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The functional organization of the crayfish lamina ganglionaris

II. Large-field spiking and nonspiking cells

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Summary. 1. The functional properties of the multicolumnar interneurons of the crayfish lamina ganglionaris were examined by intracellular recording and the cell structures were revealed with the aid of Lucifer yellow or horseradish peroxidase iontophoresis.

2. The multicolumnar monopolar cell M_5 (Fig. 1) responds to a light pulse with a depolarizing compound EPSP and a burst of action potentials. Both the EPSP amplitude and the spike rate decay toward a lower level plateau in less than 200 ms after light onset. M_5 is subject to surround inhibition, which is associated with a compound IPSP and net hyperpolarization of the membrane potential. Direct depolarization of M_5 may provide a weak excitatory drive to medullary sustaining fibers (SF).

3. Tangenital-cell type 1 (Tan_1) (Fig. 2) has a broad expanse of neurites in the lamina (covering 10 to 15 cartridges) and a much narrower projection in the medulla (1 to 3 cartridges). The response to a light pulse (Fig. 3) has a long latency consistent with a polysynaptic receptor to Tan_1 pathway. The response consists of a nearly rectangular hyperpolarization. Light 'off' elicits a depolarization and a burst of impulses. The polarity of the 'on' response can be reversed by hyperpolarizing the membrane by 23 mV. The receptive field is broad and the intensity-response function exceeds 4 log units. Direct hyperpolarization of Tan_1 provides a strong excitatory signal to medullary SFs both in the dark and in the presence of illumination (Fig. 5). We propose that Tan_1 provides the principal steady-state excitatory drive to the SFs.

4. Tangential-cell type 2 (Tan_2) (Fig. 4) is distinguished from Tan_1 by the extent and shape of the lamina process, which is a vertically oriented neurite spanning most of the lamina in a single plane. Functionally, Tan_2 is similar in most respects to Tan_1, but the response latency is much shorter, comparable to that of monopolar cells.

5. T-cells may exhibit spontaneous impulse activity in the dark which is inhibited by a short latency hyperpolarizing light response. The receptive field, which is about 2× larger than that of the columnar monopolar cells, is correlated with a small but multicolumnar dendritic arbor in the lamina. Since T-cells are aminergic, it is possible that the amines are normally released in the dark.

6. A single amacrine cell was fully characterized (Fig. 7). It exhibited a short latency hyperpolarizing response to light onset and a strong depolarizing 'off' response. The receptive field was of intermediate dimensions (larger than that of monopolars and smaller than that of tangentials), and was subject to strong lateral inhibition. Membrane polarization excited SFs. Hyperpolarization was about twice as effective as depolarization (Fig. 7C).

7. A circuit diagram of the lamina and the lamina to medulla connections (Fig. 9) is proposed on the basis of our results and previous morphological studies. The results are consistent with three general hypotheses: a) all synapses in the lamina are sign-inverting; b) the lamina to medulla projections appear to be mediated by sign-inverting synapses to a single functional class of transmedullary neurons; and c) the neurons of the external chiasma constitute a hierarchy of parallel lamina to medulla pathways with receptive fields varying from 8° (nonspiking monopolar cells) to 180° (Tan_2) and response dynamics varying from purely transient (columnar monopolars) to steady state (tangential cells).

Abbreviations: *CHE* external chiasma; *LG* lamina ganglionaris; *SF* sustaining fiber

Introduction

The lamina ganglionaris (LG) is organized to analyze the output of the receptor mosaic and transmit the coded visual signals via an array of parallel output channels (mainly the columnar monopolar cells). The morphological studies of cell structures and of the synaptic connectivity document or imply extensive lateral interactions among the lamina neurons (in lobster, Hamori and Horridge 1966a, b; in crayfish, Hafner 1973; Nässel 1977; Nässel and Waterman 1977; in diptera, Strausfeld and Campos-Ortega 1977). These lateral interactions have been proposed to subserve visual adaptation and lateral inhibition.

In the accompanying paper (Wang-Bennett and Glantz 1987), we describe the functional properties of four small field monopolar cells in the crayfish lamina ganglionaris. The nonspiking monopolar cells (M_1–M_4) transmit a graded mosaic representation of the distribution of corneal illumination to the medullary columnar neurons and secondarily to the sustaining fibers (SF). In the literature, except for a few physiological accounts of morphologically unidentified cells, the large field neurons of arthropod lamina are known exclusively by their morphology, and their functions can only be inferred from their synaptic connectivity. For example, in flies the monopolar cells L_1–L_3 and the single columnar T-cell all are nonspiking and have small receptive fields (Järvilehto and Zettler 1973). These properties were distinguished from the large field hyperpolarizing neurons (attributed to amacrine cells, Strausfeld and Nässel 1981, and to tangential neurons, Shaw 1981), and the depolarizing and spiking response attributed to L_4 and L_5. On morphological grounds, M_5 in crayfish is analogous to L_4 in Diptera. This multicolumnar centripetal neuron does not receive direct receptor input and presumably interacts via reciprocal connections with other M_5s. Tangential processes containing dense core vesicles are found distal to the lamina (in lobster, Hamori and Horridge 1966b; in crayfish, Elofsson et al. 1977). These processes are postsynaptic to retinular cells and presynaptic to lamina monopolar cells M_1–M_4 and have been ascribed to lamina amacrine neurons (Strausfeld and Nässel 1981). One amacrine cell serves several cartridges and each cartridge receives lateral branches from several amacrine cells. Thus amacrine cells would appear to play a role in intercartridge interactions. Three classes of centrifugal cells are described in crayfish: Tan_1, Tan_2, and a small field centrifugal, CE (Strausfeld and Nässel 1981). In flies, Tan_1 is presynaptic to retinular cells and dipteran analogs of monopolar cells M_1–M_4. From this evidence, Tan_1 has been assigned the role of a delayed inhibitory feedback pathway. Tan_2 is presynaptic to L_4 in insect eye (analogous to crayfish M_5). Based on the available anatomical evidence, it is hypothesized that the lamina ganglionaris possesses two separate information channels: 1) a small field channel from retinular cells to M_1–M_4 with feedback gain control from Tan_1; and 2) a large field channel from retinular cells to amacrine cells to M_5 which involves a feedback pathway from Tan_2.

In this paper, we characterize the following cell types: multicolumnar centripetal monopolar cell M_5, lamina amacrine cells, T-cells, two centrifugal cells (Tan_1 and Tan_2), and the efferents to the medulla. We focus on the physiological evidence of lateral inhibitory and/or excitatory inputs and address the issue of lamina to medulla network connections, including intercartridge relations.

Materials and methods

Adult crayfish (*Procambarus clarkii* or *Pacifastacus leniusculus*) measuring 8–10 cm (rostrum to telson) were obtained from either Western Scientific Supply Co. (W. Sacramento, CA) or Gulf Coast. The preparatory procedures, recording and histological techniques follow those reported in the accompanying paper (Wang-Bennett and Glantz 1987).

As reported in the first study, most impalements were done in the external chiasma. To study the intercartridge connections, some impalements were done in the lamina ganglionaris where most of the axonal processes are only 2–5 μm. Membrane polarization was controlled with WPI amplifier (Model M-707) equipped with bridge circuit. The injected current was varied with the aid of a potentiometer connected in series with the voltage output of a Tektronix pulse generator (Model 161). Stimulus procedures were identical to those in the companion report. Data was stored on an F.M. tape recorder.

To examine the interactions between lamina neurons and SFs, the tape recorded extracellular SF recordings were replayed through a window discriminator. Single units were isolated by waveform and spike amplitude, as described in previous studies (Glantz et al. 1984). The isolated impulses were then displayed on a storage oscilloscope and chart recorder. When the SF impulse rate exceeds about 100/s the limited frequency response of the chart recorder results in nonuniform impulse amplitudes (summed or truncated) as in Figs. 5 and 7.

Results

M_5 – the lamina sustaining unit

Anatomical evidence reveals that in most arthropod compound eyes there is at least one lamina monopolar cell that has a multicolumnar dendritic arboriztion and no direct connections from photoreceptors. In Diptera, for example, L_4 is a third

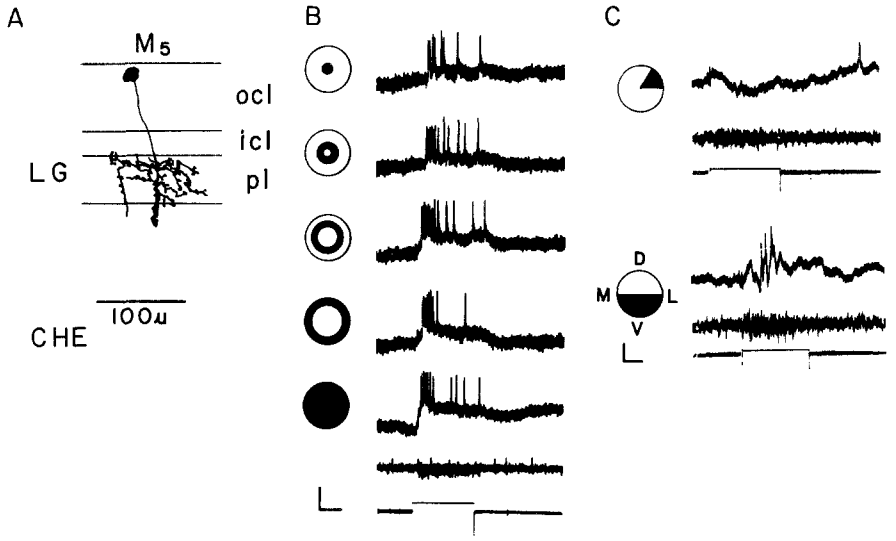

Fig. 1A–C. Lamina spiking cells. **A** Camera lucida drawing of a spiking monopolar neuron M_5. *LG* lamina ganglionaris; *CHE* external chiasma; *ocl* outer cell body layer; *icl* inner cell body layer; *pl* lamina plexiformis. **B** The responses of M_5 (in A) to stimuli in different portions of the visual field. Responses consist of a transient depolarization with superposed high frequency spikes and a lower level plateau phase. Calibration bars 2 mV, 200 ms. The trace above the stimulus marker (bottom) is a simultaneous recording of the sustaining fibers in the optic peduncle. **C** Inhibition and hyperpolarization of M_5. This recording is derived from an impalement within the lamina ganglionaris. Stimuli directed outside the excitatory field (dorsoposterior quadrant) elicit a transient depolarization followed by a hyperpolarization. Termination of stimulus results in a slow rebound depolarization and a delayed burst of spikes. Stimuli directed to the excitatory field (lower half of eye) elicit a transient discharge and a sustained depolarization. The plateau response in this cell also exhibited subthreshold oscillations (with a 120 ms period). Scale 2 mV, 200 ms. The middle trace in each group is a recording of the sustaining fibers in the optic peduncle. Bottom trace is the stimulus marker

order cell with input from lamina amacrine cells and it forms reciprocal synapses with the surrounding L_4's. These lateral reciprocal interactions may mediate the inhibitory network observed from the receptive field analysis (Arnett 1971, 1972; McCann 1974; Mimura 1974). Similarly, Golgi EM studies in crayfish (Nässel and Waterman 1977) indicate that neither M_5 nor Tan_1 is directly postsynaptic to receptor terminals. Thus, these two cell types are of a higher order than the nonspiking lamina monopolar cells M_1 to M_4.

Our dye fill results in crayfish (Fig. 1A) show that M_5 is a multicolumnar monopolar cell with a soma in the outer cell body layer (ocl) and dendrites in both lamina plexiform layers. The lateral spread of the dendrites covers a range of 25 to 112 μm (a cartridge has a mean width of 18 μm). The collaterals of the primary axon typically consist of several small knobs which give the axon a varicose appearance. We have traced the axon terminals into the distal region of the external medulla (not shown).

When impaled close to the axon terminals in the CHE, the responses of M_5 to stimuli in different parts of the visual field consist of a depolarizing compound EPSP, with transient and tonic phases and superposed spikes (Fig. 1B). In these instances, the latency to the start of the depolarizing response is 60.2 ± 1.8 ms (SE, $n=5$). This latency measurement is 3 ms longer than that of the simultaneously monitored medullary SFs (57 ± 11 ms, SE). The initial spike rate was 100 Hz and declined to 20 Hz in 300 ms. The mean spike amplitude was 5.1 ± 1.0 mV (SE, $n=4$). The wide dendritic distribution in Fig. 1A is associated with a relatively broad receptive field of 72° by 12° (X by Y) compared to that of the columnar cells (15° × 8°). As the area of illumination increases, the peak depolarization and spike rate increase; a result indicative of spatial summation. The M_5 intensity-response function (not shown) covers a broad range exceeding 4 orders of magnitude.

M_5 is also subject to surround inhibition. The clearest example of the interplay of excitation and inhibition was recorded in the lamina near the dendrites (Fig. 1C). With stimuli to the inhibitory field (dorso-lateral sector), the intracellularly recorded compound PSP (Fig. 1C, top) exhibited a short latency transient depolarization and a delayed hyperpolarizing component which peaks at 180 to 300 ms poststimulus onset. The time frame of the early component corresponds to that of the transient burst of spikes observed in the terminal impalement (Fig. 1B). The delayed hyperpolarizing

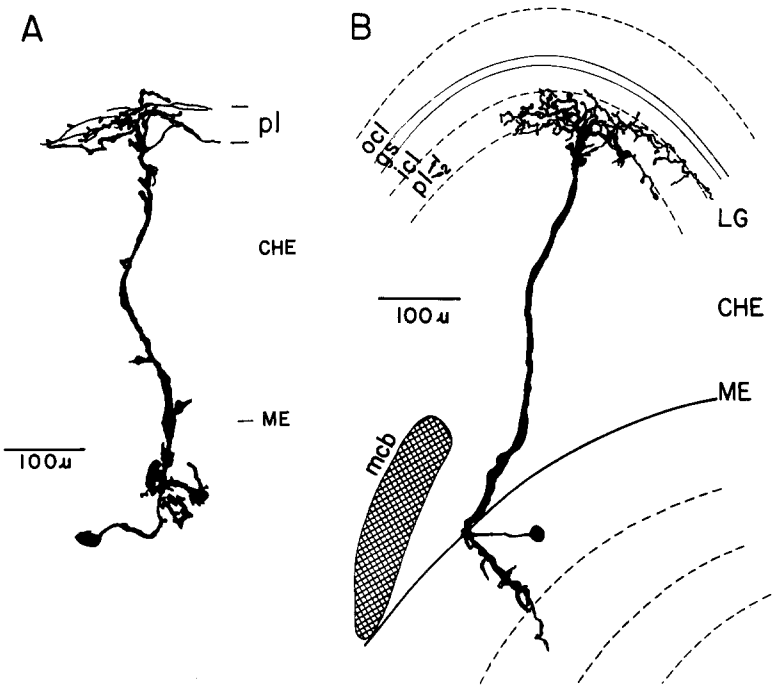

Fig. 2A, B. Tangential cell type 1 (Tan_1). **A, B** The morphology of two Tan_1 cells filled with Lucifer yellow. The cell bodies are located in the outer medullary region, and the axons ascend to the lamina plexiform layer (*pl*). Lateral branches cover 224 μm in **A** and 275 μm in **B**. *ME* medulla externa; *gs* glia sheath; *mcb* medullary cell body region. Dashed lines in ME indicate three different bands

component is always associated with inhibition of the discharge. Stimulus termination elicits a rebound depolarization and one or several impulses (Fig. 1C, top). The reversal potential (E_{rev}) for the late hyperpolarizing component is negative to the resting potential. The excitatory receptive field of this neuron was located in the ventral half of the monocular visual field (Fig. 1C, bottom).

In two preparations we examined the effect of extrinsic current in M_5 on the simultaneously monitored SFs. Two SFs were isolated in one preparation and one SF in the second. Polarization of M_5 in the dark (with varied currents of both polarities) had no effect on the SF discharge rate. Depolarization of M_5 by 10–20 mV in conjunction with a visual stimulus produced a small (11 to 22%) enhancement of the light elicited SF response (data not shown), which was statistically significant in one instance ($P<0.05$), but marginal in the others ($0.05<P<0.10$). Hyperpolarization of M_5 was associated with small but statistically insignificant effects ($P>0.25$) of either sign on the three SFs. We infer that the M_5 depolarizing light response is at best a minor contributor to the SF excitatory pathway.

Tangential cell type 1 (Tan_1)

The morphology of Tan_1 has been described in detail by Hafner (1973), Nässel (1977), and Strausfeld and Nässel (1981). Tan_1 does not receive direct input from photoreceptors. The axonal processes invade the lamina in a bistratified pattern. The lamina processes of adjacent Tan_1's overlap each other and form a hexagonal network in the distal lamina. Although the location of the cell body was undetermined in the earlier studies, it was assumed that Tan_1 is a centrifugal cell by analogy to Tan_1 in Diptera.

We localized the cell body of Tan_1 to the distal edge of the medulla (Fig. 2A, B). The cell body neurite in Fig. 2A actually projects out of the plane of the medulla. The size of the cell body is 16 μm by 21 μm. A fine neurite connects the cell body to the dendrites, which form a dense plexus in the distal band of the ME. The Tan_1 axon connects the medulla to the lamina where an extensive network of branches spreads out laterally for 172 ± 53.4 μm (SE, $n=4$) and covers 10 to 15 cartridges. The arborization in the lamina typically covers 5 to 10× the area of the medullary arborization. A similar result is indicated by Nässel (1977).

Tan_1 responds to a light pulse with a nearly rectangular hyperpolarizing response ($V_{max}=-20$ mV). The response is graded throughout the intensity range. Light off elicits a rebound depolarization and burst of spikes (Fig. 3A). Occasionally the cell discharges in the dark. The latency of the light response (84.5 ± 11.2 ms, SE, $n=4$) is much longer than that of the SF measured in the same preparations (77.3 ± 8.4 ms, SE, $n=4$). The response latency suggests Tan_1 is a fourth or even higher order cell in the visual pathway.

In contrast to the small field hyperpolarizing monopolar cells, Tan_1 derives excitatory (hyperpolarizing) input from all or most of the monocular visual field (Fig. 3A). In tests with variable diameter and broad field stimuli, we found that Tan_1 exhibits spatial summation over its entire field. The dynamic range of the Tan_1 I-R function, measured with large field stimuli, is about 4 log units (Fig. 3B). The resting membrane potential is -14.4 ± 4.0 mV (SE, $n=5$). The light response can be abolished or inverted by superposing the response on a steady hyperpolarizing current (Fig. 3C). The reversal potential for the light response is -22.5 ± 10.6 mV (SE, $n=2$) below the resting potential. This yields an absolute measure of E_{rev} of -37 mV.

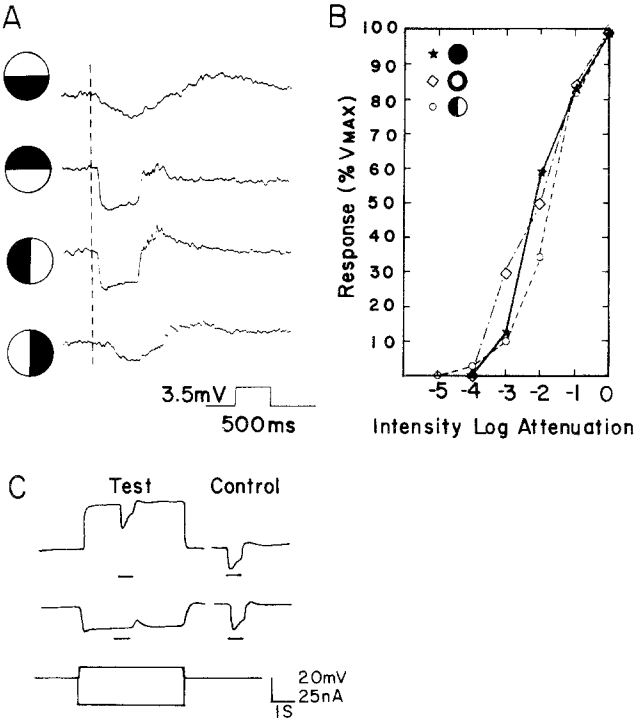

Fig. 3A–C. Physiology of Tan_1. **A** Tan_1 response waveforms are slow and show no distinct transient. Spikes are recorded during the rebound depolarization of the 'off-response'. The receptive field is broad and always additive. Dashed line indicates light stimulus onset. **B** Intensity-response functions for 3 stimulus patterns (upper left corner) extend over at least 4 log units. **C** The reversal potential measurements indicate a reversal of the light response at -30 mV below the resting potential. The top trace shows the Tan_1 light response in the presence of a depolarizing current (13 nA). Middle trace shows that a 29 nA hyperpolarizing current abolishes the light on-response while eliciting an enhanced off-response. Control light responses are measured immediately after the test stimulus. The bottom trace indicates the polarity and amplitude of the injected current. Bars beneath the light response indicate timing of light pulses

Tangential cell type 2 (Tan_2)

This cell type can be distinguished from Tan_1 by its more extensive and vertically oriented arborization in the lamina plexiform layers. We localized the soma of Tan_2 in the medullary cell body region (hatched area in Fig. 4A), which is consistent with its location in Diptera (Shaw 1981; Strausfeld and Nässel 1981). In Diptera Tan_2 is a centrifugal neuron. In two instances, when the impalement was made in the medulla, dye coupling of two to four Tan_2's were observed. Figure 4A shows portions of four Tan_2 axons which were filled simultaneously; the cell filled directly by iontophoresis is represented by a solid area. Judging from the gradient of dye diffusion, coupling occurred at the neurite to dendritic region. In contrast to Tan_1, the medullary branches of a single Tan_2 cell penetrate a broad field. Although the neurites in the medulla and lamina appear to occupy comparable superficial layers in Fig. 4, they are actually displaced vertically. The Tan_2 axon exhibits an abrupt curve between the medullary and lamina processes. The two segments shown in Fig. 4 were viewed in entirely different focal planes. The axon ascends in the CHE, and bifurcates proximal to the lamina. The lamina neurite consists of two major vertical branches, which course parallel and proximal to almost the entire lamina. Each large branch gives rise to many finer branches which project distally through the lamina cartridges. The vertical extent of the tangential lamina process is 892 μm in Fig. 4A.

In contrast to the light response of Tan_1 which exhibited a transient hyperpolarization followed by a modest decay toward a plateau phase, the response waveform of Tan_2 generally exhibited two hyperpolarizing phases; an initial rapid phase followed by a second slower phase. Thus the response amplitude continued to increase over the duration of the 500 ms light pulse (Fig. 4B). Furthermore, following the light pulse, Tan_2 exhibited a hyperpolarizing 'off' response (Fig. 4B). The resting membrane potential was -15 mV ($n=2$) and the mean latency to the light response was 46.3 ± 3.3 ms (SE, $n=3$) which is comparable to that of the second order columnar monopolar cells. The broad dendritic field is correlated with strong spatial summation over a large visual field and we found no evidence of lateral inhibition even with stimuli to the whole eye. Discrete synaptic activity in the form of spontaneous hyperpolarizing IPSPs were commonly recorded in the medulla.

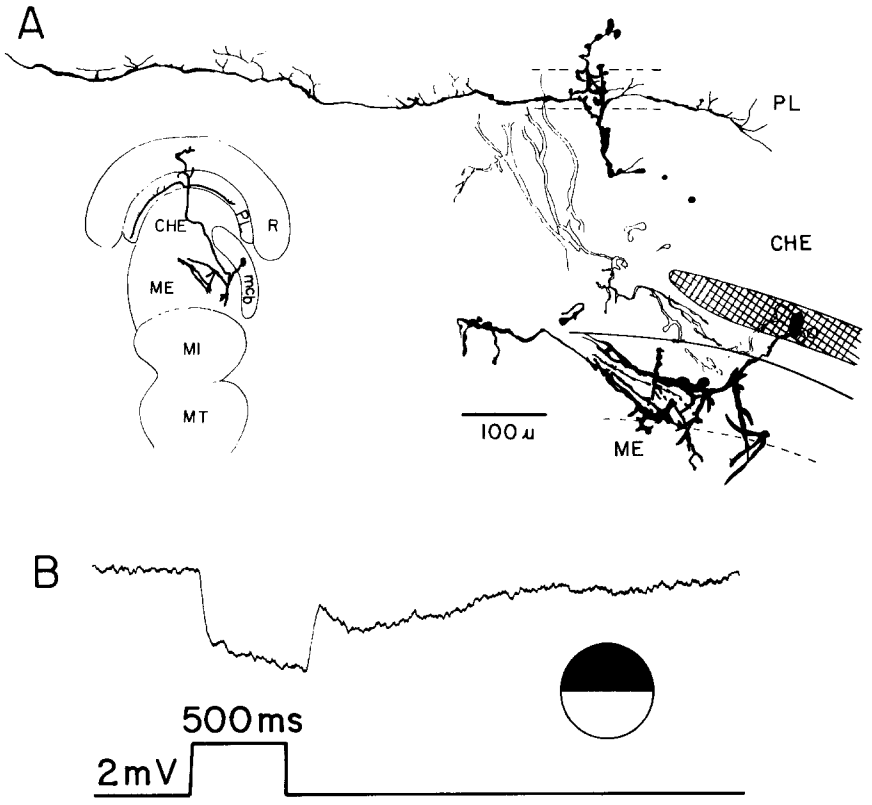

Fig. 4A, B. Tangential cell type 2 (Tan_2). **A** Tan_2 morphology. The cell body is located in the medullary cell body region (indicated by a grid). Dye-coupling of four cells was observed. The impaled cell is indicated by the solid area. The inset shows the position of this cell in the eye. Axonal branches in the medulla penetrate the columnar structure of the ME. The medullary processes are viewed from the dorsal side of the eye. The course of the axon is not entirely clear. The vertical extent of the lamina processes is 892 μm and is the broadest cell encountered. The lamina processes are viewed from the medial side of the eye. The finest branches extend distally beyond the lamina into the region of the receptor axons. *CHE* external chiasma; *mcb* medullary cell body region; *ME, MI, MT* medulla externa, interna, and terminalis; *PL* lamina plexiformis; *R* receptor axons. **B** Response waveform of Tan_2. *Note:* A second slower phase of hyperpolarization during constant illumination and a hyperpolarizing 'off' response

Tangential cell to SF functional pathway

Considering the tangential cell's broad receptive field and massive projection to the lamina, one would expect these neurons to play an important role in visual information processing. At the present time, however, we only know that in Diptera (Strausfeld and Nässel 1981) the morphological synaptology suggests that tangential cells provide a feedback signal (presumably delayed inhibition) from the medulla to a subset of lamina monopolars. A similar function could be inferred in lobster, where unidentified lamina tangential fibers are presynaptic to monopolar cells (Hamori and Horridge 1966b).

The activity of optic tract sustaining fibers (SFs) was used as an assay to explore tangential cell function. Seven experiments were performed in which current was injected into a tangential cell and the action on one or two SFs was assessed. In each instance, the tangential cell was subsequently identified via examination of the Lucifer Yellow injected neuron. Figure 5 presents the results of one type of experiment. Hyperpolarizing current pulses were injected into Tan_1 (the morphology of this particular cell is in Fig. 2A) while the preparation was in the dark. Extrinsic hyperpolarizing current elicited an abrupt acceleration of the SF discharge rate. The mean acceleration was $175 \pm 55\%$ (SE, $n=8$) of the dark discharge rate (3/s). During the current step, a light pulse illuminated the SFs excitatory field and the SF exhibited a transient burst. A comparison of the SF rate during this burst to the SF response elicited in the absence of extrinsic current (in Tan_1) (Fig. 5) indicated that the current in Tan_1 enhanced the SF light response by 17 to 86%. Similar results were obtained in 5 experiments. With currents adjusted to produce a 20 mV hyperpolarization of Tan_1, the SF average rate increased from 39 to 57/s; a rate change of $46 \pm 12\%$ (SE), which is significantly above zero ($t=3.8$, $P<0.025$). The average slope of the SF rate change versus Tan_1 membrane potential was 0.77 Hz/mV hyperpolarization. Similar tests were also conducted with depolarizing pulses. The results varied from a 6% reduction to a 22% enhancement. The mean ($\pm$SE) action of depolarizing pulses on SF rate was $7.2 \pm 4.8\%$, which was not significantly different from zero ($t=1.5$, $P>0.1$).

In a second aspect of this experiment, we probed the SF tonic response by injecting current into Tan_1 during continuous illumination of the SF excitatory field. Although the results were highly variable (enhancements of 16 to 500%), they were qualitatively similar to the Tan_1 action

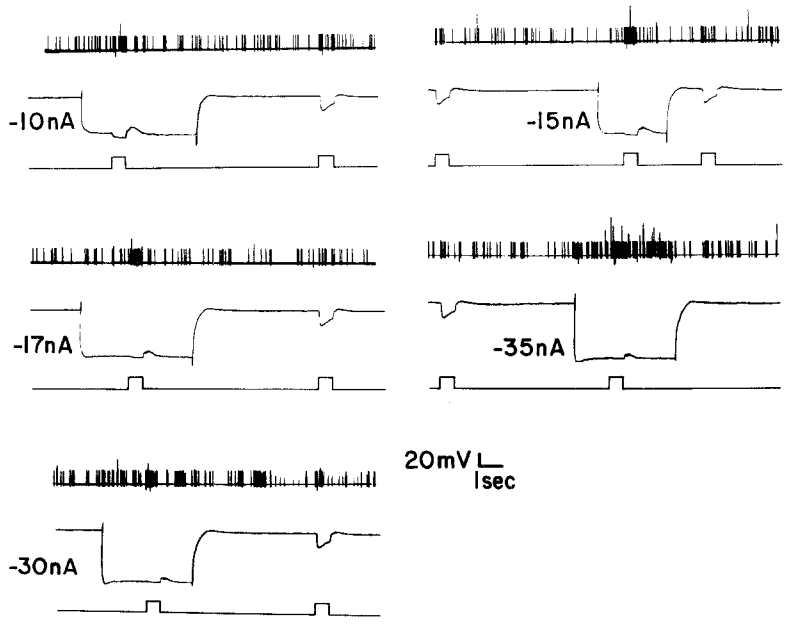

Fig. 5. Effect of Tan_1 membrane polarization on SF activity. Hyperpolarizing current of −10 to −35 nA elicited an acceleration of the SF discharge rate. When a 500 ms light pulse was presented during the hyperpolarizing currents, the SF firing rate was 17 to 86% higher than that of the control light response recorded in the absence of current. To compensate for the effect of light adaptation, control stimuli were presented both before (right) and after (left) the light-current pair. Upper trace in each panel is optic-tract recording of SF impulses isolated with a window discriminator. The impulses appear nonuniform because of the limited frequency response of the chart recorder. The middle trace is the membrane potential of Tan_1, bottom trace indicates timing of light pulses

on SF transient responses. The mean modulation of the tonic rate by hyperpolarization was $201 \pm 85\%$ (SE), which was also significantly above zero ($t = 2.36$, $P < 0.05$). Depolarization was without effect. For 5 cases in which depolarization was tested, the mean $\pm$ SE was $1.6 \pm 4.6\%$. Taken together, the results indicate that Tan_1 hyperpolarization is sufficient, but not necessary, for the excitation of SFs.

In two preparations, the same procedures were carried out on Tan_2. The results were qualitatively similar to those of Tan_1.

T-neuron

Elofsson et al. (1977) described one type of columnar T-neuron whose soma was proximal to the lamina plexiform layers and exhibited histofluorescence indicative of dopamine. The T-neurons appear to be capable of assuming two functional states. In either state, the T-neuron exhibited hyperpolarizing responses to illumination, but in one condition the cell exhibited a tonic discharge (Fig. 6D) and in the other, it was nearly silent. Small shifts in membrane potential appear to determine the dark discharge rate. The response waveform of the cell in the nonspiking state (shown in the inset of Fig. 6B) is indistinguishable from that of the nonspiking monopolar cells. The light response was associated with an 18% increase in membrane conductance (Fig. 6B) which is also similar to the value obtained for monopolar neurons. Furthermore, the response latency was 46.5 ± 2.1 ms (SE, $n = 4$) and the simultaneously recorded SF latency was 57 ± 3.5 ms. All of these properties suggest that the T-neuron is a functional analogue of a monopolar cell (Järvilehto and Zettler 1973). There, are, however, two important differences. The normally quiescent T-neuron can fire action potentials in conjunction with transient depolarizations occasionally elicited by visual stimuli and in association with spontaneous depolarizations. Furthermore, when we examined the receptive field, we observed that the largest responses were elicited with broad field stimuli (Fig. 6B, inset). The receptive fields were measured in three preparations and the mean dimensions were $24 \pm 6° \times 22 \pm 5°$ ($X \times Y \pm$ SE), about twice the size of monopolar cell fields. It is possible that the larger fields are associated with the multicolumnar neurite in the lamina or the broad expanse of neurites in the CHE (Fig. 6A). The change in membrane resistance was proportional to the voltage response (Fig. 6B).

In the spiking state, the T-neuron (Fig. 6C) exhibits a sustained discharge in the dark which is inhibited by illumination (Fig. 6D). The inhibition is associated with a modest hyperpolarization of the axonal membrane. The frequency of the tonic discharge can be increased by depolarizing current and diminished by hyperpolarization. This result suggests that a shift in membrane potential may be responsible for the appearance of the two functional states we observe. Functionally these cells resemble small field versions of the optic tract dimming fibers (Wiersma and Yamaguchi 1966).

The T-neurons were also tested for possible input to SFs. Polarization of either polarity in the

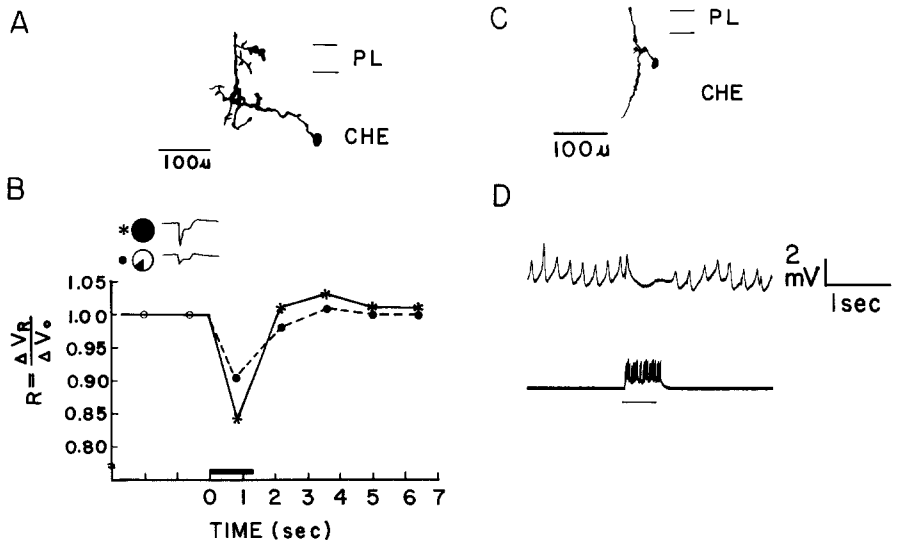

Fig. 6A–D. T-neuron. **A** Morphology of a T-neuron filled in the lamina. The soma of this cell is just outside the chiasma. Branching is observed on cell body neurite, on the axon in CHE, and in the lamina. No medullary process was observed in this cell. **B** (Inset) Light response waveform is similar to that of the nonspiking monopolar cells, but response amplitude increases with stimulus area. The hyperpolarizing light response is associated with an 18% decrease in membrane resistance. **C** Morphology of a second T-neuron in lamina. **D** Top trace shows the spiking activity in the dark and the inhibition of spikes by illumination. Bottom trace is the response of a single SF to the same stimulus (bar beneath SF trace)

dark was without effect. Hyperpolarization during a light pulse increased the SF mean rate by 21%. The rate change was highly significant ($P<0.01$). Depolarization elicited an insignificant ($P>0.10$) 6% decline in SF rate.

Lamina amacrine cell

Nässel (1977) described two types of multipolar amacrine cells, one of which (the only amacrine cell we dye filled) is shown in Fig. 7A. Several thick neurites project from the center of the cell (presumably the cell body). The great majority of branches are distributed in the proximal lamina and distal CHE. Some finer processes ascend to the distal lamina plexiform and inner cell body layers. The light response latency (30–50 ms) is similar to that of hyperpolarizing monopolar cells. This is consistent with dipteran synaptology, where amacrine cells are postsynaptic to receptor terminals. The light response waveform is complex with 3 separable components; a hyperpolarizing transient at light-on which decays to a hyperpolarizing steady plateau and a transient depolarization at light-off (Fig. 7B). The amacrine cell receptive field is of intermediate size (36° by 14°). The receptive field of the cell, illustrated in Fig. 7, occupied a 36° arc along the anterior rim of the cornea. Stimuli directed toward the center of the eye elicited only 'off' responses. When the central and annular stimuli were presented jointly (Fig. 7B, bottom), the hyperpolarizing transient was diminished by 70%. Comparison of responses to other stimulus pairs suggest that lateral inhibition was associated with a 40 to 50% response reduction.

We were able to drive the SFs by injecting hyperpolarizing current into the lamina amacrine cell (Fig. 7C, top). In this instance, a hyperpolarizing current of −4 nA elicited a prolonged burst of spikes in the SFs. To our surprise, however, depolarizing currents also excited SFs, although less effectively.

Efferents

Wiersma and Yamaguchi (1966, 1967) reported that some 'activity fibers' (multimodal corollary discharge neurons), which arise in the ventral nerve cord, can modulate the excitability of the optic tract units. A previous study in this laboratory documented the morphology of several ascending multimodal and mechanosensory interneurons with terminals in the supraesophageal ganglion and the optic ganglia (Wang-Bennett and Glantz 1985). In the present study, we encountered four cases of efferent inputs to the medulla externa. In each instance we observed a one to one correspondence between optic tract efferent spikes and PSP's recorded intracellularly in the medulla. The delay from optic tract spike to PSP was about 5 ms (Fig. 8A). Both hyperpolarizing and depolarizing PSPs were recorded. The hyperpolarizing PSPs which we observed at the start of one experiment (Fig. 8A), later reversed their polarity (Fig. 8B), thus suggesting a reversal potential near the membrane resting potential. One cell, which was morphologically labelled, appeared to be a medullary local interneuron (Fig. 8C). In another instance, mechanical pressure applied to the thorax elicited a burst of spikes in the medullary neuron. Furthermore, this spiking cell responded to illumination with a graded depolarization. A partial dye fill re-

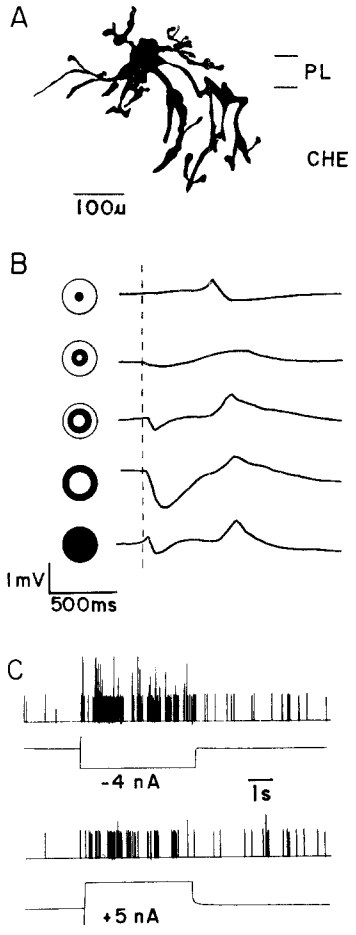

Fig. 7A–C. Multipolar neuron. **A** Morphology of a multipolar cell that corresponds to MP_1 of Nässel's (1977) classification. Several axon fibers radiate from the cell body, which is found on the distal margin of the lamina. **B** The receptive field of this cell is a 36° arc along the anterior rim of the eye. Stimuli to the central region of the cornea elicit only 'off' responses. **C** The effect of amacrine cell membrane polarization on SF activity. Top pair of the traces, hyperpolarizing current of −4 nA elicits a burst of spikes in SFs. The response latency is less than 10 ms. Bottom pair of the traces shows depolarizing current of +5 nA is also excitatory, but less effective in eliciting SF spikes. Upper trace in both panels are window discriminator outputs

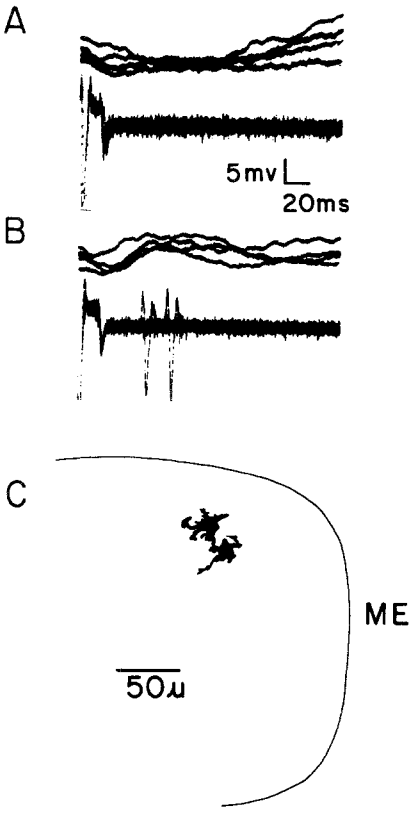

Fig. 8A–C. Efferents to the optic ganglia. Impalement was in the ME (top traces). **A** Five traces exhibiting time-locked hyperpolarizing PSPs were triggered on the positive slope of the efferent optic tract spikes (lower trace). The latency to the occurrence of the PSP is 5 ms. **B** Same reference event as in A, but later in same experiment. The compound PSPs have a short latency hyperpolarizing component (latency = 5 ms) and a delayed depolarizing component (latency = 30 ms). Four traces were triggered at the negative slope of the efferent spikes. **C** Morphology of the above cell. This medullary cell was located in the distal band of ME. Outline shows the edge of the ME

vealed processes extending to the lamina. On several occasions a concerted effort was made to test for efferent input to the tangential cells. We found no supporting evidence.

Discussion

Amacrine cells

The identification of the cell types we describe is guided by the Golgi and other light-microscopic studies of decapod lamina by Hanström (1924), Hafner (1973), Nässel (1976, 1977), Stowe (1977), and Stowe et al. (1977). Unfortunately, E.M. studies of the associated synaptology is more limited. The analysis of Nässel and Waterman (1977) was confined to crayfish receptor to monopolar cell synapses. *Homarus vulgaris* is the most closely related organism for which synaptology is documented for the multicolumnar lamina neurons (Hamori and Horridge 1966b). The lobster lamina cartridge is quite similar to that of crayfish; i.e. a stratified plexiform with lateral retinular cell terminals surrounding centrally disposed monopolar cells. Hamori and Horridge (1966a, b) also described two classes of tangential fibers. One class was of local origin, with somata proximal to the cartridges and with inclusions such as dense core vesicles and secretory granules suggestive of a neurosecretory function (Hamori and Horridge 1966a). Since the ultrastructure of the catechol-

amine-containing amacrine cells (Elofsson et al. 1977; Strausfeld and Nässel 1981) are the only known cell class to fit this description, we infer that these transverse fibers are amacrine cell projections. Hamori and Horridge (1966b) found that the principal amacrine cell input is from retinular cells (in several cartridges) and outputs are distributed primarily to monopolar cells (also in several cartridges) and secondarily to other amacrines and the second class of transverse fibers (Tan-cells?). The implication of receptor input to amacrines is consistent with our results, which indicate that amacrine cell response latencies, polarity and waveform are similar to those of monopolar cells but with a broad receptive field. These results are at odds with a single report on an amacrine cell in the fly (Ioannides 1972, cited in Laughlin 1981), which claims that the amacrine cell responds to light with a graded depolarization. The synaptology we infer from Hamori and Horridge (1966b) is generally consistent with Strausfeld and Nässel's (1981) description of dipteran amacrine cell synaptology, although in flies amacrine to monopolar cell synapses are restricted to the multicolumnar monopolar, L_4 (Strausfeld and Campos-Ortega 1977). A similar connection in crayfish lamina would be consistent with the fact that the amacrines and M_5 were alone among the broad field cells in their susceptibility to lateral inhibition. If amacrines synapse on M_5, then it follows that the amacrines provide visual excitation to M_5 via a sign-inverting synapse (Fig. 9).

On the output side, we have shown that polarization of the amacrine cell membrane provides a powerful excitatory input to medullary SFs. Since the amacrine cell has no projection to the medulla, the excitation must be transmitted via monopolar or tangential cells. Because both depolarization of M_5 and hyperpolarization of tangentials excite the medullary SFs, our results cannot distinguish between these alternative pathways. If the amacrines operate via a sign-inverting synapse, then amacrine hyperpolarization would excite M_5, and amacrine depolarization would excite the tangentials. Since the amacrine cell can excite SFs with polarization of either polarity, it is possible that both M_5 and Tan-cells are postsynaptic to the amacrines.

Tangential cells

The second class of transverse fibers described by Hamori and Horridge most likely belong to Tan_1 and/or Tan_2. These fibers are described as emanating from a thick process proximal to the lamina,

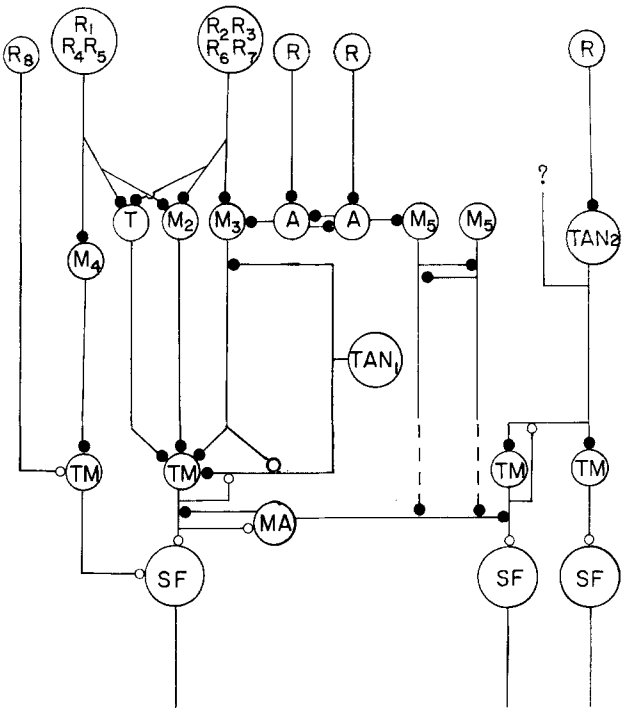

Fig. 9. A proposed connectivity scheme for identified lamina and medullary neurons. Small filled circles indicate sign-inverting synapses, open circles are sign-conserving synapses. *R* receptor; *M* lamina monopolar cell; *A* lamina amacrine neuron; *T* T-cell; *Tan_1*, *Tan_2* tangential cells; *TM* transmedullary columnar neuron; *MA* medullary amacrine cell; *SF* sustaining fiber

but with the somata probably located in another ganglion. They indicate that these cells obtain a principal input from a spatially broad array of retinular axons and a secondary input from amacrines. Furthermore, they show that these tangential fibers are presynaptic to unidentified monopolar cells in numerous cartridges. Our results indicate short latency (46 ms) light responses in Tan_2 (but not Tan_1). These latencies are similar to those of monopolar cell responses (Wang-Bennett and Glantz 1987) and would thus be consistent with direct receptor input (Fig. 9). The Tan_1 response latency is 30 to 40 ms greater than that of monopolar, amacrine or Tan_2 cells. This latency difference would imply that the Tan_1 visual input is several synapses removed from the columnar monopolar cells. In flies (Strausfeld and Nässel 1981), Tan_1 has no documented input in the lamina, but Tan_2 has input from amacrine cells.

If we put aside the difference in response latency, however, Tan_1 and Tan_2 appear to be closely related. The similarities include location of somata, overal distribution of neurites in lamina and medulla, hyperpolarizing light responses, broad receptive fields, an absence of lateral inhibition, and

comparable functional connections to SFs. In regard to these connections, it is interesting to note that the strength of the Tan_1 to SF connection (estimated from the SF rate change per mV hyperpolarization) is about 3 times that of the hyperpolarizing monopolar cell (0.77 versus 0.25 Hz/mV) (Wang-Bennett and Glantz 1987). Furthermore, in contrast to the columnar monopolar cells, the Tan-cell light response exhibits little (Tan_1) or no (Tan_2) decay during our light pulses. Thus the Tan-cells have the properties appropriate to convey a steady-state illumination signal from the lamina to the medulla and the SFs.

When considered in purely functional terms, the Tan-cells resemble broad field afferents with inputs and outputs parallel to the columnar projection of the monopolar cells. Morphologically, however, they appear to share too many features with dipteran tangentials to dismiss a possible centrifugal role. Thus, it is possible that Tan_1 derives its input in the medulla (e.g. from columnar monopolars) and expresses its actions in the lamina.

The multicolumnar monopolar cell (M_5)

To our knowledge, there is no documented synaptology for the multicolumnar monopolar cell in any decapod. In flies, the analogous multicolumnar monopolar neuron, L_4, derives input via amacrine cells. A similar connection in crayfish would be sign-inverting (Fig. 9), since the amacrine light response is hyperpolarizing and the M_5 response is depolarizing. Neurons with response properties similar to M_5 have been observed in the fly CHE (Arnett 1971, 1972), but were not identified morphologically. Furthermore, the dipteran analogs exhibited small receptive fields of near ommatidial dimensions.

There is a striking similarity between the M_5 and medullary SF response forms but the physiological evidence supports only a relatively weak functional relationship. Since the M_5 response latency exceeds that of SFs by 3 ms, M_5 cannot contribute to the SF transient depolarization. Furthermore, the application of tetrodotoxin to the optic ganglia does not block or diminish the SF light-evoked compound EPSP (Waldrop and Glantz 1985a). This could indicate that the M_5 input can be conveyed without spikes or that its contribution is too weak to detect in this circumstance.

Surround inhibition observed in lamina recordings of M_5 were associated with a net hyperpolarization of the M_5 membrane, and the hyperpolarization exhibited a reversal potential of 65 mV below rest. These features clearly indicate postsynaptic inhibition. It is possible that the inhibitory synaptic input is derived from adjacent M_5 cells (by analogy with the L_4–L_4 reciprocal synapses in Diptera) (Fig. 9).

T-cells

The synaptic connections of the T-cells are unknown. At least one T-neuron is an aminergic columnar neuron and a part of the lamina to medulla projection (Elofsson et al. 1977; Strausfeld and Nässel 1981). In Diptera, the T-neuron is postsynaptic to photoreceptors (Strausfeld and Campos-Ortega 1977), to amacrines and the L_2 monopolar cell (Shaw 1984). Our results reveal T-cell responses with latency and time course similar to those of the non-spiking monopolar cells. Thus, we assume that T-cells have photoreceptor input (Fig. 9). If the putative T-cell transmitter, dopamine, is released as a function of the T-cell membrane potential (and/or action potentials), then our results would suggest that dopamine is normally released in the dark in the medulla (or lamina, since the amacrine cells are also aminergic). Illumination would suppress dopamine release. This speculation has potentially important implications for the nocturnal decapods (Aréchiga and Wiersma 1969). Biogenic amines are potent modulators of arthropod nerve cell and organismic behavior (Harris-Warrick and Kravitz 1984; Hoyle 1985), and octopamine can control the sensitivity of retinular cells in *Limulus* (Evans et al. 1983; Kass and Barlow 1984). When SFs are monitored during prolonged periods of dark adaptation, they exhibit several qualitative changes indicative of heightened excitability which are not inconsistent with aminergic action. The changes include increased spontaneous activity and pronounced after discharges which are not observed in light-adapted animals.

A hierarchy of parallel projections

An interesting, but somewhat disturbing, feature of our results is the almost boring consistency with which lamina neurons modulate the SF discharge. In every cell class examined, from hyperpolarizing monopolars to Tan_2 to depolarizing M_5 cells, we found that membrane polarization of the same polarity as the light response was an excitatory signal to the SFs. There are probably a number of possible explanations for this circumstance, but two seem worth mentioning. The first is that the lamina is obviously a complex network. Polarizing current in any cell type is likely to affect one or several other cell types. This is particularly relevant to any

consideration of amacrine and tangential cell function. A second rationale concerns the dimensions of the receptive fields. The lamina neuron receptive fields can be viewed as an ordinal array, from the smallest (nonspiking monopolar cells) to the largest (Tan_2). The virtue of such an array is that different corneal light distributions are optimal for different classes of lamina neurons. Thus, at low light levels, Tan_2 may extract an adequate signal from its broad receptive field, while the monopolar cell signal is buried in noise. This capability would be enhanced by the wide aperture of the dioptric apparatus in the dark. At higher light levels, the more numerous columnar cells with smaller receptive fields could provide the more significant signals and with higher spatial resolution. The various parallel channels (Fig. 9) could be funneled through a common pathway, such as a transmedullary neuron, with its own broad field gain control mechanism, the medullary amacrine cells (Waldrop and Glantz 1985b).

Efferent modulation of visual activity

The role of efferents in the crayfish visual system was first described by Wiersma and Yamaguchi (1967). They observed a concurrence of spontaneous motor activity ('the excited state'), an increased discharge rate in 'activity fibers' (corollary discharge neurons) and enhanced SF light responses, i.e. a two- to four-fold increase in the light elicited firing rate. Subsequently, Aréchiga and Wiersma (1969) documented a 10–40 ms delay between activity fiber impulse bursts and subsequent SF bursts. The 'excited state' and activity fiber discharge did not alter the SF activity in the dark. The implication is that the activity fiber acts not on the SF per se, but on the visual pathway to the SF. More recently, we have shown that several ascending interneurons, which originate in the thoracic and/or abdominal ganglia, have projections to optic neuropils including the medulla. The results of this study indicate that interneurons of the medulla are postsynaptic to these multisegmental cells and may provide a link in the pathway mediating the activity-dependent modulation of visual excitability. Although tangential cells were observed to exhibit discrete synaptic potentials in the medulla, we were unable to correlate these events with action potentials of optic tract efferents.

A proposed circuitry for lamina and medullary neurons

The following account should be taken as a first approximation, intended to bring some cohesion to our data and, where possible, to offer a possible explanation for some phenomena. The account is principally based upon the data in this and the companion report. The synaptic connectivity scheme in the lamina is in part compiled from Nässel and Waterman (1977) and Hamori and Horridge (1966b). The gaps in the documented synaptology are filled with results on analogous cells in Diptera (Strausfeld and Campos-Ortega 1977; Strausfeld and Nässel 1981; Shaw 1981, 1984) and where no useful data is available we made some educated guesses based upon our physiological data. We assume that each morphologically defined neuronal class is functionally homogeneous. We also assume (for the sake of simplicity) that the sign of synaptic action of a given neuronal class and in a given synaptic layer is the same for every synapse formed by that neuron class (e.g. amacrine cell synapses are sign-inverting in every cell class postsynaptic to amacrine cells).

A minimal connectivity scheme is shown in Fig. 9. Some of the connections are documented in the published synaptology of decapods or the proposed connection (or some equivalent) is required by our physiological results. The filled circles indicate sign-inverting synapses. This could be the exclusive mode of synaptic action in the lamina. We will illustrate the rationale for this scheme by focusing on the proposed amacrine cell connections.

We propose that the amacrine cells are driven by retinular cells via a sign-inverting synapse. This follows from the short-latency, hyperpolarizing light response. The response is similar to that of the monopolar cells (M_1–M_4), which are known to be postsynaptic to retinular cells (Nässel and Waterman 1977). Such a connection is also consistent with the synaptology we infer from Hamori and Horridge (1966b), and it is consistent with the connectivity of dipteran amacrines.

Amacrine cells provide visual input to M_5 via sign-inverting synapses, and make similar connections to other amacrines and the hyperpolarizing monopolars M_1–M_4. The rationale for the amacrine to M_5 connection is as follows. The sign and latency of the M_5 light response indicate that M_5 is of higher order than M_1–M_4 (which rules out receptor input), but its receptive field is too small to be provided by Tan_1 or Tan_2 input. The choice is thus narrowed to the M_1–M_4 group or the amacrine cells. The documented synaptology in decapods does not contain any references to output connections by M_1–M_4 in the lamina, but amacrine cells are observed to synapse on unidentified monopolar cells (Hamori and Horridge 1966b).

The amacrine cell receptive field and response time course are appropriate to drive M_5. The proposed pattern of connectivity is also consistent with that established in the fly lamina.

The sign-inverting synapse from amacrine to amacrine and from amacrine to M_1–M_4 is based on the fact that both cell types exhibit strong lateral inhibition and depolarizing 'off' responses to surround stimuli. The proposed connections are consistent with Hamori and Horridge's (1966b) findings, but Tan_1 could supplement and/or substitute for the amacrine cell input in either case.

The input to Tan_1 is problematic if we adhere to the convention of a fixed postsynaptic response sign for each type of neuron. If we assume that Tan_1 derives its input in the medulla as in Diptera and that it is a third order neuron, then a sign conserving synapse from a columnar monopolar cell is not an unreasonable speculation.

The proposed lamina to medulla projection is based upon the fact that SFs are excited by polarization of lamina neurons of the same sign as that of the light response. For M_1–M_4, T-cells, and tangential cells, the effective current (hyperpolarizing) should diminish transmitter release by the lamina neuron. Since the SF light response is associated with a large increase in conductance (Waldrop and Glantz 1985a), it is not unlikely that the SF is driven by a neuron which increases transmitter release in response to illumination. Thus, for all of the above mentioned cell types, it is reasonable to postulate the presence of a sign-inverting synapse between the lamina neurons and the synapse which drives the SFs. The same arguments apply with respect to the excitation of the medullary amacrine cells (MA in Fig. 9), which appear to be excited in parallel with the SFs (Waldrop and Glantz 1985b). A second constraint on the SF excitatory pathway is the close correspondence between the SF excitatory receptive field and the distribution of SF dendrites in the medulla (Kirk et al. 1983). This correlation implies a principal role for the columnar projection in the medulla. All of these constraints are satisfied by the convergence of the hyperpolarizing lamina neurons on the transmedullary monopolar array. Functional distinctions among the transmedullary cells are possible, even likely, but there is presently no empirical basis for making these distinctions.

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