Characterization of dendrites as nonlinear computation devices

Abstract

From the spines to the soma, signal processing in the neuron is intrinsically nonlinear. In this paper we present first results of a project whose objective is to identify/characterize dendrites as nonlinear devices in the hope that the resulting model will be of use in bio-inspired connectionist architectures. The methodology used is based on the extension of the Wiener-Volterra formalism to Multiple Input-Multiple Output (MIMO) systems. The project starts by applying the method to a computer model of the Purkinje cell as a guide for the design of real neurophysiological experiments data, as well as an aid for the interpretation of results.

Information processing in the brain takes places in a number of different scales from the single neurons to the brain as a whole, the characteristics of each stage being dictated by the physiology of the intervening units and the architectural implementation of the corresponding scale. The conventional view amongst brain modelers is that the neuron is the basic unit of computation, following pioneering work by McCulloch & Pitts. In the models, the neuron is represented as a non-composite device that performs linear sum of the (possibly) weighted inputs and passes the sum through a static nonlinearity. Nevertheless, in recent years, much attention has been paid to the processing stages within the neuron with the result that new computational capabilities have been discovered in connection with previously neglected parts of the neuron, most significantly, the dendritic tree and spines. These capabilities are associated with the nonlinearities intrinsic to the physiology of the dendrites and spines and most importantly, but not exclusively, with their active properties. This is so because the essence of computation is nonlinearity. A composition of linear fuctions, no matter how complicated or deep, is in the end another linear function. Computation, in a broad sense, cannot therefore be accomplished just with linear units.

In the following, we take a closer look at the phenomenological nonlinearities found in neurons. The first nonlinear process encountered in normal operation of neurons is the synapse itself. Unlike most model that place the nonlinearity in the postsynaptic elements of the computation, the output of a real synapse is not merely a linear sum of the inputs but the result of a complex process that includes presynaptic mechanisms such as paired-pulse facilitation, augmentation/depression and post-tetanic potentiation. Some of these mechanisms have been postulated to underlie specific functions such as gain control or temporal responsiveness in neurons of the V1 area. Also, due to the change in electrical properties of the postsynaptic membrane, the postsynaptic potential or PSP tends to saturate with stronger and stronger inputs. Therefore, the PSPs of two synapses (typically) adds sublinearly.

The second nonlinear processing of signals takes place along dendrites. Active dendrites have enhanced computational properties with respect to passive dendrites which already show nonlinear processing of information. Dendrites often exhibit differentiation of synaptic weights even within a given subregion. Furthermore, dendritic morphology and the nonuniform distribution of membrane conductance represent new possibilities for nonlinear combination of inputs.

But that is not the end of it: thousands of excitable channels permate the membrane and are responsible for new nonlinear transformations of the inputs, for example, the subthreshold amplification of excitatory postsynaptic potentials (EPSP). In fact, potassium channels are known to counteract this amplification and the resulting time evolution of the EPSP is the result of the distribution of excitable channels along a given dendritic path as much as of the initial shape. These active channels can produce and sustain dendritic action potentials (although this point is somehow controversial), and make possible the propagation of antidromic action potentials from the soma. Other possibilities suggested in the literature are coincidence detection and multiplication of signals.

What can we learn of these nonlinearities present in all stages of real neuron computations? Can we distill from it practical knowledge applicable in the world of connectionism?

In this paper a step-by-step strategy is iniciated in the hope that kowledge about separate computing elements is essential for a thorough understanding of their complex interactions in real neurons. The choice of a computer model as a starting point for the nonlinear analysis of neurons is also inspired by this strategy in a twofold sense: first because a detailed identification of computer models of neurons as nonlinear systems is expected to help us understand equivalent studies in *in vivo/in vitro* experiments; but also because the differences found between results obtained for models and for real neurons can help improve the models by pointing to the operational differences. In section 2 a brief description of the Wiener-Volterra methodology will be sketched; in section 3 the basic properties of original model of the Purkinje cell used in this paper will be summarized; in Sec. 4 the *in silico* experiment designed to obtain the nonlinear properties of the model dendrites is described and, finally, in section 5, the wiener kernels thus obtained are presented and discussed.