Interaction of synaptic plasticity rules lead to structure formation in balanced random networks

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Cortical networks are characterized by inhomogeneities in structure and dynamical properties and these seem to play an important role in their functioning [BM14]. After a number of negative answers given in the past (see e.g. [MAD07]), we present here a minimal model of a balanced state network of spiking neurons in which a delicate interplay of different forms of synaptic plasticity leads to stable effects of self-organization which are robust with respect to parameter changes in the learning rules. Using analytically tractable reduced neuron and synapse models, we are able to carry out an analysis of the influence of the different plasticity rules and their interactions.

Specifically, we study random, balanced state networks of excitatory (E) and inhibitory (I) (ratio 4 : 1) leaky integrate and fire model neurons, receiving as input either a constant depolarization or Poisson noise resulting in asynchronous irregular network activity. Synaptic connections are current-based with exponential kernels, in accordance with fast acting excitatory and inhibitory neurotransmitters. There are three synaptic plasticities in the model: Hebbian STDP rules at E-E and I-E connections [HNA06] and a synaptic scaling rule at the postsynaptic site of E-E connections. Starting from initially constant or uniformly distributed weights, the network expresses long-tailed distributions of firing rates and synaptic weights after a transient phase. A fraction of the excitatory cells develop predominantly strong outgoing synaptic connections; we call them driver cells. Drivers have a strong dynamical influence on their postsynaptic targets and form subnetworks, similar to leader neurons found experimentally [EJM$^+$08]. We investigate analytically and numerically the nature of the interaction of the different plasticity mechanisms that allow for the self-organized development of driver neurons. To get the analytical approximation of the synaptic changes in the network we consider reduced, analytically tractable models. We model pairs of cells driven by Poisson input (as a proxy for network input) and synaptically connected by a delta synapse of initial strength w and subject to excitatory or inhibitory STDP (restricted to pairwise nearest neighbor interactions). We study how the average change in synaptic efficacy Δw is influenced by the initial synaptic strength w and the firing rates of the pre- and post-synaptic cells.

For the excitatory STDP rule we found that, as expected, weak synapses get weaker due to STDP (as the integral of the STDP kernel is negative), but strong connections get increasing positive feedback. We obtained a reasonable approximation of the actual synaptic dynamics, capturing all the important properties of the simulated system: negative impact of STDP for weak synapses and growing positive impact of the stronger ones, see Figure **??** (left).

For inhibitory STDP that is modeled as an additive Hebbian STDP rule as motivated by experimental findings [HNA06], we find that inhibitory weights converge to stationary values depending on the postsynaptic firing rate; higher postsynaptic rates cause higher IPSP amplitudes, but usually inhibitory weights do not saturate at the maximal value due to effects of negative feedback, due to a self-regulatory property of the Hebbian inhibitory STDP rule. We find an analytical solution for the stationary weights in the simplified model, see Figure **??** (right).

Regarding driver neurons, a delicate interplay of all three plasticity rules is necessary for their emergence. Topologically, driver cells are distinguished by a lower than mean inhibitory in-degree (as a result of random network connectivity) that in the initial, static network leads to reduced inhibitory currents that such cells receive. This configuration results in increased firing rates, which in turn make it more likely that the cell's outgoing synapses undergo LTP (mediated by STDP) and win the competition over the limited synaptic resources (introduced by the homeostatic plasticity that regulates the total incoming excitatory weights to every neuron). Inhibitory STDP is necessary for the development of driver neurons. Without it, postsynaptic partners of potential driver cells also increase their firing rates and thus compete for the limited available pool of synaptic efficacy and prevent a clustering of strong weights at single cells, characteristic for driver cells. This recruitment in "waves" also explains the higher degree of connectivity in driver cell subnetworks. **Figure 1**, see `https://db.tt/3hWRUZjY`

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