Influence of dendritic topology on firing patterns in model neurons activated by synaptic stimulation of the dendritic tree

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Neuronal firing patterns are influenced by both membrane properties and dendritic morphology. Distinguishing two sources of morphological variability (metrics and topology) and using synaptic stimulation of the dendritic tree, we investigate the extent to which model neurons that have the same metrical and membrane properties can still produce different firing patterns as a result of differences in dendritic topology. Within a set of trees that have the same number of terminal segments and the same total dendritic length, we show that type of firing (bursting or regular), but not frequency of firing, is strongly influenced by dendritic topology.

Recordings of the electrical activity of neurons display a wide range of firing patterns. Experimental and theoretical studies have shown that differences in firing patterns between neurons can arise from differences in membrane properties, such as the types and densities of ion channels. Several studies have also emphasized the contribution of the morphological variability of the dendritic tree. Mainen and Sejnowski (1996), for example, showed that models of neocortical neurons that have the same channel densities and kinetics but differ in their dendritic shape and size can generate firing patterns ranging from regular spiking to bursting when stimulated at the soma with a fixed current injection. However, this study did not distinguish between the possible separate roles of the two sources of morphological variability: metrics and topology. Metrics include, for example, the total surface area of the dendritic tree and the lengths and diameters of its segments, whereas topology is the way in which the different segments of the tree are connected (e.g., giving rise to trees with a different degree of symmetry). Distinguishing these two sources of morphological variability, Van Ooyen et al. (2002) showed that within a set of dendritic trees that have the same metrical and membrane properties, the firing frequency strongly correlates with dendritic topology as expressed by the mean dendritic path length. If active dendritic channels are present, it was shown that topology influences not only firing frequency but also type of firing (regular, bursting).

Both Mainen and Sejnowski (1996) and Van Ooyen et al. (2002), however, used a fixed current injection at the soma to invoke action potentials, which is a biologically unrealistic way of stimulating the neuron. In the present study, we therefore stimulate the model neurons by means of synapses that are distributed over the whole dendritic tree. We model AMPA synaptic input, and the time course of conductance changes follows an alpha function. Each synapse is randomly activated, whereby the time intervals between the synaptic activations are drawn from a negative exponential distribution. Over the length of the complete simulation, this results in a Poisson distribution of synaptic activation times. To study the influence of the topological structure of the dendritic tree on neuronal firing, we use a set of neurons consisting of all the topologically different trees with 8 terminal segments. (For the basal dendrites of rat pyramidal neurons, for example, most topologically different tree types can actually be found for small trees.) All the segments in the tree have the same length, so that the total dendritic length is the same for all tree types. We study both the situation in which the diameters of dendritic segments are the same throughout the whole tree, and the situation in which the diameters of the segments obey Rall's 3/2 power law (so that the diameters of the segments decrease at each branch point). Active channels are present in the dendrites, and ion channel types and densities are identical for all trees. Ion channel types and densities are as in Mainen and Sejnowski's (1996) two-compartmental model and as in the study by Van Ooyen et al. (2002). The simulations are carried out in NEURON. The firing patterns are recorded from the axo-somatic compartment, and the observed firing patterns are correlated with dendritic topology as expressed by the mean path length. The mean path length is the sum of all dendritic path lengths measured from tip to soma divided by the number of terminal segments. The firing patterns are characterized by the firing frequency and the burstfactor. The burst factor quantifies the amount of bursting (the occurrence of action potentials in doublets and triplets) in the firing pattern.

We show that with synaptic stimulation of the dendritic tree, unlike with somatic stimulation, there is little variation in firing frequency between different tree topologies. With somatic stimulation, the firing frequency is higher in asymmetrical trees than in symmetrical trees (Van Ooyen et al., 2002). With dendritic stimulation, however, this "advantage" of asymmetrical trees is reduced because in asymmetrical trees the synapses are on average farther away from the soma than in symmetrical trees. The variation in firing frequency is especially low for the situation in which the diameters of the segments in the tree obey Rall's power law.

Unlike the frequency of firing, the type of firing (whether action potentials occur in bursts or not) is strongly influenced by dendritic topology as expressed by the mean path length. This is true for trees with equal diameters as well as for trees that obey Rall's power law, and for both dendritic and somatic stimulation. In all cases, there is a sudden increase in bursting when the mean path length of the trees is bigger than a critical value. Moreover, after this transition, there is a strong correlation between the amount of bursting (as expressed by the burstfactor) and the mean path length. The strongest correlation is found in the most biologically realistic situation: in neurons that obey Rall's power law and that are stimulated at the soma. In conclusion, we have shown that with synaptic stimulation of the dendritic tree, type of firing (bursting or regular), but not frequency of firing, is strongly influenced by dendritic topology.

References

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