Active dendrites implement probabilistic temporal logic gates.

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The recognition of patterns is a primary function of the brain. Often, relevant patterns occur on time-scales that vary in length. For example, place and grid cells encode location [7] and therefore activate in sequential patterns that depend on an animal's varying movement speeds. Encoded in these patterns are directed paths through an environment that are important to – for example – find the way back out of a maze. Further patterns on time-scales on the order of hundreds of milliseconds have been observed elsewhere in cortex, for example in the sequential codes for different odors in the olfactory bulb [1], and the segmentation length of speech signals in auditory cortex [2].

Neuron models used in the theoretical analysis of cortical circuits predominantly model the passive integration of synaptic currents, and are therefore limited to the short and fixed time-scale determined by the passive electrical properties of neurons. Since these integrate-and-fire neurons cannot inherently solve the problem of long, temporal integration, the implementation of the required working-memory is relegated to the dynamics of attractor networks [5] and synapses undergoing fast, plastic changes [4]. Here, we argue that intricate biophysical mechanisms along dendrites of pyramidal neurons, that have recently been detailed in experiments [3], implement an elegant alternative solution we call *active dendritic sequence processing* (ADSP).

ADSP relies on the dynamics of NMDAr ion channels that activate when multiple spikes arrive at a local cluster of synapses in a short period of time. Their opening due to the availability of Glutamate and high enough postsynaptic depolarization induced by overlapping EPSPs leads to supra linear *dendritic plateau potentials* that can last for up to hundreds of milliseconds. However, they do not actively propagate along the dendrite and are subject to the strong attenuation of the dendritic cable as well as functional dendritic compartmentalization [6].

We call clusters of synapses that can initiate a plateau a dendritic segment that functions as a coincidence detector and only weakly interacts with neighboring dendritic segments. When one segment initiates a plateau potential in response to strong, coincident input, neighboring segments increase their resting voltage for the duration of the plateau, enabling them to initiate a plateau themselves. A cascade of overlapping plateau plateau potentials can start in distal segments and propagates towards the soma. A successful cascade leads to a neuronal UP-state that signifies the recognition of a sequential pattern of coincident spike inputs on a time-scale of the plateau-length times the number of dendritic segments in the cascade.

In the tradition of McCulloch & Pitts, we abstractly model this dendritic computational behavior as temporal logic gates in a tree structure, with a second time-scale that enables local memory for asynchronous computation. To reflect richer computational functions, AND and OR - type gates can be implemented by requiring at least N child segments to have initiated a plateau for the current node to be active and be able to initiate its own plateau. This deterministic model of neural computation extends naturally to stochastic synapses as the probability of a neuronal UP-state is directly proportional to the number of coincident spikes at individual segments. In a population ensemble of neurons with the same input connections and independent synapses, the number of coincident output spikes encodes this signal strength.

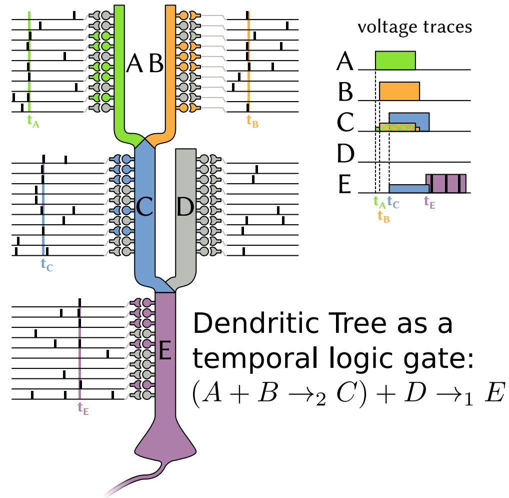

Figure 1: Plateaus in response to spike volleys interact in the morphology of dendritic segments. The function of this dendritic tree can be expressed as a temporal logic gate.

We show that ADSP can solve the temporal integration problem on long and varying time-scales with the example of path integration from place cell activity. The temporal logic gate model directly maps dendritic morphology to computational function. Cells other than pyramidal neurons may implement the same general computational principle by other biomechanistic implementations. We connect the sub-symbolic and dynamic processes of dendritic integration to logical functions on symbols defined by coincident spike events, addressing a long standing problem of connectionist models to explain and account for the inherent structure of reasoning.

References

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