaining unit is most sensitive at this temporal frequency, see Fig. 2C). There was no significant difference between the responses to horizontal and vertical gratings, so these results are treated together. Figure 5A and 5B show examples of the responses of a unit to gratings of 1 and 6 cycles/30° respectively. Figure 5C gives the response (difference between maximum and minimum spike rate) as a function of spatial frequency, averaged over 4 experiments in 2 units after normalization.

In the sustaining unit, grating contrast and resulting response (peak to peak spike rate) are in good approximation linearly related for contrasts of up to 25%. This is shown in Fig. 6. Therefore, assuming that the curve of Fig. 6 is similar for all spatial frequencies, Fig. 5C can be considered as a modulation transfer function. Fourier transforming this modulation transfer function yields the line spread function of the sustaining unit, which is shown in Fig. 7. The half-width of its central lobe is approximately 2°, thus somewhat broader than the half-width of the photoreceptor angular sensitivity (about 1.4°, Smakman et al. 1984), but approximately the same as that of the presumed subunit of the on-off unit, $(2.3 \pm 0.2)°$ (Jansonius and van Hateren 1993). The distance between the centre of the main lobe and the minimum of the sidebands is approximately 3°. This distance is in good agreement with the distance estimated from the moving edge experiment of Fig. 4. The central

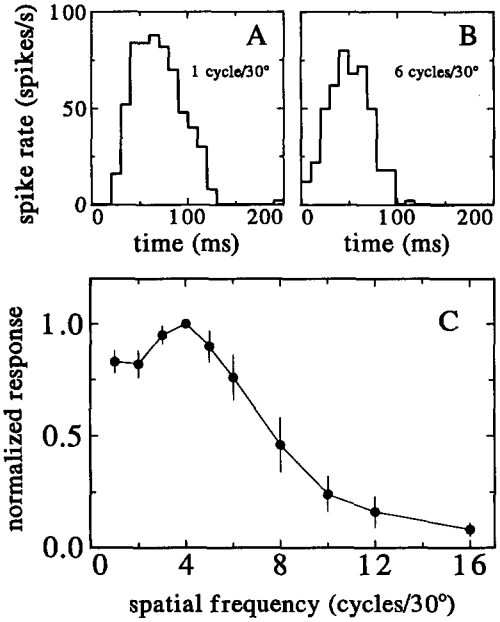

Fig. 5A–C. Response to moving sinusoidal gratings of contrast 25% (i.e., varying between 0.75 *I* and 1.25 *I* with a mean value of *I*) and temporal frequency 5 Hz. **A** Response to a grating of spatial frequency 1 cycle/30°. Average of 200 cycles (40 s recording), bin-width 10 ms. **B** Response to a grating of 6 cycles/30°. Average of 200 cycles (40 s recording), bin-width 10 ms. **C** Response as a function of spatial frequency. Average of 4 experiments, after normalization per unit to the maximum response

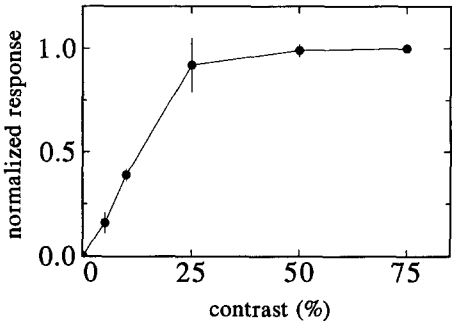

Fig. 6. Normalized peak to peak spike rate in response to a moving sinusoidal grating as a function of contrast (modulation depth). Average of 2 units. Spatial frequency 1 cycle/30°, temporal frequency 5 Hz

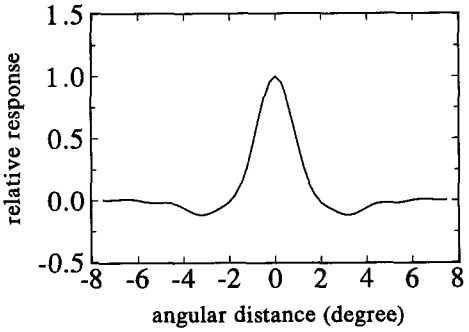

Fig. 7. Line spread function of the sustaining unit, calculated by Fourier transforming its modulation transfer function (Fig. 5C). The datapoint 0 cycles/30° was determined to be 0.7 by extrapolation. Taking 0.5 or 0.9 instead of 0.7 yields the same half-width and the same position of the minimum, but increases (0.5) or decreases (0.9) the depth of the inhibitory zone by approximately 12%

Table 1. Temporal and spatial properties of various cells in the retina and the lamina of the blowfly at a background intensity of approximately $I = 20$ cd/m^2

	Photo-receptor	LMC	On-off unit	Sustaining unit
Temporal resolution (Hz)	50[f]	56[c]	14[d]	25[f]
Spatial resolution (°)	1.4[a,b]	1.4[c]	2.3[e]	2[f]
Receptive field (°)	1.4[a,b]	1.4[c]	10[e]	2[f]

Data from Smakman et al. 1984[a]; van Hateren 1984[b], and unpublished[c]; Jansonius and van Hateren 1991[d], 1993[e] and this study[f]. Temporal resolution is given as the frequency at which the high-frequency roll off reaches 50% of the maximum response. Spatial resolution is defined as the half-width of the line spread function. The size of the receptive field is given as the half-width of the spatial sensitivity profile, except for the on-off unit, where the full extent is presented. Due to the square sensitivity profile of this unit, however, the full extent only slightly exceeds a half-width

lobe of Fig. 4 is, however, slightly broader than that of Fig. 7. This difference is presumably caused by temporal smearing. Generally, the response of a neuron to a moving edge depends on the speed of the edge in proportion to both the spatial and the temporal properties of the neuron (see e.g. Srinivasan and Bernard 1975). If the edge moves very slowly, then the response merely depends on the profile of the receptive field. A very fast moving edge, however, elicits a response similar to the temporal step response of the neuron. At an intermediate speed, the width of the response is determined both by the width of the receptive field and by temporal smearing. The latter situation is true for the experiment of Fig. 4, as the half-width of the temporal step response of the sustaining unit (about 70 ms) is not negligible with respect to the response width of 100 ms.

Table 1 presents a summary of the basic temporal and spatial properties of the spiking units in the first optic chiasm of the blowfly (extracted from this study, and from Jansonius and van Hateren 1991, 1993). We added data from photoreceptor and LMC to enable a proper comparison.

Discussion

The main results reported in this article are the following. Firstly, we found that the temporal resolution of the light-adapted sustaining unit is not as good as that of the photoreceptor, but still substantially better than that of the on-off unit. We showed that the sustaining unit does not display fast temporal adaptation like the on-off unit. Secondly, we found that the receptive field of the sustaining unit (measured by means of moving edges) and its line spread function (calculated from the response to moving sinusoidal gratings) have similar size and profile: a central lobe with a half-width of approximately 2° surrounded by a circular inhibitory zone located at about 3° from the centre of the main lobe.

In particular the dark-adapted spatial properties of the sustaining unit have been investigated thoroughly by Arnett (1971, 1972) in the fly *Phaenicia sericata*. Confirming Arnett's results, we found no discharge in darkness, and sustaining discharge during steady illumination. Also the measured horizontal size and profile of the receptive field and line spread function (Fig. 4A–C and 7) are in good agreement with Arnett's data. Vertically, however, we found inhibitory zones adjacent to the central lobe as well, whereas Arnett reported horizontal inhibition only. This discrepancy indicates a difference between the light-adapted *Calliphora* and the dark-adapted *Phaenicia*.

As the basic temporal and spatial properties of both the sustaining and the on-off unit are, in some detail, known by now, it seems worthwhile to reconsider the correspondence between the anatomy and the physiology of the fly's lamina (see Laughlin 1981, 1984; Shaw 1981, 1984). Unfortunately, almost all anatomical studies of the fly lamina are based on *Musca*, and not on *Calliphora* (review: Nässel 1991; Shaw 1981, 1984). Therefore, the following discussion (comparing *Musca's* anatomy with *Calliphora's* physiology) must be read with some reservation: the lamina of *Drosophila* for example, differs in some respects from that of *Musca* (Meinertzhagen and O'Neil 1991).

At present, there are only 6 connections known between lamina and medulla that are not strictly centrifugal (functionally, as indicated by the synaptology; see Shaw 1981; Nässel 1991). These probably centripetal connections are 3 types of second-order Large Monopolar Cells (LMCs, L1–3), two third-order monopolar cells (L4–5), and the basket cell T1. Arnett (1972) suggested that the on-off and the sustaining spiking activity in the chiasm might originate from the LMCs, generating spikes proximally to the lamina. Nowadays, however, the blowfly LMCs are generally believed to be purely graded potential neurons (e.g. Laughlin and Hardie 1978; Laughlin and Osorio 1989; van Hateren and Laughlin 1990; Hardie and Weckström 1990; Straka and Ammermüller 1991). Based on a single staining by Järvilehto and Zettler (1973), T1 is also assumed to be a graded potential neuron. Therefore, only the two monopolar cells L4–5 remain as candidates for the anatomical counterparts of the on-off and the sustaining unit, assuming the validity of Arnett's (1972) lesion experiment showing centripetal spike transmission. A single staining by Hardie (Hardie 1978, cited in Shaw 1981) suggests that L4 is indeed a spike generating cell.

Both L4 and L5 are postsynaptic to amacrine cells (*Musca*, Nässel 1991). Amacrines form a lateral network in the lamina, with radial processes extending into 6–17 cartridges (Shaw 1981). Both the sustaining unit and the subunit of the on-off unit have, however, a line spread function with a half-width of approximately 2°, only slightly more than that of a single neuro-ommatidium. This suggests that the amacrines do not operate as wide-field neurons, but as an ensemble of functionally more or less independent units (see also the discussion by Shaw 1984). The lateral inhibition in the receptive field of the sustaining unit and between the subunits

of the on-off unit could originate in the reciprocal synapses between amacrines. Although the response of Hardie's stained L4 apparently resembles that of the sustaining unit (Shaw 1981), we now believe that it might be more likely that L4 corresponds to the on-off unit. L4 has, unlike L5, connections with corresponding cells in neighbouring cartridges, which could provide the anatomical substrate for the spatial pooling of subunits in the on-off unit (Jansonius and van Hateren 1993).

What kind of information is coded by the sustaining unit that makes it different from other, parallel channels from lamina to medulla? Although the unit has a good spatial and temporal resolution, and is thus able to transfer details in space and time, it is surpassed in this respect by the LMCs (e.g. Laughlin 1981; van Hateren 1992a, b). A stimulus parameter coded at most only poorly by the LMCs and not at all by the on-off unit is the level of background illumination. As the sustaining unit keeps on spiking as long as the light is on, its spike rate might be a measure of this parameter. We have not yet tested this directly, though. Thus one function of the sustaining unit could be to transfer, along with the photoreceptors R7 and R8, information about the absolute level of light intensity to more central parts of the nervous system. However, although the sustaining unit continues spiking during steady illumination, its response rapidly adapts after a change of intensity. The unit produces a large increase of the spike rate in response to small increments, but the spike rate returns almost completely to its background value within 500 ms (Fig. 1 B). Therefore, the sustaining unit seems primarily a highly sensitive ON detector, with coding of the absolute level of light intensity as a possible subsidiary function.

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