## Impact of Correlated Activity and STDP on Network Structure

Changan Liu<sup>1,2,†</sup> and Zhong Dai<sup>3</sup>

Abstract Synaptic strengths between neurons are plastic and modified by spontaneous activity and information from the outside. There is increasing interest in the impact of correlated neuron activity and learning rules on global network structure. Here the networks of exponential integrate-and-fire neurons with spike timing-dependent plasticity (STDP) learning rules are considered, by providing the theoretical approximation of spiking cross-covariance between connected neurons and the theory for the evolution of synaptic weights. Background input mean and variance highly affect the spiking covariance, even for the fixed baseline firing rate and connection. Through analyzing the effects of covariance and STDP on vector fields for pairwise correlated neurons under fixed baseline firing rate, we show that the connections from a neuron with lower input mean to that with higher one will strengthen for balanced Hebbian STDP. However, this situation is reversed for Anti-Hebbian cases. Moreover, for potentiation dominated STDP, the synaptic weights for the networks of neurons with lower input mean are more likely to be enhanced. In addition, these properties found from coupled neurons also hold for large recurrent networks in both theories and simulations. This study provides a self-consistent theoretical method for understanding how correlated spiking activity and STDP shape the network structure and an approach for predicting structures of large networks through the analysis of simple neural circuits.

**Keywords** Correlated activity, network structure, phase plane, synaptic weights

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## 1. Introduction

Many studies have explored how spike timing-dependent plasticity (STDP) shapes the distribution of synaptic weights of a group of synaptic connections to a single neuron [4, 23, 27, 43, 49]. Here, more challenging problems of understanding how correlated activity and STDP shape the global structure of a recurrent network of spiking neurons are considered. Related questions have been addressed before in a number of studies [8, 10, 12, 16–21, 24, 29, 32, 33, 35, 42, 45, 48, 50]. The generally

<sup>&</sup>lt;sup>†</sup>the corresponding author.

Email address: changanliu@email.sdu.edu.cn (C. Liu), zhongdai07@mail.sdu.edu.cn (Z. Dai)

<sup>&</sup>lt;sup>1</sup>Department of Systems Biomedicine, School of Basic Medical Sciences, Shan-

dong University, Jinan, Shandong Province, 250012, China

<sup>&</sup>lt;sup>2</sup>Department of Mathematics, University of Houston, Houston, TX 77204, United States

<sup>&</sup>lt;sup>3</sup>School of Control Science and Engineering, Shandong University, Jinan, Shandong Province, 250061, China

antisymmetric shape of the STDP window, in which reversing the ordering of preand postsynaptic spikes reverses the direction of synaptic change, led to the proposal that this synaptic modification rule should eliminate strong recurrent connections between neurons [1,42]. This idea has been expanded by Kozloski and Cecchi [29] to larger polysynaptic loops in the case of balanced STDP which the magnitudes of potentiation and depression are equal. The case of enhancing recurrent connections through pair-based STDP was also proposed by Song and Abbott [42] and was explored by Clopath and her colleagues [8] later in a more complex model. Clopath and her colleagues proposed a STDP model in which the synaptic changes depend on presynaptic spike arrival and the postsynaptic membrane potential. They use this model to explain the connectivity patterns in cortex with a few strong bidirectional connections. Their plasticity rule lead not only to the development of localized receptive fields but also to the connectivity patterns that reflect the neural code. An excessively active group of neurons has been shown to decouple from the rest of the network through STDP [33], and in presence of axonal delays, STDP enhances recurrent connections when the neurons fire in a tonic irregular mode [32].

Babadi and Abbott have shown that large network properties can be explained by the effect of STDP on pairwise interactions of neurons receiving Poisson input based on the baseline firing rates [5]. Gilson and his colleagues developed a theoretical framework based on the assumption that spike trains can be described as Poisson processes, and they applied this framework to analytically describe the network dynamics and the evolution of the synaptic weights in a series of five papers [16-20]. Most of these previous studies are based on the assumption that the input and output of neurons follow Poisson process, which leads to tractable models and frameworks. However, such strong assumption does not fully reflect a number of properties of actual neurons. One of the main issues is the background noisy input in neuronal firing, although the Poisson model captures such input indirectly through the probabilistic nature of the firing of spikes. So it can not provide a mechanistic explanation of neuronal response variability. Poisson-like spike generation, by itself, is highly reliable and deterministic. However, background input in neural responses is believed to result in part from the fact that synapses are very unreliable [2]. Background input is therefore due to unreliable synapses, or inherited from the input from the rest of the network, and is not due to spike generation. For the integrate-and-fire neuron model, the output is a filtered, thresholded and deterministic function of the input. Thus, such model captures many of the qualitative features, and is often applied as a starting point for conceptualizing the biophysical behavior of single neurons [44].

There is evidence showing that actual neurons respond as integrate-and-fire neurons [37] through biological experiments, which implies such neuron models are closer to the real ones. Here the networks built of the general type of integrate-and-fire neurons: exponential integrate-and-fire (EIF) neurons [13] are considered, which have been shown to match spiking dynamics well in certain cortical areas [6]. In this paper, how correlated spiking activity and STDP affect the evolution of network structure under the same fixed baseline firing rate is illustrated, which may not be captured by following the assumption of Poisson-like neurons.