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Dendritic integration of motion information in visual interneurons of the blowfly

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Dendritic integration plays a key role in the way information is processed by nerve cells. The large motion-sensitive interneurons of the fly appear to be most appropriate for an investigation of this process. These cells are known to receive input from numerous local motion-sensitive elements and to control visually-guided optomotor responses (e.g., Trends Neurosci., 11 (1988) 351–358; Stavenga and Hardie, Facets of Vision, Springer, 1989). The retinotopic input organization of these cells allows for in vivo stimulation of selected parts of their dendritic tree with their natural excitatory and inhibitory synaptic input signals. By displaying motion in either the cells' preferred or null direction in different regions of the receptive field we found: (i) Responses to combinations of excitatory and inhibitory motion stimuli can be described as the sum of the two response components. (ii) Responses to combination of excitatory stimuli show saturation effects. The deviation from linear superposition depends on the distance and relative position of the activated synaptic sites on the dendrite and makes the responses almost insensitive to the number of activated input channels. (iii) The saturation level depends on different stimulus parameters, e.g. the velocity of the moving pattern. The cell still encodes velocity under conditions of spatial saturation. The results can be understood on the basis of passive dendritic integration of the signals of retinotopically organized local motion-detecting elements with opposite polarity.

An experimental analysis of dendritic integration often suffers from the problem that it is usually not possible to place excitatory as well as inhibitory input signals onto the dendrite at deliberate locations. However, this can easily be done in the large motion-sensitive interneurons in the third visual ganglion of the blowfly *Calliphora erythrocephala*. These neurons spatially pool the output signals of several hundreds of local, motion-sensitive elements [2, 4, 10]. On each side of the brain there reside about 50 large-field neurons. They can be identified individually by their unique anatomical and physiological properties. This allows to repeat an experiment with the same cell in different animals. Due to their retinotopic input organization, selected branches of the dendrites can be stimulated in vivo by visual motion in the respective parts of their receptive field. Since these cells are directionally selective, excitatory as well as inhibitory stimuli can be applied by displaying motion in the preferred or null direction, respectively.

Two properties of the fly's motion vision system are generally attributed to these cells: (i) The output of the optomotor system spatially integrates over local motion-sensitive elements from different parts of the visual field in a highly nonlinear way. The non-linearity makes the response largely independent of the stimulus size. Nevertheless, the system is still able to respond to changes in e.g. stimulus velocity [3, 9, 13, 22]. (ii) The local motion-sensitive elements consist of two mirror-symmetrical subunits with opposite preferred directions. They most likely converge with excitatory and inhibitory synapses on the large-field cells, respectively [2, 8]. According to theoretical analysis the system would acquire the largest possible direction selectivity if the signals of these subunits are subtracted from each other in a linear way [2, 6].

The present paper shows that the large-field cells in the fly's third visual ganglion acquire both of these computational properties by surprisingly simple means. The experimental analysis is done on the VS cells. The 11 VS cells represent one subpopulation of the large-field neurons [13, 14]. They have a simple T-shaped anatomy (Fig. 1) and are depolarized by downward motion and hyperpolarized by upward motion in a graded way. The depolarizing phase may be superimposed by spike-like activity [12, 13].

In the first experiment, the spatial sensitivity distribution of the VS cells was determined by stimulating them with motion in either preferred or null direction pre-

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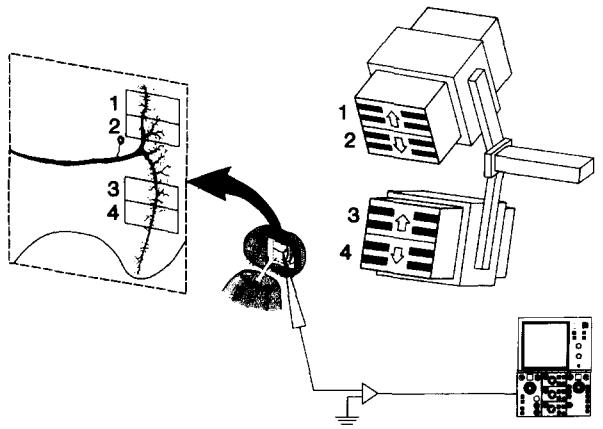
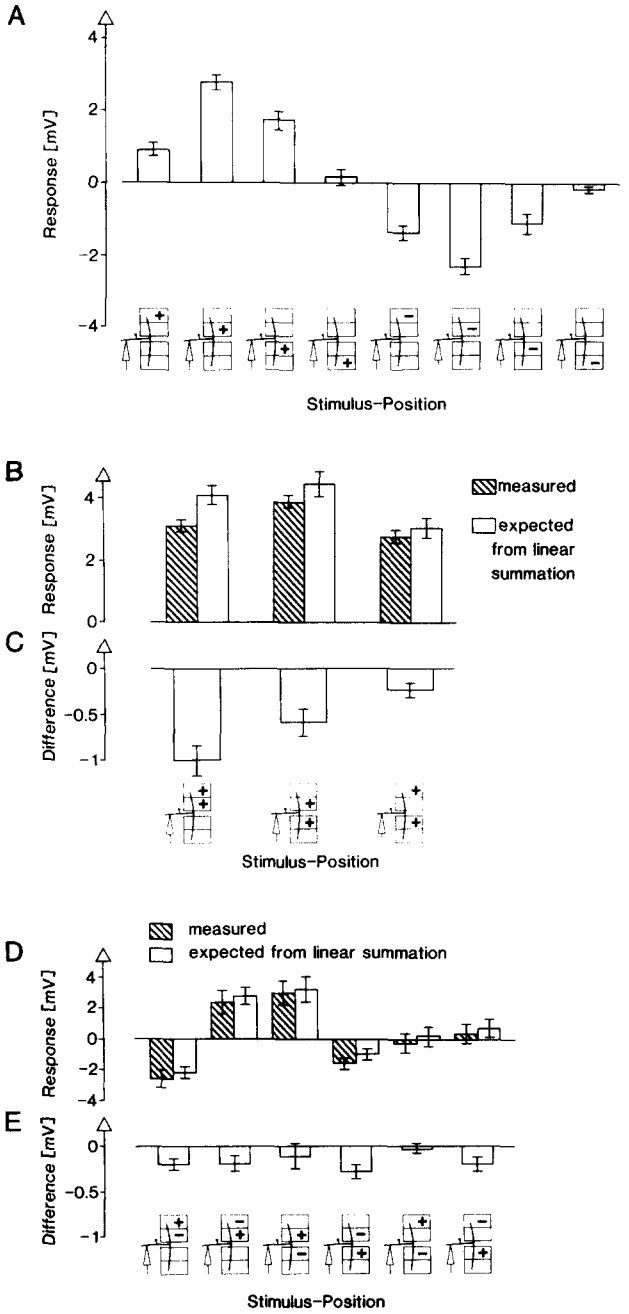


Fig. 1. Experimental set-up. A fly facing two monitors (Tektronix 608) is shown schematically from behind. The backside of the head capsule is opened (for details of the preparation see ref. 6) and a VS cell can be seen lying directly underneath the surface of the brain. The VS cell is zoomed on the left side of the figure. It has a horizontally oriented axon and vertically oriented main dendrite. In contrast to other large-field neurons of the fly [9] the simple T-shaped anatomy of the VS cells facilitates the topological placement of the stimuli on the dendrite with respect to the recording site. The monitors were arranged in the visual field of the fly such that motion stimuli displayed on the upper monitor (fields 1 and 2) stimulated the dorsal dendritic branch of the cell, and motion stimuli displayed on the lower monitor (fields 3 and 4) stimulated the ventral dendritic branch of the cell. The angular width of each field was 40° in horizontal, and 28° in vertical direction as seen by the fly. Stimuli were generated by an image synthesizer (Picasso, Innisfree) and consisted of an one-dimensional grating of 87% contrast. When activated, the grating was moving vertically for 2 s in either the cell's preferred or null direction. The recording electrodes were made from glass capillaries (Clark Electromedical Instruments, GC100F-10) and pulled on a P77 Brown-Flaming puller. When filled at the tip with a 3% solution of Lucifer Yellow (Aldrich Chem.) in 1 M lithium chloride, they had a resistance of 30–60 MΩ. Signals were amplified and fed to a personal computer (IBM PS/2) via an A/D-converter (Metra Byte uCDAS-16G, Keithley Instruments) at 1 kHz. Responses shown in Fig. 2A,B,D and in Fig. 3 represent the mean steady-state amplitudes obtained by averaging the membrane potential over the 2nd half of the stimulus period of 2 s, and subtracting the average membrane potential during a period of 1 s preceding the onset of stimulation.



sented in one out of four vertically displaced locations (see Fig. 1). Their sensitivity is largest for motion in field 2 and smallest for motion in field 4 (Fig. 2A). These data will now be used to compare the responses to simultaneous motion stimulation in two fields with the linear superposition of the responses induced by each of the stimulus constituents. The difference between the measured responses and the responses 'predicted' in this way represents a measure of the nonlinearity of the underlying synaptic interactions. In the present experiments pairwise stimulation was restricted to fields 1–3.

For composite stimuli consisting of two excitatory motion fields, the measured response is always smaller than the sum of the individual response components (Fig. 2B). The deviation from the sum is the larger, the smaller the distance between the stimuli and thus the closer the activated dendritic areas (Fig. 2C). These results are expected if it is assumed that the synapses are not connected to the main dendritic trunk via high resistance connections. Then, activation of one synaptic site should change the driving force as well as the input impedance at neighboring dendritic locations, leading to nonlinear synaptic interactions when both synaptic sites are activated simultaneously. Of course, these interactions should decrease with increasing electrotonic distance between the synaptic sites (see e.g. refs. 1, 15, 16, 18, 19, 21).

For composite stimuli consisting of excitatory and inhibitory stimuli, the measured responses are also smaller

Fig. 2. Average response recorded in the axon of VS cells (VS 3–5) in response to various motion stimuli. Due to their similar response properties the data of VS cells 3, 4 and 5 were pooled. Data are the mean ± S.E.M. of the recordings obtained from 14 different VS cells. Each neuron was tested with 3–10 sweeps per stimulus condition. The location of each stimulus with respect to the stimulated part of the dendrite is shown in the pictogram below each response bar with a '+' and a '−' sign indicating preferred and null direction motion, respectively. The pattern was a square-wave grating with a spatial wavelength of 14° which was moving at 28°/s. All other stimulus parameters are given in the legend of Fig. 1. A: dependence of the response on the vertical position of the stimulus. B: dependence of the response on the relative position of two excitatory stimuli. The responses to the composite stimuli (hatched bars) are compared with the values expected from a linear superposition of the responses to the single stimulus constituents (open bars). C: difference between measured and expected values from the data shown in B. Note that the differences were calculated for each cell individually and then averaged. D: dependence of the response on the relative position of an excitatory and an inhibitory stimulus on the dendrite. As in B, the responses to the composite stimuli (hatched bars) are shown together with the values expected from linear superposition (open bars). E: difference between measured and expected values from the data shown in D. Mean values and errors were calculated as in C. ←

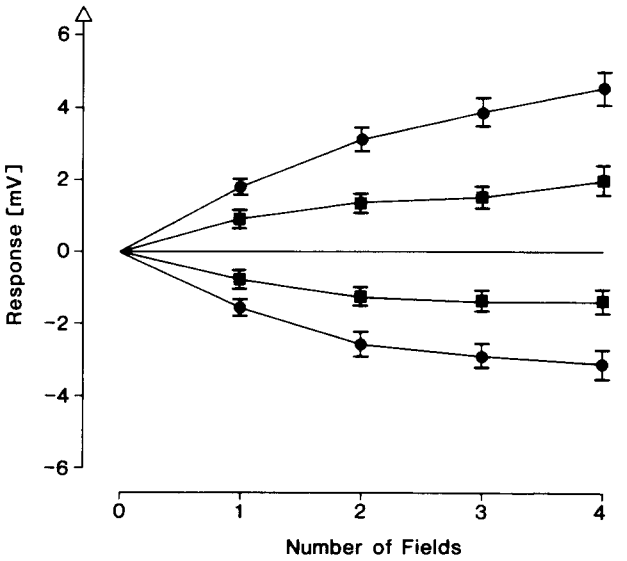


Fig. 3. Average response of VS cells (VS 1–6) in response to preferred (upper curves) and null direction motion (lower curves) at two different velocities (v=35°/s, v=106°/s) displayed in a variable number of fields. The pattern was a sine-grating and had a spatial wavelength of 9.3°. All other stimulus parameters are given in the legend of Fig. 1. Data are the mean ± S.E.M. of the recordings obtained from 18 (v=35°/s) and 14 (v=106°/s) different VS cells, respectively. Each neuron was tested with 1–7 sweeps per stimulus condition. The number of fields in which motion was presented is indicated on the x-axis. To make the values independent of the position of the stimulus the data obtained in response to motion in one, two and three fields, respectively, were averaged from the responses to the four, six and again four possible stimulus combinations available under the corresponding conditions. At v=106°/s the pattern is moving at a temporal frequency of 11.4 Hz which is beyond the optimum of the fly motion detection system and, therefore, yields smaller steady-state responses. When fitted with a saturation function of the form $f(x)=A\,x/(x+c)$ the following parameters were found for the different stimulus conditions (from top to bottom): (1) A=8.7 mV, c=3.7; (2) A=3.0 mV, c=2.3; (3) A=−1.9 mV, c=1.4; (4) A=−4.5 mV, c=1.7.

than the sum of corresponding responses to motion of the stimulus constituents (Fig. 2D,E). However, these differences are considerably smaller than during stimulation with two excitatory stimuli. Hence, excitatory and inhibitory stimuli superimpose almost linearly, independent of their relative position. Such a behavior is expected from a passive dendritic tree if the equilibrium potentials for the respective excitatory and inhibitory inputs are quite symmetrical with respect to the resting potential [17]. This is likely to be the case in the VS cells because with an average value of about 38 ± 3 mV as measured in axon and also in main dendritic branch the resting potentials of these cells are comparatively low (see also ref. 13). This is to say that similar driving forces can be realized for both excitatory and inhibitory synaptic input.

In another experiment, the response of the VS cells was determined as a function of the number of stimulus fields in which a pattern was moving either in the cell's preferred or null direction. This was done at two pattern velocities. For all stimulus conditions the membrane potential change increases with an increasing number of stimulated fields (Fig. 3). The increase is significantly below the sum of the components and can be fitted by saturation curves. Two aspects of these data are particularly noteworthy. (i) The corresponding data for motion in preferred and null direction are about symmetrical around the resting potential. This again substantiates that the excitatory and inhibitory synaptic currents of the VS cells are driven by similar electromotive forces. (ii) The saturation curves that can be fitted to the data obtained at different pattern velocities do not approach the same saturation plateau but level off at different plateaus. Hence, the response amplitudes of the VS cells, as of other cells in the third visual ganglion of the fly [9] and the behaviorally determined optomotor responses [22], tend to be relatively invariant to changes in the size of the stimulus pattern. Nevertheless, they still code for changes in other stimulus parameters such as pattern velocity.

This important property of the VS cell cannot simply be a consequence of synaptic saturation, since then the response curves should approach a common saturation level irrespective of pattern velocity. A possible explanation arises from the fact that the large-field cells receive their input from two types of local motion-sensitive elements with opposite preferred directions via excitatory

and inhibitory synapses [2, 5, 8]. As a consequence of the low direction selectivity of the retinotopic input elements, preferred direction motion, for instance, excites not only the excitatory but also, to a smaller extent, the inhibitory input channels [5]. Therefore, the membrane potential is expected to saturate with an increasing number of activated input synapses at a value which corresponds to a mixture of the equilibrium potentials of both excitatory and inhibitory membrane channels [20]. Since the degree of direction selectivity of the input elements depends on stimulus parameters such as velocity [6], the mixed reversal potential and, accordingly, the saturation level of the cell is expected to change along with them just in accordance with the present experimental results.

In conclusion, the specific membrane properties of the VS cells and the nature of their synaptic input allow them to achieve three important properties of the optomotor pathway: (i) Fairly linear interaction between excitatory and inhibitory synaptic input allowing for an almost quantitative subtraction of the responses of their oppositely directed antagonistic local input elements. This results in a comparatively high direction selectivity. (ii) Relative invariance of the response with respect to the number of activated input synapses and, thus, the size of the stimulus pattern. (iii) Response amplitudes that still vary with other stimulus parameters such as pattern velocity. Our experiments show that in order to explain these features no complicated network interactions need to be assumed: They simply follow from basic properties of the motion-sensitive input elements and the biophysical design of the postsynaptic large-field neurons.

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