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# Consequences of realistic network size on the stability of embedded synfire chains

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**Abstract**

Cortical activity in vivo is characterized by asynchronous irregular spiking. Additionally, precise spike synchronization is observed with respect to the experimental protocol. Attempting to model this behavior, theoretical studies have focused on two extreme cases: random and feed-forward networks (synfire chains). Here, we combine both descriptions by successively converting an isolated synfire chain into a completely embedded one. This method systematically reveals the effects of different aspects of the embedding scheme on the stability of the system. At realistic network sizes common-input correlations play a major role. Surprisingly, their impact is reduced by the dynamics of the embedding recurrent network.
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*Keywords:* Recurrent network; Synfire chain; Common-input correlation

## 1. Introduction

In the absence of specific stimuli, cortical activity in vivo is characterized by asynchronous irregular firing of the neurons at a low rate. However, the same system exhibits precise spatio-temporal spike patterns with respect to the experimental protocol (e.g. [9,10]). During the past decade several theoretical studies (e.g. [3]) explored the existence and stability of asynchronous irregular activity states in random networks of integrate-and-fire neurons. The mechanism of spike synchronization and the generation of spatio-temporal spike patterns in divergent-convergent feed-forward networks ("synfire chains", [1]) is also well understood (e.g. [5]).

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Recent simulation studies pointed out the destabilizing effect of introducing non-random elements into balanced random networks. The embedding of feed-forward subnetworks increases the tendency of the whole network to start oscillating in a synchronous manner [2,7]. This finding is challenging for a concept of the cortical network in which synfire chains serve as the building blocks or substrate for processing. So far, theoretical descriptions of destabilizing mechanisms in synfire chains have been documented only for the simple case, in which the "embedding" is modeled by providing the neurons in an isolated chain with independent Poissonian background inputs [2,11]. Both studies derive an upper bound $w_{\text{crit}}$ on the number $w$ of neurons in each synfire layer, above which the asynchronous ground state is unstable. This upper bound on group size is well above the minimal $w$ required for a stable propagation of synchronous spike volleys [4]. Thus, there is a range of $w$ where a stable asynchronous ground state and a stable synchronous mode coexist. The question arises whether this state space structure required for functionally relevant synfire chains is also exhibited by more realistic network architectures.

In the present study, we systematically investigate how the interactions between a feed-forward and a random architecture affect the stability of the asynchronous state. For this purpose we focus on three aspects which were not taken into account in the case of an isolated synfire chain with uncorrelated Poissonian background:

(i) Cortical neurons receive a large amount of their synaptic inputs from the local area ($\approx 1$ mm$^3$, [6]). Consequently, it is reasonable to assume that neurons of the same layer in a synfire chain share not only the inputs of their preceding group but also a certain amount of inputs from the background. Hence, the total background inputs of different neurons in a synfire group are correlated, even if the individual inputs are described by Poisson processes.

(ii) Due to finite size effects, the asynchronous irregular states in unstructured random networks exhibit some small degree of global oscillations [3], even for network sizes of the order of $10^5$. Therefore, the assumption that the neurons in the chain are driven by stationary Poisson inputs may have to be abandoned.

(iii) A major postulate of the isolated chain theories is that the activity in the chain does not affect the embedding network. It remains to be seen whether the neglect of these feedback connections can be justified.

## 2. Model

The behavior of an embedded synfire chain is studied with the help of computer simulations [8]. The nodes of the considered network architectures are modeled as single compartment leaky integrate-and-fire (I & F) neurons (membrane time constant $\tau_{\text{m}} = 10$ ms, membrane capacity 250 pF, resting potential 0 mV, spike threshold $\vartheta = 20$ mV, refractory period 0.5 ms). Interactions between neurons are described by $\delta$-function shaped synaptic currents resulting in exponential postsynaptic membrane potential responses (amplitude $\hat{h} = 0.14$ mV for excitatory and $-5\hat{h}$ for inhibitory synapses). Each neuron receives $K_{\text{E}} = 9000$ excitatory and $K_{\text{I}} = 2250$ inhibitory

inputs from the local region. In addition, there are $K_X = 9000$ non-local excitatory inputs. All synaptic delays are chosen to be 2 ms. Each layer in the synfire chain consists of $w$ neurons. The chain is fully connected, i.e. every neuron in the chain (except those in the first layer) receives exactly $w$ inputs from all neurons in the preceding group. Intra-chain connections are assumed to be purely excitatory, the remaining $K_E - w$ excitatory inputs are provided by the local excitatory background.

In the simplest background model, which we refer to as the *independent Poisson* case, background inputs are described by uncorrelated Poissonian processes with rates $(K_E - w)v$, $K_I v$ and $K_X v_X$ for the excitatory and inhibitory local and the non-local contributions, respectively ($v = 7.7$ s$^{-1}$, $v_X = 1.5 \ \vartheta/K_X \hat{h} \tau_m$). The rates are chosen such that in a stationary state the neurons will respond in a self-consistent way with a firing rate of $v$. Three different embedding paradigms extending the simple scheme of an isolated chain with independent Poissonian background inputs are considered:

*Finite Poisson case*: As a first step we randomly draw the background inputs of the individual neurons in the chain from two large but finite pools of $N_E = 90\,000$ excitatory and $N_I = 22\,500$ inhibitory non-interacting Poissonian processes. This way, we take the common input correlation caused by finite network size into account, while the Poisson approximation still holds. The numbers $N_E$ and $N_I$ approximately correspond to the number of neurons found in the local vicinity of a pyramidal neuron ($\approx 1$ mm$^3$) in rat cortex [4,6]. External inputs are still modeled by uncorrelated Poissonian processes with rates $K_X v_X$. The input statistics of a single neuron is identical to the independent Poisson case. However, due to the overlap between the input ensembles, the background inputs of different neurons in the chain exhibit a certain degree of correlation.

*Interacting background*: In the next stage, background inputs are chosen from a large random network of interacting pools of $N_E$ excitatory and $N_I$ inhibitory I & F neurons ($N_E$ and $N_I$ as in the previous case) driven by a Poissonian external source with rate $K_X v_X$ [3]. For the given parameters, the resulting state of the background network is characterized by more or less asynchronous irregular firing. However, the collective activity exhibits some small degree of oscillation. The input overlap structure is statistically identical to the finite Poisson case. Feedback from the chain to the recurrent background network is still absent.

*Complete embedding*: In the last step, the behavior of a completely embedded synfire chain is studied. Here, background inputs of the chain as well as the rest of the network are randomly drawn from the total network (including the synfire chain). This way, feedback connections between the chain and the recurrent network emerge as well as loops inside the chain.

## 3. Results

To quantify the network dynamics under the four different conditions (independent Poisson case included), we record the spikes of the neurons in the 16th layer for 1 s, compute the population activity histogram (bin size 10 ms) and determine the ratio $F$ between its variance and mean (Fano factor).

Fig. 1 shows the measured Fano factors as a function of the group size $w$ for three different embedding scenarios. In all cases we observe a transition from low Fano
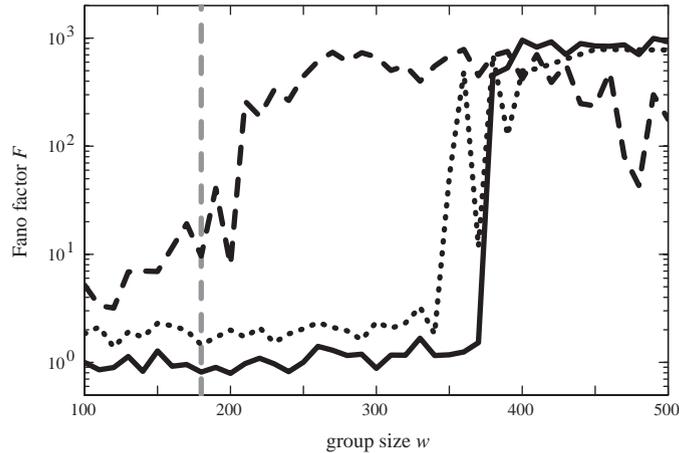
Fig. 1. Ground state stability of embedded synfire chains for different background models: independent Poisson (solid curve), finite Poisson (dashed curve), recurrent I & F network (dotted curve). The population activity in layer 16 of synfire chains with different group sizes $w$ (horizontal) is characterized by the Fano factor $F$ (vertical, bin size 10 ms). The transition from low to high Fano factors indicates the entrance into the synchronous mode. The vertical dashed gray line marks the minimal group size required for a stable propagation of synchronous spikes.

factors at small $w$ to high values at larger $w$, indicating the transition of the system from the asynchronous into the synchronous regime. The latter is characterized by dense volleys of synchronized spikes which spontaneously emerge out of the asynchronous state and stably propagate along the chain. In the remainder we focus on the location of the transition point $w_{crit}$.

Observe that the value of $w_{crit}$ for finite Poisson background (dashed curve) is considerably smaller than the one we find for the independent Poisson case (solid curve). In fact, here the transition into the synchronous regime occurs close to the minimal group size required for a stable propagation of synchronized spikes (vertical gray dashed line; [5]). Hence, there is no appreciable range of group sizes left where synchronized spike volleys can be initiated in a controllable manner and stably travel along the chain.

Surprisingly, replacing the Poisson background by a recurrent random network (dotted curve) causes $w_{crit}$ to return to larger values. The impact of background correlations seems to be compensated by the dynamics of the background network. Adding feedback connections from the chain to the rest of the network does not change this situation as long as the network load is small, i.e. as long as the size of the synfire chain is small compared to the total network size (not shown). In contrast to the network designs without feedback, here for the first time the length of the embedded chain becomes relevant.

## 4. Discussion

In the present work we demonstrated that the finite size of the local cortical network seriously challenges the functional relevance of feed-forward subnetworks. Due to

correlations caused by common input, a clear separation between an excited synchronous state and a quiescent ground state can only be achieved with difficulty. The dynamics of the embedding recurrent network seems to compensate for the effects of the common input. The underlying mechanism still needs to be uncovered.

Clearly, it is important to establish to what extent the results are dependent on the simplifying assumptions. The simulations presented are based on $\delta$-type synaptic currents, but we were able to verify that the results qualitatively hold when $\alpha$-function shaped currents, generating postsynaptic potentials with finite rise times are used instead. We are currently investigating whether the observed effects persist in heterogeneous networks with synaptic delay and amplitude distributions and variability of the membrane time constant. Finally, it is clear that the membrane potential statistics depends on the synapse model. Whether synapses modeled by currents, as studied here, and more realistic models involving conductances lead to qualitatively different system behaviors is an open question.

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