Dendritic Computation in a Point Neuron Model

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Abstract. Biological neurons possess elaborate dendrites that perform elaborate computations. They are however ignored in the widely used point neuron models. Here, we present a simple addition to the commonly used leaky integrate-and-fire model that introduces the concept of a dendrite. All synapses on the dendrite have a mutual relationship. The result is a form of short term plasticity in which synapse strengths are influenced by recent activity in other synapses. This improves the ability of the neuron to recognize temporal sequences.

Keywords: Spiking neural networks · Dendritic computation · Point neuron model

1 Introduction

Biological neurons are 3-dimensional structures consisting of a cell body (soma), an axon and dendritic arborization. The variety in dendritic tree morphology among neurons has always suggested a role for dendrites in the functionality of the neuron. Over the past decades, thanks to new optical stimulation methods and recording techniques [1,8,9], it has become clear that dendrites are not merely passive electrical components. Instead, they are found to integrate inputs in a nonlinear fashion [3,11,13] and participate actively in computations [2,10,12].

While dendrites are function critical, they are often not taken into account when simulating spiking neural networks. Especially in the machine learning context, point neuron models such as the leaky-integrate-and-fire (LIF) model are widely used. As suggested by their name, point neuron models ignore the existence of dendrites and mimic the integration of all inputs on the neuron soma. They are popular because they seem to be a good trade-off between capturing biological neuron behaviour and computational complexity. Li et al. [6] formulated a synaptic current in order to integrate dendritic nonlinearity into a point neuron model. This current was based on electrophysiological recordings and neuronal simulations. The addition of the current resulted in computational abilities such as direction selectivity.

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In a study by Branco et al. [3], dendrites were observed to be sensitive to the sequence of synaptic inputs. Different sequences of the same inputs result in different somatic response magnitudes. The underlying mechanism was observed to rely on NMDA receptor activation, causing synapses to differentially influence each other, dependent on the relative timing of their activations. In this work, we investigate the extension of the computational LIF neuron model to mimic this dendritic functionality. Synapses are enabled to influence each other, based on the relative timing of activation. We investigate the impact of this extension on the capacity of the neuron to discriminate spatiotemporal inputs.

2 Materials and Methods

2.1 Network Structure

We consider networks that consist of an input layer, an output layer and an inhibitory layer (see Fig. 1). The input layer is fully connected to the output layer, and both consist of only excitatory neurons. The output layer connects to the inhibitory layer with a one-to-one connectivity. The inhibitory layer consists of inhibitory neurons and implements lateral inhibition across the output layer (see Fig. 1). Weights from the input to the output layer are uniformly drawn from [0, 0.5]. Inhibitory neurons are activated by a single input spike and connect to excitatory neurons with weight magnitude of 5, resulting in fairly strong inhibition. This network architecture implements a winner-take-all (WTA) mechanism.

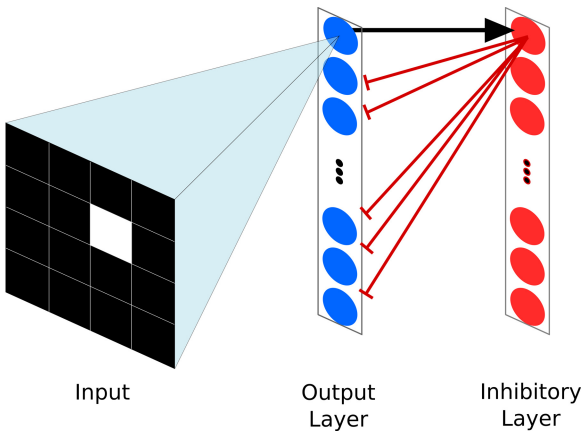

Fig. 1. Network architecture. Inputs are connected to the excitatory output layer in an all-to-all fashion. Lateral inhibition between excitatory neurons is implemented with an inhibitory layer.

2.2 Neuron Model

Neurons are of type leaky integrate-and-fire (LIF). In the absence of input spikes, the neuron membrane potential (u) change is described by a simple differential equation:

$$\tau_{\text{leak}} \frac{du}{dt} = -(u - u_{\text{rest}}) \tag{1}$$

With τ_{leak} the membrane time constant. Upon input spike arrival, the membrane potential is increased by amount w, the synaptic efficacy. If the membrane potential u reaches a threshold value of u_{thres}, an output spike is sent to all outgoing synapses and u is reset to the resting potential u_{rest} and insensitive to excitatory input for a refractory period T_{refr} (see Table 1 for an overview of parameter values).

To implement inter-synaptic influencing and STDP, a synaptic trace (x) keeps track of recent synaptic activity. Each synapse has a synaptic trace that decays exponentially:

$$\tau_{\text{x}} \frac{dx}{dt} = -x \tag{2}$$

with τ_{x} the decay time constant. Every time a presynaptic spike arrives at the synapse, the synaptic trace is set to 1. The value of x thus indicates recent synaptic activation.

Table 1. Simulation parameters.

Parameter	Value
u_{rest}	-65 mV
u_{thres}	-63 mV
T_{refr}	30 ms
τ_{leak}	10 ms
τ_x	8 ms
η	0.05

2.3 Synaptic Relations

To mimic dendritic functionality, we introduce a synaptic relation (r) between every pair of synapses. The efficacy of a synapse is then determined by both the synaptic weight and the recent activity of other synapses with which it has a non-zero synaptic relation r (Fig. 2). Upon spike arrival, the synaptic efficacy w_{i} of synapse i is computed as:

$$w_{\text{i}} = w_{\text{proper,i}} + w_{\text{sr}} \tag{3}$$

$$w_{\mathrm{sr}} = \sum_{j=0}^{N} r_{\mathrm{i,j}} x_{\mathrm{j}} \tag{4}$$

with w_{proper} the synaptic weight, and w_{sr} the contribution of synaptic relations. $r_{\mathrm{i,j}}$ is the magnitude of the synaptic relation between synapse i and j. The synaptic trace (x) is a variable that decays exponentially to 0, hence $r_{\mathrm{i,j}} x_j$ will be small except if a spike recently arrived in synapse j. As the efficacy of a synapse can now change transiently, the term w_{sr} implements a form of short term plasticity induced by recent presynaptic activity.

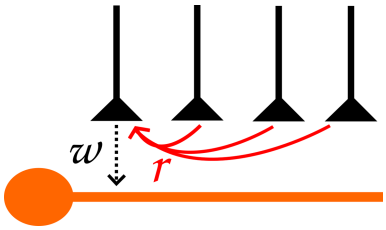

Fig. 2. Synaptic efficacy is influenced by both the synaptic weight (black, dotted arrow) and the synaptic relations (red, solid arrows). (Color figure online)

2.4 Learning Rule

The magnitude of the proper weights can be learned using a form of spike-time dependent plasticity (STDP). When a neuron is caused to fire, it's incoming synaptic weights are updated. All weights are depressed except if a presynaptic spike immediately preceded the postsynaptic spike (see Fig. 3). Using this learning rule, a synapse that does not contribute to spike generation is systematically depressed. Note that if a neuron never fires, it weights will remain static. The positive weight change (potentiation) is given by ηx with η the learning rate and x the synaptic trace. In case of depression, a negative weight change of fixed magnitude ($\eta/2$) is applied.

Winner-take-all (WTA) mechanisms are long thought to be present in biological networks. In combination with STDP, WTA networks achieve unsupervised feature learning [4,5,7]. Here, a WTA mechanism is implemented with lateral inhibition provided by the inhibitory layer. Hence, output neurons compete for input patterns and activation of the winning neuron is reinforced through the STDP update.

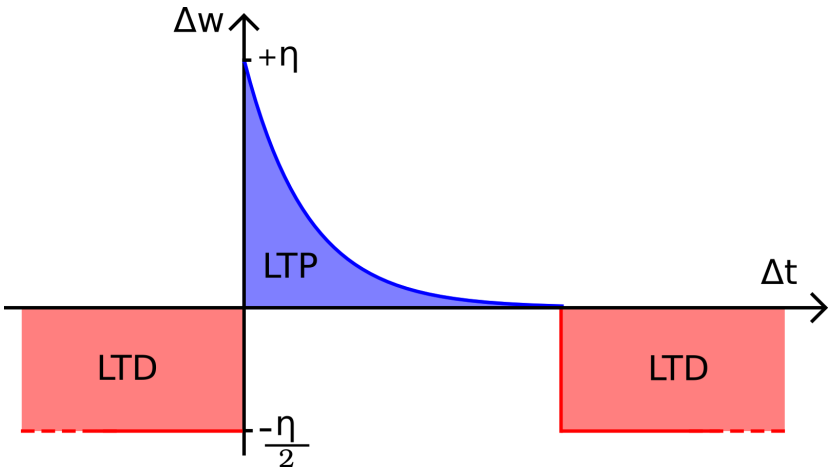

Fig. 3. STDP learning rule. Synaptic weights updates (Δw) are positive (ηx) if the postsynaptic spike shortly follows the presynaptic spike and negative otherwise. $\Delta t = t_{\text{post}} - t_{\text{pre}}$. LTP = long term potentiation, LTD = long term depression.

3 Results

3.1 Direction Sensitivity

To illustrate the impact of the proposed dendritic mechanism, the reaction of two neurons to two input sequences is compared. The neurons differ only in synaptic relations, which were hand-tuned to increase sensitivity for either the first sequence or the second sequence. The first sequence consist of 5 inputs that fire subsequently with a 5 ms interval. The second sequence is the same as the first, but in reversed temporal order. Figure 4 plots the membrane potential of the two neurons. As can be seen from the membrane potential response, the short term plasticity introduced by inter-synaptic relations causes neurons to be sensitive for the order in which inputs arrive.

3.2 Random Sequences

Random sequences are used to assess the increased capacity of temporal sequence discrimination. The input population consists of 16 neurons. One hundred random input sequences were generated, with each input neuron firing once per sequence and fixed inter-spike times (Fig. 5A). Output layers with random synaptic relations (uniformly sampled from [0, 0.5]) are compared to output layers without synaptic relations. Due to strong lateral inhibition only one output

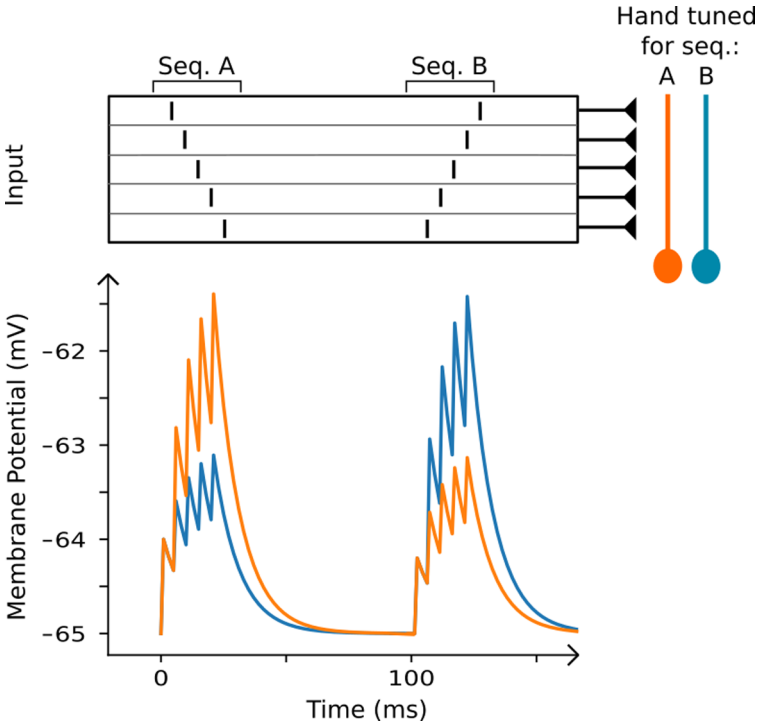

Fig. 4. Inter-synaptic relations cause temporal sensitivity. **Top panel:** Two input sequences are given to two output neurons. The output neurons differ only in inter-synaptic relations. **Bottom panel:** Response of the membrane potentials. The spiking threshold was set high to prevent spiking.

neuron fires in response to an input sequence (see Fig. 5B). As a metric for discrimination capacity, the fraction of neurons in the output layer that is activated by at least one of the input sequences is used. The output layer size is varied from ten up to one hundred neurons. Regardless of the output layer size, the presence of short term plasticity induced by synaptic relations, increases variation in activated output neurons (Fig. 5C).

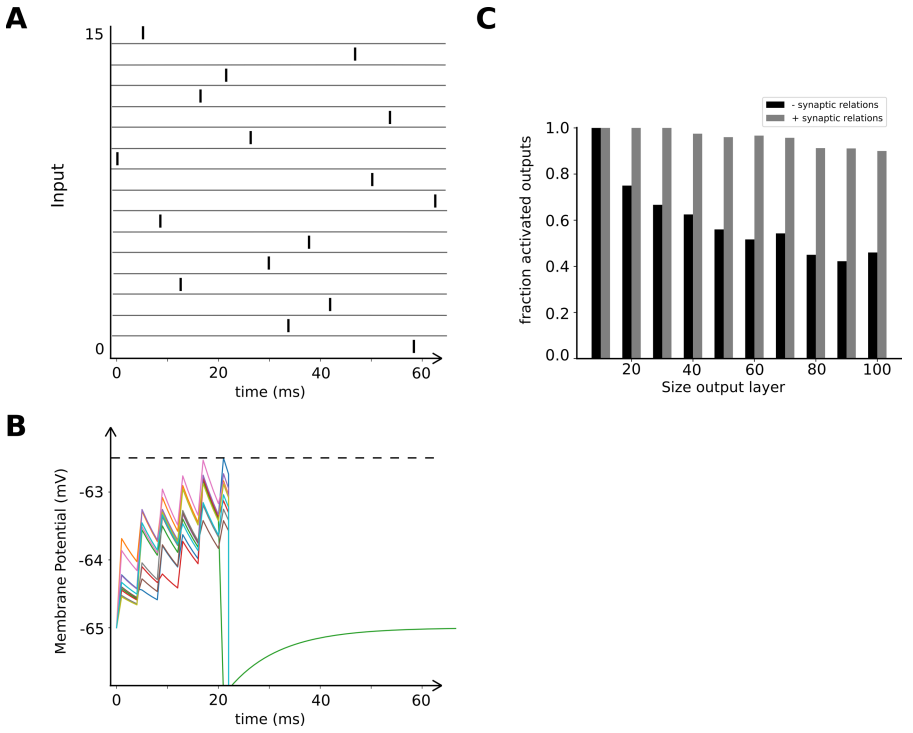

Fig. 5. Discrimination of random sequences without learning. **Panel A:** Example input sequence. **Panel B:** Example response of 10 competing output neurons to the sequence pictured in panel A. Dashed line indicates firing threshold. **Panel C:** Fraction of output neurons activated by at least one input sequence, for different output layer sizes.

3.3 Synaptic Relations Improve Unsupervised Learning

To test the learning capacities of spatiotemporal sequences, we stimulate an output layer of 50 neurons with inputs consisting of a moving pixel on a four by four grid (see Fig. 1). Every time step, the pixel moves to an adjacent tile with a 10% probability of changing direction. During the training phase the output layer receives continuous input while weights are updated according to the STDP rule. During the test phase, the learning updates are halted and the response to continuous input is recorded, in order to establish the receptive field of the output neurons.

Training is repeated for two categories. In the first, all synaptic relations have the same magnitude and hence do not contribute to input discrimination. In the second category, synaptic relations are drawn uniformly from [0, 0.5].

When all synaptic relations are identical, receptive fields develop only as a consequence of the STDP-based weight learning. Figure 6A shows the spatiotemporal receptive fields for a selection of 3 output neurons. The top panel plots the location of the moving pixel, for each time the output neuron was triggered

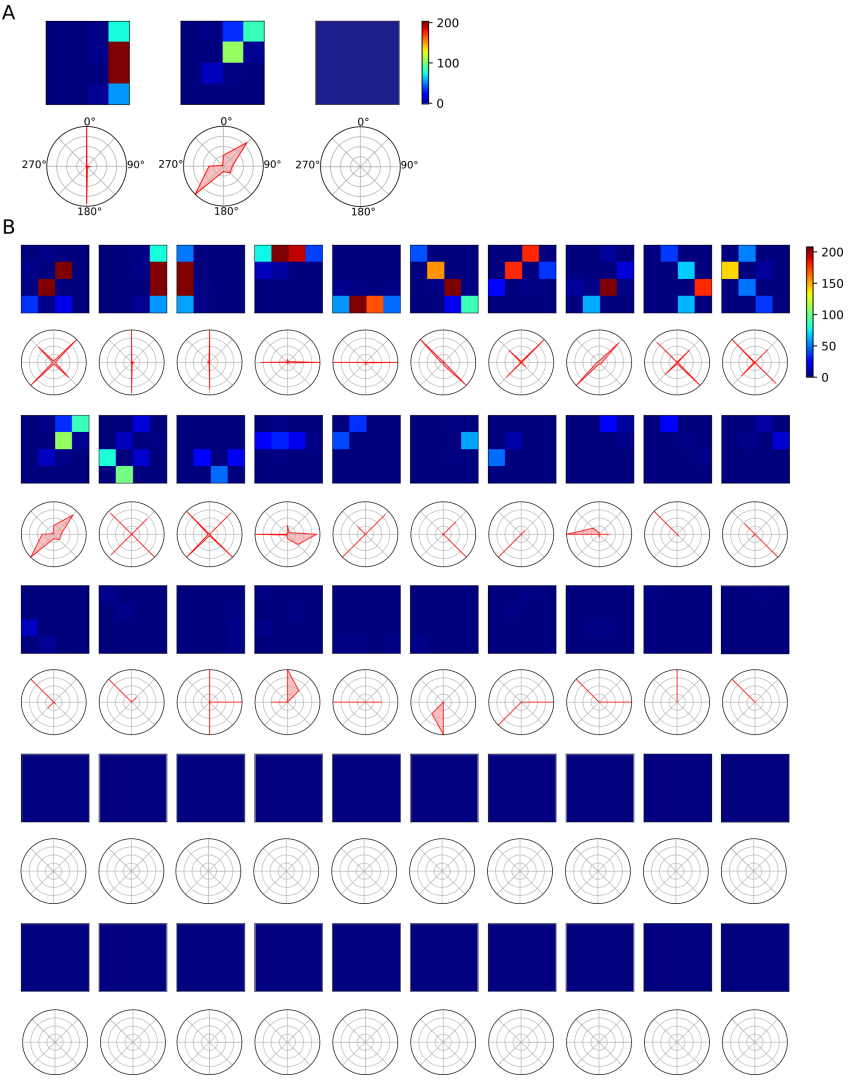

Fig. 6. Spatiotemporal receptive fields of output neurons with **identical synaptic relations**. **A:** Location (top) and direction (bottom) of moving input pixel on moment of neuron activation, for a selection of output neurons. **B:** Spatiotemporal receptive fields for all output neurons, sorted by activity magnitude.

during test run. The bottom panel indicates the direction in which the pixel was moving. Some neurons develop a spatially confined receptive field. The leftmost depicted neuron is sensitive for both upwards (0°) and downwards (180°) movement in the rightmost column. The middle neuron is mainly activated by movement along the diagonal 45°–225° axis, but to a lesser extent also to other directions on that location. Other neurons, like the third shown, are never

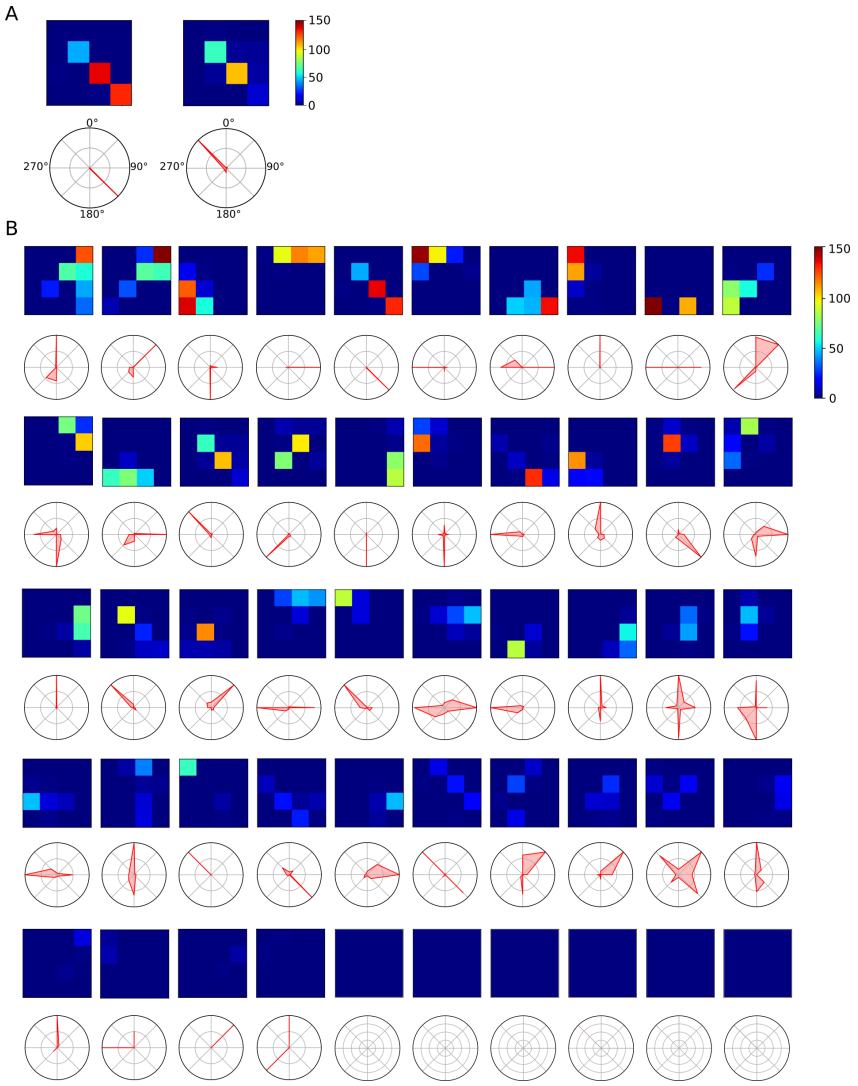

Fig. 7. Spatiotemporal receptive fields of output neurons with **randomized synaptic relations**. **A:** Location (top) and direction (bottom) of moving input pixel on moment of neuron activation, for a selection of output neurons. **B:** Spatiotemporal receptive fields for all output neurons, sorted by activity magnitude.

activated as they are always inhibited by other output neurons that win the competition. Figure 6B shows the receptive fields of all 50 output neurons. Less than half of the neurons form meaningful receptive fields. Note that most frequently active neurons are sensitive for at least 2 opposing directions of movement.

Figure 7 shows the result for the second category, with randomized synaptic relations. It is clear from Fig. 7B that more output neurons have developed

meaningful receptive fields. This can be explained by the increased direction sensitivity of output neurons. Figure 7A shows two output neurons that have a similar spatial receptive field, however they are sensitive for movement in the opposite direction. The addition of random synaptic relations hence enabled neurons to discriminate inputs based on their temporal order. Indeed, most of the active output neurons have a single dominant direction to which they are sensitive.

4 Conclusions

The computations performed by dendrites are known to be crucial for biological neurons. in this work we present a simple method to include some of the observed functionality into a point neuron model, commonly used in spiking network simulations. Inclusion of synaptic relations results in a form of short term plasticity that makes the neuron sensitive to the precise temporal order of inputs. This increases the capacity of a neuron to discriminate between spatiotemporal inputs, as exemplified by directional sensitivity. This capacity, also observed in biological neurons, should be helpful for interpreting temporal data. This can be useful at the input level, for instance when dealing with video data, but it can also be useful for neurons in more downstream layers, as they continuously receive sequences of inputs from other neurons.

In this work, the magnitude of the synaptic relations have been sampled in a random fashion, whilst in biological neurons this value would be related to the spatial adjacency of synapses on the dendritic arbour. In further work, we will explore the use of distance based relationships. In addition, it may also be interesting to apply an unsupervised learning rule, similar to the STDP used in this work, to adjust the synaptic relations based on the inputs provided to the network.

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