

Chapter III

Forward Dendritic Spikes: A Mechanism for Parallel Processing in Dendritic Subunits and Shifting Output Codes

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ABSTRACT

Neurons send trains of action potentials to communicate each other. Different messages are issued according to varying inputs, but they can also mix them up in a multiplexed language transmitted through a single cable, the axon. This remarkable property arises from the capability of dendritic domains to work semi autonomously and even decide output. We review the underlying mechanisms and theoretical implications of the role of voltage-dependent dendritic currents on the forward transmission of synaptic inputs, with special emphasis in the initiation, integration and forward conduction of dendritic spikes. When these spikes reach the axon, output decision was made in one of many parallel dendritic substations. When failed, they still serve as an internal language to transfer information between dendritic domains. This notion brakes with the classic view of neurons as the elementary units of the brain and attributes them computational/storage capabilities earlier billed to complex brain circuits.

ARE NEURONS THAT SIMPLE?

The quintessential feature allowing any processing of electrical signals within individual neurons is that their narrow elongated dendrites make them electrically non-uniform, enabling long electrical distances between different parts of the same neuron. Whatever electrical events take place in the dendrites, they are not the same as in the soma or the axon. These compartments are not totally isolated and signals travel from one another as in an electrical circuit. From early studies, neurophysiologists concluded that neurons were essentially input/output devices counting synaptic inputs in their dendrites, a numeric task that transform into a temporal series of action potentials or spikes, each one triggered when a certain voltage threshold is reached by temporal summation of the synaptic currents at a specialized region near the soma-axon junction. This simple working scheme enables the transformation of myriads of inputs scattered in a profusely branched dendritic arbor into a temporal sequence of binary axonal spikes that can be read by target cells in terms of frequency. Indeed, frequency modulation of spikes may perform with equivalent accuracy as the fine tuning capabilities of graded communication that prevail in non neuronal cells. For a while, researchers felt this was good enough for a single cell, and the uncomplicated view of dendritic trees as not-very-clever receiving black boxes settled in for decades. This classical picture is, however, incomplete. Such a basic scheme holds only in a few neuron types (if any).

Typically, neurons receive several thousand synaptic contacts, each conveying information from as many afferent cells. In order to understand how such a huge amount of inputs are integrated, it is useful to examine the output first. Lets have a look to it. The output range across neuron types in the Nervous System goes from regularly firing (pacemaker-like) to almost silent neurons. The later type fire spikes at extremely low rates lacking any apparent temporal structure.

In fact, it constitutes a most interesting case as it applies to several neuron types in the cortex of mammals. One may argue that the few action potentials fired by these near-silent neurons have a strong informative load and they are signaling the recognition of particular combinations of inputs bearing a strong physiological meaning. While this is reasonable, some questions follow. If only some input combinations produce outgoing spikes, do neurons consider irrelevant the vast majority of their inputs, which cause no output? Would that mean that the fate of most presynaptic spikes is to become useless noise in brain circuits? If so, why bother that much to produce them anyway? And, is the postsynaptic cell structure or the specific assortment of electrogenic machinery genetically assembled to make the neuron recognize these critical combination of inputs that initiate a few outgoing *superspikes*? From the point of a working neuron, these and many other similar questions can be reduced to two major questions. First, how the thousands of inputs are selected within dendrites to end in a few outgoing spikes? And second, is there any benefit or function in the remaining inputs failing to produce output? The answers have to be found in the computational operations performed in the dendritic arborization of the neurons. Formerly viewed as a black box, we shall try to introduce ourselves within the dendritic apparatus to unveil the secrets of this miniature communication center.

CHANNELS IN DENDRITES: A CONCEPTUAL REVOLUTION

Based on modeling studies, some authors, suggested that the overall firing pattern is somehow engraved in the architecture of the dendritic tree (Mainen et al., 1995). Indeed, some architectonic dendritic prototypes have been preserved in specific brain nuclei spanning long periods of brain evolution. Although this may be indicative of a common integrative function being preserved

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