

THE consequences of dendritic geometry for the processing of synaptic information was analysed in two types of motion-sensitive neurones in the visual system of the fly. These neurones differ conspicuously in the morphology of their dendrites but receive their input from the same type of local motion-sensitive elements. Intracellular recording and activating selected regions of the dendrite by visual motion showed that, in accordance with cable theory of nerve cells, the way in which postsynaptic signals interact is essentially determined by the structure of the dendritic tree.

## Processing of synaptic information depends on the structure of the dendritic tree

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### Introduction

Ever since neuroanatomists discovered the fascinating anatomical variety of neurones there has been speculation regarding the computational significance of all this diversity. The advent of theoretical approaches and computer modelling put the possible functional consequences of dendritic geometry for the processing of synaptic information on a sound theoretical basis, although direct experimental evidence is still scarce.<sup>1–7</sup> Identified visual interneurons in the fly brain represent a good system in which this fundamental question of computational neurobiology can be addressed experimentally. This is because first, selected dendritic regions of these neurones can be activated via their natural synaptic input and second, different types of these neurones possess substantially different dendritic shapes but have the same kind of synaptic input.

In the theoretical framework of a passive dendritic tree, saturation is the only possible non-linear interaction between synaptic inputs of the same polarity.<sup>2</sup> More sophisticated non-linear interactions can only occur if there are active (i.e. voltage-gated) ionic channels in the dendritic membrane. However, even linear superposition of postsynaptic signals, though simple from a mathematical point of view, is not easily accomplished by dendritic pooling. Only if the synaptically induced membrane potential changes are small compared with the leak conductance of the cell are the postsynaptic potentials predicted to superimpose linearly. However, when the conductance changes become larger the postsynaptic potential saturates increasingly. For two synaptic sites this means that the joint activation of both inputs should lead to a postsynaptic potential that is less than the sum of the

postsynaptic potentials obtained if each of the inputs is stimulated alone. The strength of this non-linear interaction is predicted to depend on the electrotonic distance between the two synaptic sites and, thus, on the specific membrane parameters and the geometrical properties of the neurone.

This prediction was tested in the large motion-sensitive visual interneurons ('tangential cells') in the third visual neuropil of the blowfly *Calliphora erythrocephala*.<sup>8</sup> There are approximately 50 of these cells in each half of the brain, and they can be identified individually owing to their characteristic structural and functional properties. With their extended dendritic trees the tangential cells pool the output signals of several hundreds of columnar elements.<sup>9–12</sup> Owing to the retinotopic organization of these input elements, motion in visual space is projected like a two-dimensional image on the dendritic tree of the tangential cells<sup>13,14</sup> (Fig. 1). This allows activation of restricted parts of the dendrite by motion in localized areas of the cell's receptive field. Since the dendrites of different types of tangential cells differ tremendously, but share a common set of synaptic input channels, the functional implications of dendritic geometry can be analysed.

### Materials and Methods

The experiments were performed with 1- to 5-day old female blowflies (*C. erythrocephala*). The preparation for intracellular recording was as described previously.<sup>10</sup> Recording electrodes, filled at the tip with a 3% solution of Lucifer Yellow (Sigma) in 1 M lithium chloride, had a resistance of 30–60 M $\Omega$ . Signals were

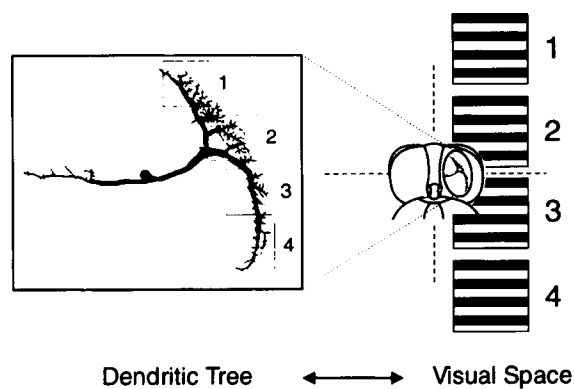


FIG. 1. Retinotopic projection of the visual field on to the dendritic tree of a large-field neuron in the fly's third visual neuropil. A fly's head facing four visual stimulus fields is shown schematically from behind. The back of the head capsule is opened and a large-field cell can be seen lying directly underneath the surface of the brain. The cell is zoomed in the left part of the figure. The retinotopic input organization of the large-field cells allows selected parts of the dendritic tree to be activated by visual motion. The dendritic projection areas of the four stimulus fields are indicated by four rectangles that are superimposed on the cell.

amplified and fed for subsequent data evaluation to a PC (IBM PS/2) via an A/D converter (Metra Byte uCDAS-16G, Keithley Instruments) at 1 kHz.

The cells were activated by motion in four adjacent stimulus fields (Fig. 1), each with an angular width of 40° in horizontal and 28° in vertical direction, as seen by the fly. Stimuli were generated on Tektronix 608 monitors by an image synthesizer (Picasso, Innisfree) and consisted of a one-dimensional sinewave grating of 9° spatial wavelength and 87% contrast. When activated, the grating moved for 2 s at 28° s<sup>-1</sup>. The analysis is based on the mean steady-state responses to pre-

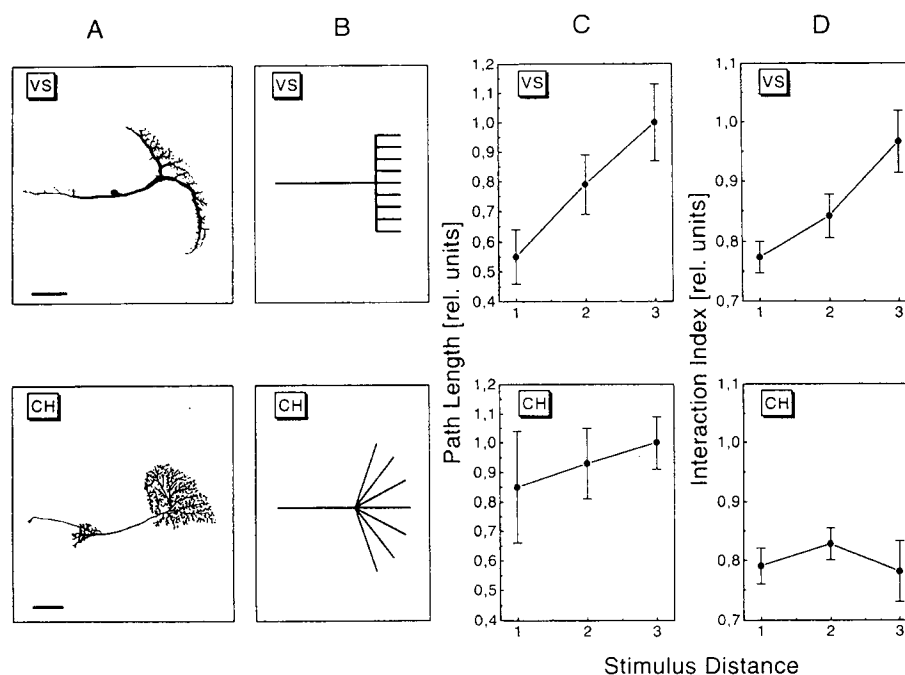
ferred direction motion as determined during the last second of the stimulation time.

## Results

The experiments presented here were performed on two classes of cells which exhibit particularly pronounced differences in their dendritic geometry (Fig. 2A, B). The so-called VS-cells<sup>15</sup> have an almost straight primary dendrite from which small second order dendrites branch off like the teeth of a comb. The so-called CH-cells<sup>16</sup> are characterized by main dendrites which branch off almost at one point, giving rise to a structure with a palm-like topology. Both cell types respond to motion in their preferred direction mainly by graded depolarizations with amplitudes of up to 10 mV.<sup>14,16,17</sup> Selected parts of the dendritic tree of these neurones were activated by motion in four vertically displaced regions of the receptive field (Fig. 1).

To quantify the structural differences between the VS- and CH-cells, we measured the path lengths between postsynaptic sites for the two cell types on the basis of reconstructed material. A grid consisting of four vertically displaced sectors was superimposed on the dendritic tree. These sectors roughly correspond to the projection areas of the four visual stimulus fields used in the electrophysiological experiments. As an approximation for the electrotonic distance between the various synaptic sites, the dendritic path length was determined between the tips of each major branch in a given sector with any major tip in the other sectors. For the two cell types, the dendritic path lengths between different postsynaptic sites depends in a different way on the distance of the stimuli in visual space by which

FIG. 2. Interaction between postsynaptic signals depends on dendritic geometry. (A) Anatomy of two types of large-field motion sensitive cells (VS-, CH-cells; CH-cells from Ref. 24). (B) Cartoons of the two cell types to emphasize the difference of the geometry of their major dendritic branches. (C) Normalized mean length of the dendritic path that connects the tips of the major dendritic branches with one another as a function of the distance between the four stimulus fields in visual space from which the various tips receive their input. This dependence is different in the VS- and CH-cells. The data are mean  $\pm$  s.e.m. obtained from three cells of each type. (D) Dependence of the interaction index on the distance of the stimulus fields in visual space. The interaction index is given by the ratio of the responses to simultaneous motion in two stimulus fields and the sum of the responses to motion in each of the two stimulus fields alone. All data are the mean  $\pm$  s.e.m. of recordings obtained from 20 VS-cells and 12 CH-cells. Scale bars: 0.2 mm.



they are activated (Fig. 2C). As a consequence of the comb-like structure of the VS-cells, their dendritic path length increases considerably with increasing distance of the stimuli in visual space. In contrast, the corresponding pathlength of the CH-cells increases only weakly, as is expected from the palm-like structure of their dendritic tree.

Do these structural differences between the two cell types affect the way in which synaptic input signals originating in different parts of the dendritic tree interact with each other? To analyse this question the responses of the cells were determined for motion in each of the four stimulus fields alone as well as in all possible combinations of two stimulus fields. The ratio of the responses to simultaneous motion in two areas and the sum of the responses induced by motion in each area alone was calculated as a measure of synaptic interaction ('interaction index'), a value of 1 corresponding to a linear attraction and smaller values designating an increasingly stronger saturation of the postsynaptic signals. At least under the stimulus conditions used in the present experiments, the interaction index was  $< 1$  for all combinations of stimuli, as may be expected for a passive dendritic tree. However, when the interaction index was plotted as a function of the distance between the stimuli in visual space (Fig. 2D), pronounced differences between the two cell types were observed. For the VS-cells, the interaction index increased monotonically with increasing distance between the two stimulus fields, in accordance with our previous experiments.<sup>19</sup> This means that the saturation is more pronounced if the visual stimuli are close to each other and decreases with increasing distance of the visual stimuli. In contrast, for the CH-cells the interaction index does not depend in an obvious way on the distance between the two stimulus fields. Thus, the level of saturation is virtually unaffected by the distance of the stimuli in visual space.

## Discussion

The anatomical and electrophysiological data shown in Figure 2 suggest that the structure of the dendritic tree is reflected in the way postsynaptic signals interact with each other. Changes in the level of saturation that are achieved by increasing the distance between the stimulus fields in visual space are paralleled by changes in the dendritic path length between the postsynaptic sites that are activated by the stimuli. When the dendritic path length changes significantly with the field's distance, the strength of interaction between the corresponding postsynaptic signals also varies considerably. On the other hand, small variations of the dendritic path length are associated with a virtual absence of changes of the interaction index.

These conclusion have to be qualified. Cable theory predicts that the interactions between synaptic inputs in a passive dendrite depend on the electrotonic dis-

tance between the corresponding postsynaptic sites. The dendritic path length determined in this study, however, represents only a crude estimate of the electrotonic distance. This is because the width of the dendrites varies considerably along a given branch and the biophysical membrane properties may not be homogeneous all over the dendrite. All these anatomical and biophysical details have to be known in order to account for the numerical values of the interaction index. Since, however, these parameters are likely to vary for a given cell in essentially the same way for all dendritic paths from the distal to the proximal branches, such changes are unlikely to affect qualitatively the dependence of the interaction on the stimulus distance. Passive cable theory predicts different results for the non-linear interaction depending on the time course of the response and the time constants of the capacitative currents. In the fly tangential cells, however, the transient responses at motion onset are determined not only by the biophysical properties of the cell itself but also by the dynamical properties of the local input elements. Since the latter are not known, only the steady-state response levels were taken into account where the response settles after approximately 1 s.<sup>18</sup> Since VS- and CH-cells do not have the same sensitivity in their entire receptive fields,<sup>14,19</sup> motion in the different stimulus fields leads to responses of different size. As a consequence, a small response may interact with another one more or less linearly, just because of its small size rather than due to a large electrotonic distance between the corresponding postsynaptic sites. Nevertheless, since VS- and CH-cells are affected by the consequences of spatial sensitivity gradients in a similar way, these are unlikely to be the major determinant of the characteristic dependence of the interaction index of both cell types on stimulus distance. In principle a compressive non-linearity is not necessarily the consequence of a simple saturation in a passive dendritic tree. It could also be due to active membrane properties, such as potassium outward currents, that are triggered by depolarization of the cell. Indeed, active membrane properties have recently been revealed in both VS- and CH-cells<sup>20</sup> (Haag and Borst, in preparation), of which at least voltage dependent calcium channels were found in the dendritic tree.<sup>21</sup> Moreover, at low activation levels, the responses of the tangential cells may be considerably larger than those predicted by linear summation of the responses elicited by motion in the individual stimulus fields alone.<sup>22</sup> This hints at the possibility that facilitatory mechanisms also play a role in shaping the postsynaptic potentials. Nevertheless, the finding that saturation behaviour is similar for excitatory and inhibitory stimuli<sup>19,23</sup> clearly speaks against the assumption that the saturation effects observed in the present study are the consequence of active membrane processes. Rather, it can be explained in the most parsimonious way as the result of passive membrane properties.

## Conclusions

The experiments reported here demonstrate a relationship between the structure of the dendritic tree and an important computational property of nerve cells, i.e. the way how postsynaptic signals interact with each other. Hence, the outcome of synaptic information processing does not only depend on the nature of the synaptic signal but also depends on the topology of the dendritic tree.

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