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Cortical Synfire-Activity: Configuration Space and Survival Probability

Marc-Oliver Gewaltig [a], Markus Diesmann [b], Ad Aertsen [c]

[a] *Future Technology Research, HONDA R&D Europe (Deutschland) GmbH, Offenbach, Germany*

[b] *Dept. of Nonlinear Dynamics, Max-Planck-Institut für Strömungsforschung, Göttingen, Germany*

[c] *Neurobiologie und Biophysik, Inst. für Biologie III, Albert-Ludwigs-Universität, Freiburg, Germany*

Abstract

The synfire hypothesis states that under appropriate conditions volleys of synchronized spikes (*pulse packets*) can propagate through chains of groups of neurons. Here, we present results from network simulations, taking full account of the variability in pulse packet realizations. We repeatedly stimulated a synfire-chain of model neurons and estimated the activity (a) and response–jitter (σ) for each group in the chain over many trials. The survival probability of the activity was assessed for each point in the (a, σ)–space. The results agree well with our earlier predictions based on single neuron properties and a deterministic state-space analysis.

Key words: Pulse packets, synfire chains, spike timing, spiking neurons, firing patterns

1 Introduction

The synfire hypothesis [1] states that under appropriate conditions volleys of spikes can propagate through chains of groups of neurons. In order to describe the evolution of such short-lasting volleys of synchronized spiking activity, we introduced the notion of pulse packets [3]. Such pulse packets are characterized by two parameters: the number of spikes a in the volley and their temporal spread σ. Thus, a novel transmission function, describing probability and temporal spread of response spikes to pulse packet input, was computed [4] using simulations of a physiologically realistic model neuron [5]. Interpreting a and σ as deterministic state variables, we could predict the evolution of synchronous activity in a synfire chain network on the basis of the transmission function [4]. Here, we present results of a simulation study [5], undertaken to test whether the results from our two-dimensional state space analysis could be confirmed in network simulations, while taking full account of the variability in pulse packet realizations.

2 Methods

A synfire chain consists of a sequence of groups of neurons, interconnected in a feed-forward way by divergent/convergent connections. Each neuron in group i receives input from a number of neurons in group $i-1$ and projects its axons to a number of neurons in the subsequent group $i+1$. Neurons within a group are not mutually connected. For simplicity, we assume that all groups in the chain have the same number of neurons w, and that the connections between the neurons of successive groups are identical and complete (i.e. full connectivity). Here, we chose $w = 100$ neurons.

For the simulation studies, we used a leaky-integrate-and-fire type model neuron [5] with a membrane time constant of 10 ms. A spike is generated when the membrane potential crosses a threshold value of 10 mV above resting level. An absolute refractory period of 1 ms prevents the generation of a second spike. Relative refractory behavior is modeled by after-hyper-polarizing currents. Post-synaptic currents are modeled by an alpha function, resulting in post-synaptic potentials (PSP) with amplitudes of 0.14 mV. In order to simulate the embedding into a cortical network, each neuron was supplied with random background activity from 20,000 neurons, 80 % of which were excitatory, 20% inhibitory. PSP amplitudes and mean firing rates were chosen such that they yielded a consistent low spontaneous activity of about 2 Hz per neuron.

In a model synfire chain, activity propagation can be triggered using a stimulus which mimics the output of a group of neurons, sending activity into the chain. For a set of different stimulus configurations we performed the following experiment, using 50 trials for each stimulus configuration. In each trial a stimulus pulse packet was created by drawing a_0 spike times from a Gaussian distribution with standard deviation σ_0. We presented this stimulus pulse packet to the neurons of the first group and recorded the spike responses of all neurons in all groups. Stimulus parameters were chosen such that they covered the borders of the configuration space: one set was chosen by setting $a_0 = w = 100$ and varying σ_0 between 0 and 5 ms, the other set was chosen by setting $\sigma_0 = 0$ ms while varying a_0 between 0 and 100 spikes.

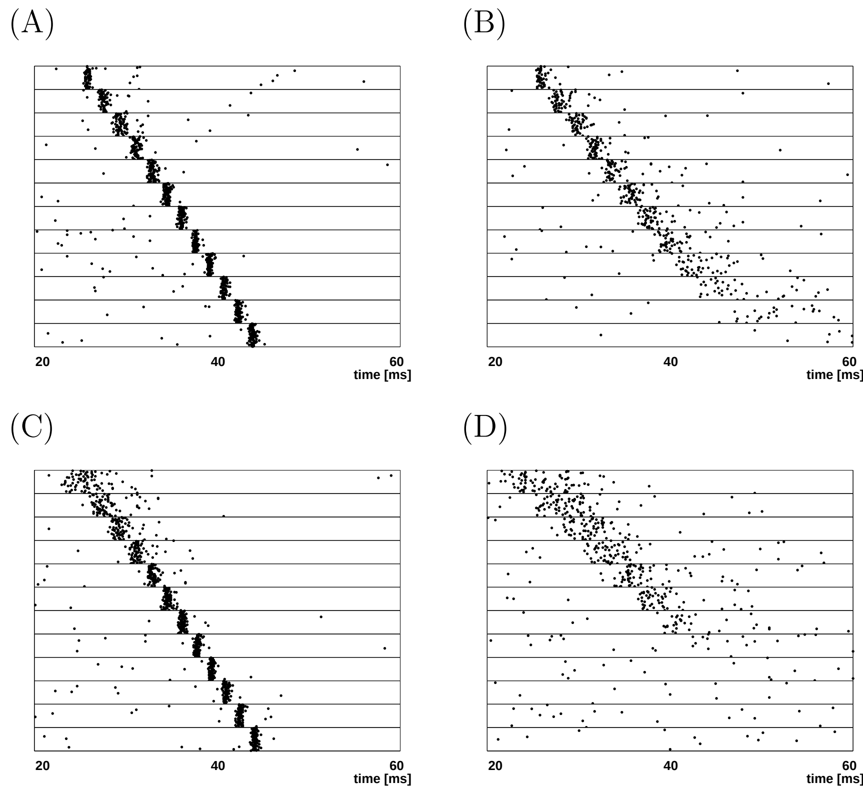

Fig. 1. Raster displays of evoked synfire activity for different stimulus parameters. Each row in a panel shows the spiking activity of a synfire group versus time. Within each row, dots correspond to spike events of a single neuron. The top row in each panel shows the first group in the synfire chain. The stimulus pulse packet is not shown. Further explanation in text.

3 Results

Fig. 1 shows four typical raster displays of propagating synfire activity. Panels A and B show cases where the chain was started with a number of fully synchronized input spikes. Observe that the spike volley in panel A (54 initial spikes) is able to build up enough activity in order to propagate along the entire chain. By contrast, panel B (52 initial spikes) shows the situation where at each group, the dispersion of the spikes increases and the activity propagation stops before the end of the chain is reached. Note, that in both cases the initial conditions were very similar and differed only by two input spikes. Panels C and D illustrate the behavior of the same synfire chain under the conditions of a large number (100 initial spikes) of broadly distributed input spikes. Panel C ($\sigma = 3.5$ ms) demonstrates that the system is able to reduce the input jitter to some residual amount. By contrast, in panel D ($\sigma = 4.0$ ms) the input dispersion increases while the number of spikes steadily reduces from group to group, until the group activity becomes indistinguishable from the background

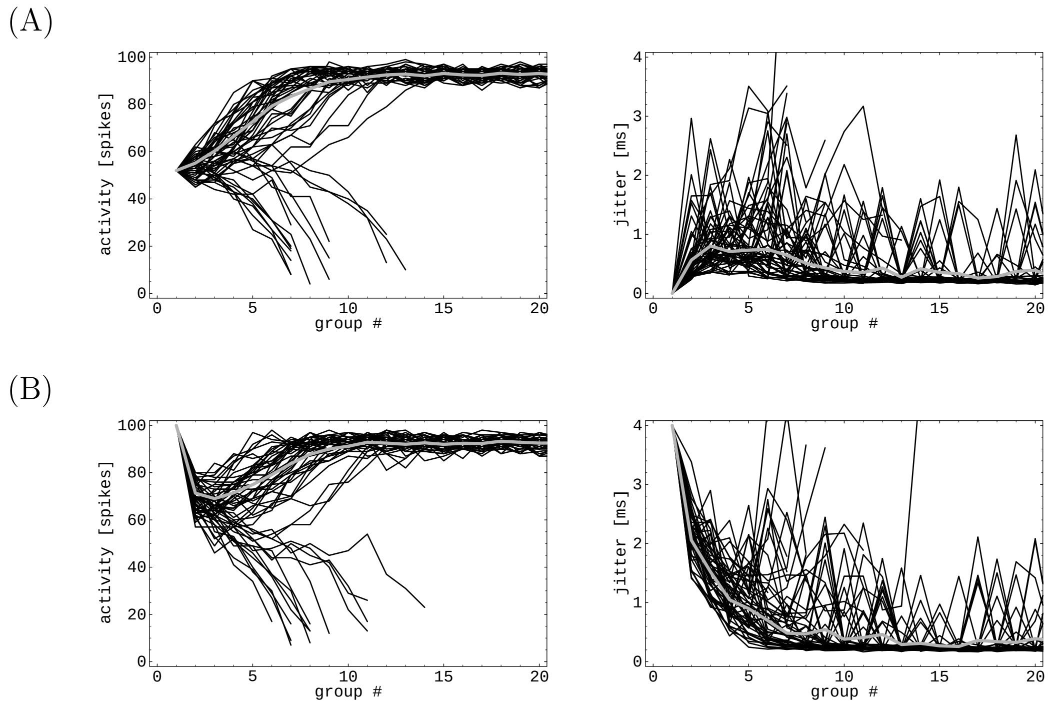

Fig. 2. Evolution of pulse packet activity a_i (left) and temporal jitter σ_i (right) versus group index i. Grey curves represent trial averages. (A) 52 initial spikes with $\sigma = 0.0$ ms. (B) 100 initial spikes with $\sigma = 4.0$ ms.

activity.

Taken together we observed two different modes of activity propagation. Either the initial stimulus is strong and/or concise enough to result in stable propagation of activity, or it is not. In the latter case, the activity propagation ceases after a few groups. Although Fig. 1 suggests that the boundary between these two modes is very sharp, it is effectively blurred by the effect of the background activity which causes large variability between individual trials.

This is variability is illustrated in Fig. 2, which shows the evolution of pulse packet activity a_i and temporal jitter σ_i, estimated from the recorded spike-trains, at each group i for different trials. Observe that neither the activity nor the time jitter evolves monotonically along the chain, not even on average. However, the averages of both measures converge rapidly towards an asymptotic value.

Assuming that the system can, at least on average, be fully described by the two parameters a and σ, we can plot the evolution of activity propagation as trajectories in the (a, σ)–configuration space. At each group i, we obtain a pair of values (a_i, σ_i). The stimulus parameters are denoted as (a_0, σ_0). Thus, the propagation of activity through a synfire chain of length ℓ can be ex-

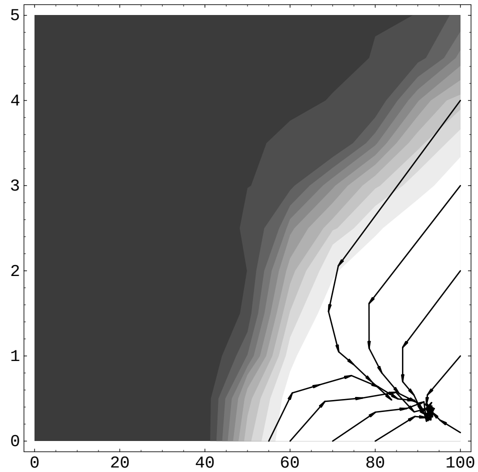

Fig. 3. Survival probability of a synfire chain at a given position in the (a, σ)-space (Light grey: high values, dark grey: low value). The superimposed trajectories show trial averages of chains which survived in at least 50 % of all trials. For a wide range of parameters the pulse packet is likely to evolve towards a stable configuration. Within this region all trajectories lead towards the same fixed-point. Note that the temporal jitter at the fixed point is well below 1 ms.

pressed by the series of pairs $\{(a_0, \sigma_0), (a_1, \sigma_1), \ldots, (a_\ell, \sigma_\ell)\}$, referred to here as a "trajectory". We say that a pulse packet "survives" if it travels along the entire synfire chain, while maintaining a minimum amount of precision and activity. The survival probability at each point in the (a, σ)–space can then be assessed by computing the fraction of the trajectories crossing a small area around (a, σ) that survive.

Fig. 3 shows the survival probability of a propagating pulse packet for different input configurations. Dark grey corresponds to a survival probability close to zero, while light grey indicates a survival probability close to one. The superimposed trajectories show trial averages of configurations which survived in at least 50% of all trials. Observe that there exists a wide range of stimulus parameters for which the pulse packet is likely (i.e. with probability P$>$ 0.5) to evolve towards a stable attractor. If the pulse packet is moved away from the attractor, it can re-synchronize and re-gain activity. In the deterministic case, the region in which the system will return to the attractor is called the *basin of attraction*; here it is distinguished by a survival probability close to one. Note the steep transition which separates the basin of attraction from the rest of the configuration space, where the survival probability is close to zero. Near the attractor, the precision of firing is well below 1 ms. We note that a steep transition of the survival probability between the stable and the instable regime demonstrates the validity of the (a, σ)-description.

4 Summary and Conclusions

Taken together, the results of these network simulations of synfire activity correspond well to our earlier predictions, based on single neuron properties [4]: For sufficiently large groups ($w \geq 100$ neurons), we observe stable propagation of synfire activity. Activity propagation can be fully described by just two parameters, the number of spikes a and their temporal jitter σ. There exists a wide range of stimulus parameters for which the pulse packet is likely to evolve towards a stable attractor. Within the basin of attraction, the survival probability is close to one. Moreover, the location of this transition matches the separatrix in our state space description [4,5]. Our findings indicate that the accuracy of activity propagation in the cortical network is precise and robust enough to explain the precision ($\sim$ 1 ms) of experimentally observed spike patterns [2,6]. Moreover, our results indicate that a combinatorial neural code, based on rapid association of groups of neurons co-ordinating their activity at the single spike-level, is feasible within the cortical network.

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