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LEARNING TEMPORAL CORRELATION BETWEEN INPUT NEURONS BY USING DENDRITIC PROPAGATION DELAYS AND STOCHASTIC SYNAPSES.

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The ability of neural circuits to respond preferentially to inputs with a given arrival time difference is required for functions such as visual speed discrimination or sound source localization. The responses of such circuits are generally well reproduced by correlation detectors using a delay line on one of the inputs (see e.g. Zanker et al., 1999). A number of models have been proposed for the direction selectivity and speed tuning of visual cortical cells using various extra-cellular delay mechanisms. For speed selective cells closer to sensory inputs, such as those feeding into the H1 cell in the fly, the delay could be generated within the cell itself, using the propagation time of EPSPs in the dendritic tree (Christodoulou et al., 1992). In this paper we examine a possible mechanism that enables neurones to learn the dendritic time delay, simply by being repeatedly exposed to inputs separated by given time intervals.

Recent results using a temporally assymetric Hebbian learning rule have shown that a neurone could learn the delay separating a dendritic input and a somatic spike (Senn et al. (to appear)). The question addressed here is that of learning the temporal delay between two inputs at different dendritic locations.

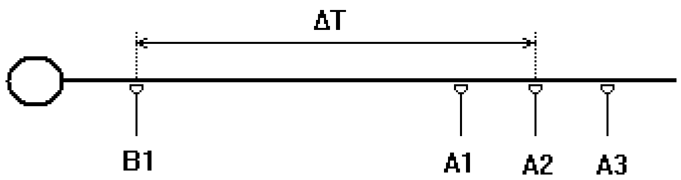

Figure 1: Spatial arrangement of synapses in the model

In the proposed model, following situation is considered. A target neurone has synaptic inputs from two neurones A and B that tend to fire successively (A and then B) with a time interval ΔT. We assume that B makes a single synaptic contact B1 relatively close to the soma, and A makes several contacts A1, A2, A3 at increasing distance from the soma (figure 1). The dendritic propagation time from A2 to B1 corresponds to the time interval ΔT. If the synaptic pair A2-B1 is reinforced, this increases the probability for the target neurone to fire when successive inputs arrive with the time interval ΔT.

It is assumed that EPSPs produced at any synapse will propagate to all the other synapses and induce learning according to a simple asymmetrical Hebbian learning rule modelled by two exponential functions. A key element in the model is the learning induced in synapses A1, A2 and A3 by an EPSP backpropagating from B1.

In a first scenario, synapses are not probabilistic. Suppose that neuron A fires with a delay ΔT after neuron B. Three EPSPs are produced simultaneously at A1, A2 and A3. Then they propagate to B1. The EPSP-A1 (from A1) will have reached B1 before the spike from B, EPSP-A2 reaches it at the same time and EPSP-A3 reaches it afterwards.

At this point, it should be noted that dendrites show a very active persistent voltage-dependent Sodium current I_{NaP} that tends to amplify EPSPs propagating towards the soma (Crill, 1999). The voltage dependence has a non-linearity such that an EPSP-B2 arriving on the back of an EPSP-A2 will be of a larger amplitude than one produced when the membrane is at the resting potential. Thus, a larger EPSP-B1 is backpropagated when inputs at A2 and B1 have a time difference ΔT.

The problem is that the backpropagating EPSP reaches the three synapses A1, A2 and A3 that have all fired recently, and hence that will all be reinforced. If the amplitude of a backpropagating EPSP decreases with distance, it is likely that A1 will be reinforced most. This is not the result that we wish to achieve, because the synaptic pair A1, B1 does not encode the time delay ΔT, but a shorter one.

To solve this problem, one can take advantage of the probabilistic nature of the neurotransmitter release. Most synapses (approx. 90%) have release probabilities p of less that 0.1. The others have p above 0.5. Thus, in a more realistic scenario, it is unlikely that synapses A1, A2 and A3 would simultaneously release neurotransmitter upon arrival of a spike from neurone A fires. Instead, if neurones A and B repeatedly fire, only individual pairings of synaptic inputs A1-B1, A2-B1 and A3-B1 will occur. In particular, when synapse A2 is active, it induces a backpropagating EPSP larger that in the two other cases and should benefit from a significant advantage in the learning rule.

In principle it should thus be possible to train neurones to detect temporally correlated synaptic inputs. Detailed simulations need to be carried out next to verify the plausibility of the proposed mechanism. Several voltage-dependent ionic currents are likely to play a crucial role. Apart from I_{NaP} mentioned above, transient potassium A-Type currents also affect propagation in dendrites (Hoffman et al., 1997) and are likely to enhance the difference between the considered pairings, but also to restrict the practical range of time-delays that can be learned.

References

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