Does a dendritic democracy need a ruler?

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1 Context

Large dendritic trees have a tendency to attenuate signals from distal synapses more than from proximal synapses. However, in hippocampal CA1 cells at rest the amplitude of an EPSP at the soma is independent of the location of the corresponding synapse on the dendritic tree [1]. The idea that synapses on different parts of the dendritic tree contribute equally to firing the neuron has been termed "dendritic democracy" [2].

Two factors contribute to dendritic democracy in CA1 cells. Firstly, active conductances on dendrites help to ameliorate the attenuation. Secondly, the size of synapses increases with distance from the soma [1, 3].

This distance-dependent synaptic scaling implies that each synapse "knows" either how far it is from the soma or the amplitude of its EPSP at the soma, which we call the *effective amplitude* of the synapse. At present, it is not clear how this happens. Two possible mechanisms that inform synapses of their distance from the soma or effective amplitude are:

1. A "dendritic ruler", where each synapse can read off its distance from the soma. This could be implemented by a concentration gradient of a trophic factor or protein.

2. "Synaptic self-regulation", where each synapse adjusts its strength in response to local electrical and chemical signals. This would be implemented by the same machinery responsible for activity-dependent synaptic plasticity.

2 Objectives

In this study we will investigate one manifestation of the "synaptic self-regulation" mechanism. We hypothesise that backpropagating action potentials following a somatic spike

provide the information necessary to a plasticity rule at the synapse. It is known that the amplitude of a backpropagating spike decays with distance, and that the delay in arrival of backpropagating spikes is greater further from the soma [4].

Before examining plasticity rules that might use this information, we first decided to investigate how reliably the delay and amplitude of backpropagating action potentials tell synapses about their distance from the soma and their effective amplitude. Statistics of the backpropagating spike other than its amplitude and delay could also contain information about the distance and effective amplitude of the spike, but in this work we concentrate on the most obvious measures.

3 Method

We investigate these questions using a model CA1 cell from the literature [5] that contains sodium and delayed rectifier and A-type potassium channels. To simulate input from the *stratum radiatum*, one thousand synapses are uniformly distributed 100–500 μm from the soma [see 6]. Each synaptic conductance is a sum of two exponentials with rise time constant $\tau_1 = 0.1\,\text{ms}$ and fall time constant $\tau_2 = 10\,\text{ms}$. The synaptic reversal potential is $E_\text{s} = 0\,\text{mV}$.

We take the effective amplitude of a synapse to be the peak deflection of the somatic membrane potential under resting conditions in response to stimulation of that synapse when its peak conductance is 0.1 nS. (The area under the EPSPs correlates very closely with their amplitudes.)

To investigate the signals available from a backpropagating spike, we simulate input to CA1 from the Schaffer collaterals with synchronous input to all synapses. The synaptic conductances are uniformly set to 0.03 nS, ensuring that there is just one spike in response to this input.

We record the postsynaptic membrane potential at each synapse. The peak of the backpropagating action potential is higher than the peak of the EPSP at every synapse, so we take the peak membrane potential deflection from rest as the amplitude of the backpropagating spike and the time to the peak membrane potential from the synaptic input as the delay of the backpropagating spike .

4 Results

Figure 1 shows the backpropagating spike amplitude correlates negatively with distance and positively with effective amplitude. Amplitudes below 35 mV predict the effective

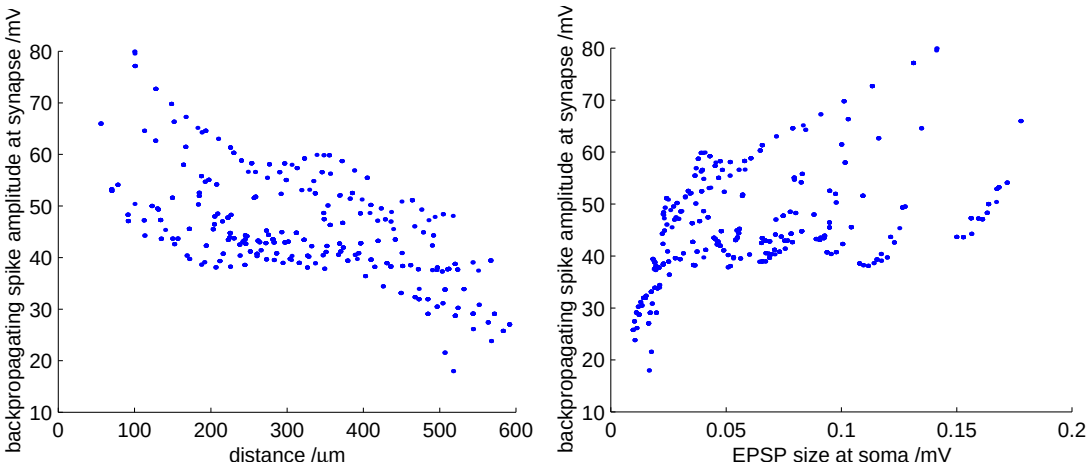

Figure 1: Correlation of backpropagating spike amplitude with distance (left) and effective amplitude (right) of synapse.

amplitude well, amplitudes between 35 mV and 65 mV predict the amplitude poorly but amplitudes larger than 65 mV may be better predictors.

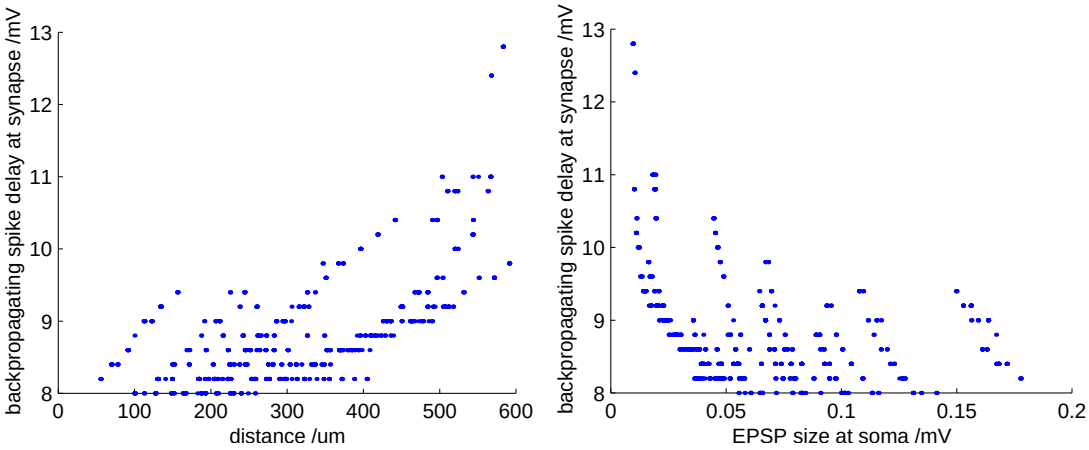

Figure 2: Correlation of backpropagating spike delay with distance (left) and effective amplitude (right) of synapse.

Figure 2 shows the backpropagating spike delay correlates positively with distance and negatively with effective amplitude. However, the delay is not a good predictor of the effective amplitude or distance of a synapse. The pattern of delays is consistent with the backpropagating spike travelling relatively quickly up the thicker apical dendritic trunk and slowly down the thinner branches. Thus, in a particular branch, the delay is correlated with the distance and effective amplitude of the synapse.

5 Discussion

These preliminary results suggest that neither the amplitude or delay of a backpropagating spike are good predictors of the distance or effective amplitude of a synapse. This information is therefore not sufficient to set up a distance-dependent distribution of synapses. Thus these results not rule out the need for "dendritic ruler" for a "dendritic democracy".

A number of extensions to our work could strengthen or change this conclusion. The main limitation of this study is that the cell model has a limited range of conductances. Further work will include low-voltage activated calcium channels on the dendrites. It is possible that EPSP amplitude at the soma under resting conditions is a bad measure of effective amplitude during input. We will investigate alternative measures of effective amplitude.

References

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