THE CONCEPT OF DECISION POINTS AS A TOOL IN ANALYZING DENDRITIC COMPUTATION

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ABSTRACT

The concept of decision points is introduced as a tool for analyzing computational processes in dendritic trees. Using this concept, a simplified model of a dendritic tree is derived. The various nonlinear processes in dendritic trees are interpreted as "computational decisions" made at "decision points". This simplified model provides insights into the possible role of dendritic geometry and passive biophysical properties such as R_m and R_i. First, we demonstrate the computational limitations of passive dendritic trees in which the inputs are modeled as current injections. The advantage of adding nonlinearities into dendritic trees is then demonstrated, by analyzing the spatio-temporal integration properties of various nonlinear decision points at the dendritic tree. Distal dendritic decision points are found to be suitable for performing coincidence detection of synaptic events, while proximal and somatic decision points tend to act as integrators of synaptic inputs. The spatial integration properties also vary between decision points: the synapses that significantly affect a given decision point are located in the vicinity of the point or distal to it. We compare different realistic dendritic morphologies and demonstrate that the geometry of the tree is a major determinant of its computational capabilities. This emphasizes the importance of a dendro-centric view of the neuron as a computational device.

INTRODUCTION

Neural network modelers usually consider a point-neuron as the atom of their network. The effect of the dendritic geometry and the spatial distribution of synapses on the dendrites is thus neglected[1,2,3]. Even in network models that utilize a more "realistic" neuron, the dendrite is represented by a short cable, or a "tree" with one order of branching[4]. Although these models include some of the realistic biophysical properties of neurons (as voltage dependent channels), they fail to mimic the role of the branching structure of the dendritic trees.

On the other hand, single neuron modelers, impressed by the magnificent variety of dendritic geometries found in nature, are expending a lot of effort to understand the role of this geometrical variety[5,6]. Still, there aren't systematic tools for comparing different dendritic geometries and biophysical properties of various cell types and explaining the meaning of the differences between these cells. The commonly used approach is to use detailed compartmental modeling. The results of these multi-parameter models are often hard to interpret and generalize. The computational function of the neuron depends on many complicated factors (morphology, channel density and distribution as well as input architecture) and trying to mimic the complicated reality by a complicated simulation does not lead to a general understanding of the system. However, it is still unknown which neuronal properties *are* important and which are secondary in their importance.

As an alternative to the detailed compartmental modeling approach, we propose here a simple model, based on the concept of decision points, that can help in obtaining insights into the main functional properties of dendritic trees. In general, *simple models* try to explain the function of few factors in the system, by simplifying the other factors. The concept of decision points neglects some important contributors to neuronal computation, such as the vast variety of channel types, and emphasizes the role of dendritic geometry and the passive properties of neurons. However, the nonlinear properties of neurons are introduced in a very simplified way. Hence, this new type of model serves as a bridge between strictly passive models and active models of single neurons.

THE CONCEPT OF DECISION POINTS

For the input-output relationship of the neuron, we typically emphasize the role of the soma (and the axon hillock) as a site where synaptic currents are transformed into a pattern of action potentials. Because of the convergence of the many synaptic inputs at the soma, the soma cannot be regarded as a faithful relay that delivers all the arriving information to the next "station". Many combinations of synaptic inputs can result in the same output. In other words, only part of the spatio-temporal information that arrives at the soma is expressed in the output pattern of action potentials at the axon. Hence, in the soma, a decision is made - what part of the information should be delivered to the axon. For example, in a simple isopotential integrate-and-fire model of the neuron, the only information delivered by the neuron is *when* the sum of the inputs reaches a threshold.

The soma, however, is not the only decision point in the cell. Many types of nonlinear interactions between inputs at the dendritic tree (e.g., local "veto" effect of synaptic inhibition, nonlinear summation of excitatory inputs at partly isolated dendritic arbors, activation of voltage-dependent channels) may be implemented as local decision points. The dendritic decision points are triggered by a subset of the inputs that impinge on the dendrites, and in many cases, the voltage response at the decision point affects other decision points. Decision points cannot be regarded as faithful relay points because their output does not include all the information contents of their inputs. We may say that such decision points "decide" what part of the information is to be transmitted to other decision points (specifically, to the soma).

The idea that the processing in the dendrite is done by "decisions" at "decision points" does not convey all the biophysical properties of realistic neurons, but it allows one to state some rules for dendritic computation. In the present work, the dendritic tree and the soma were assumed to be passive, and the inputs were modeled by current injections (rather than by conductance changes). The *method of moments* was used to analyze the transient voltage response of a passive dendritic tree to a current input[7,8]. To this passive analysis we then added the concept of decision points. Hence, although the voltage response in the model was calculated using the elegant methods of passive cable theory, the interpretation of the results was made from the point of view of the decision points, where nonlinear operations could take place. This "hybrid" approach is demonstrated in this chapter.

RESULTS

The somatic decision point

When a synapse is placed at a dendritic location in a passive dendrite, its efficacy on the somatic decision point will be smaller and delayed, compared to placing that synapse directly at the soma. What is the cost, in terms of efficacy and delay, of moving a synapse from the soma to the dendrites? To answer these questions, we use definitions that are based on the *method of moments*[8]. We define *attenuation cost* of placing an input at location i when the decision point is at location d as $1 - {}^{R_{tr}(i,d)}/_{R_{in}(d)}$, where $R_{tr}(i,d)$ is the transfer resistance between points i and d and $R_{in}(d)$ is the input resistance at point d (the classical steady-state definitions of input and transfer resistances are equivalent numerically to the transient-input definitions of these resistances, based on the ratio between the time-integrals of the transient[8]). For an input that is modeled by a transient current injection, $R_{tr}(i,d)/R_{in}(d)$ is the ratio between the time-integral of the voltage response at point d (the decision point) when the input is located at i and the time-integral of the voltage response at d when the input is located at d. Therefore, the attenuation cost is the fraction of the voltage response that was lost (at point d) when the input is moved from point d to point i. Similarly, we define *delay cost* of placing an input at location i when the decision point is at location d as $D_{tr}(i,d) - D_{in}(d)$, where $D_{tr}(i,d)$ is the transfer delay between points i and d and $D_{in}(d)$ is the input delay at point d (these delays are defined as differences between the centroids of transient signals[7,8]). The delay cost is the additional delay in the voltage response at d due to moving the input from d to i.

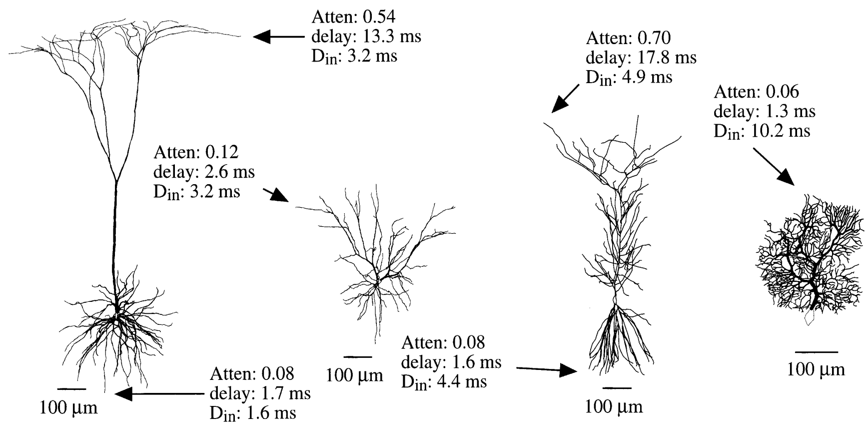

Figure 1: Attenuation cost (Atten), delay cost (delay) and input delay (D_{in}) at various points in four types of dendritic trees. The costs are calculated with respect to the somatic decision point. From left to right: pyramidal cells from layer 5 and layer 2/3 of the cat visual cortex (provided by R. Douglas); hippocampal CA1 pyramidal cell from the rat (provided by D. Amaral and N. Ishizuka); cerebellar Purkinje cell from the guinea pig (provided by M. Rapp). For comparison, the same parameters were used for all cells: R_m = 20 kΩ·cm^2, R_i = 100 Ω·cm, C_m = 1 μF/cm^2 (i.e., τ = 20 ms). For this demonstration, dendritic spines were not included in the model (however, the qualitative results, as discussed in text, holds also for the case that includes spines). The somatic input delay was about 18 ms for all cell types.

In Fig. 1, the attenuation cost and the delay cost with respect to the somatic decision point are depicted for four types of dendritic trees. To emphasize the role of geometry, all the modeled cells share the same biophysical properties. Using these properties, the attenuation cost is very small except for inputs located at distal parts of apical dendrites. The somatic input delay for the cells modeled is about 18 ms, and this is also a fair estimate for the input integration time window at the soma (see below). Hence, delay costs that are much smaller are negligible in their effect on the somatic integration (except for special cases of spatio-temporal input patterns). From Fig. 1 it is also clear that the delay cost of placing an input at the dendrites is small, except for inputs at distal parts of apical dendrites.

Although these results may depend on the biophysical properties of the modeled dendrites, it can be shown that in general, the cost of placing an input outside the soma is small. Therefore, a model of a passive dendrite with inputs that are represented by current injections has computational capabilities that are very similar to those of a point neuron. However, using the concept of dendritic decision points, nonlinearities in dendrites may be found to increase the computational repertoire of the dendrites.

Dendritic decision point compared to the somatic decision point

If some inputs should be summed together for activating a nonlinear process at a decision point, their voltage responses at the decision point must overlap. Hence, these inputs must arrive within the same time window, the width of which is governed by the width of the voltage responses. The *input delay* at the decision point may serve as an estimate for the width of this local integration time window[7,8]. In an isopotential neuron model, the input delay is the membrane time constant, τ_m, which is an estimate of the width of the voltage response to a brief input. As depicted in Fig. 1, The input delay at dendritic decision points, and hence the integration time window, can be 10 times smaller. The range of input delays may vary from one cell type to another, presenting a clear dependence of the properties of the decision points on the dendritic geometry. It can be shown that the branching is a major factor in creating the wide range of integration time windows.

An analysis of the attenuation costs and the delay costs with respect to various dendritic decision points shows a difference between the decision points in their dependence on the spatial distribution of the inputs. For a given decision point, one can define a dendritic region for the inputs that may affect significantly the voltage response at this decision point. The dendritic tree introduces hierarchy between the various decision points in the process of computation. Each decision point is affected by inputs that arrive from its vicinity and from inputs that are distal to it (the detailed analysis is in preparation).

SUMMMARY AND CONCLUSIONS

1. **The concept of decision points**, combined with **the method of moments**, is a useful tool for analyzing the computational capabilities of realistic dendritic models **that include some kinds of nonlinearities**.

2. Using the method of moments and the concept of decision points, we show that a passive model in which the soma is the only decision point, **does not add significantly to the computational capability** of the neuron (compared to a "point neuron"). This was shown by analyzing the "cost" of placing a synapse away from the soma.

3. We show that the structure of the dendritic tree provides for many decision points with various computational properties. Moreover, there are different synchronization requirements for inputs in local versus global decision points. **We suggest that the role of the spatial distribution of synapses on the dendritic tree is for making "local computation clusters".**

4. The theoretical framework demonstrated here may be used for a detailed analysis of reconstructed dendritic trees and for analyzing the effect of different biophysical properties on their integrative properties.

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