



The ground state of cortical feed-forward networks

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Abstract

The occurrence of spatio-temporal spike patterns in the cortex is explained by models of divergent/convergent feed-forward subnetworks—synfire chains. Their excited mode is characterized by spike volleys propagating from one neuron group to the next. We demonstrate the existence of an upper bound for group size: above a critical value synchronous activity develops spontaneously from random fluctuations. Stability of the ground state, in which neurons independently fire at low rates, is lost. Comparison of an analytic rate model with network simulations shows that the transition from the asynchronous into the synchronous regime is driven by an instability in rate dynamics. © 2002 Elsevier Science B.V. All rights reserved.

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1. Introduction

Cortical neurons in vivo exhibit ongoing spiking activity at rates of a few Hertz. In the presence of this background “noise” subnetworks are able to process relevant information [3]. The synfire model [1] was introduced to explain the task-related occurrence of precise spatio-temporal spike patterns [7]. A synfire chain consists of groups of w neurons which are linked by divergent/convergent connections in feed-forward manner. In a completely connected chain each neuron in group i receives w inputs from the preceding group $i - 1$ and projects to all w neurons of the succeeding group $i + 1$. We assume coupling to be purely excitatory (in contrast, [6]). The chain is regarded to constitute a subgraph embedded into a large cortical network. The excited mode

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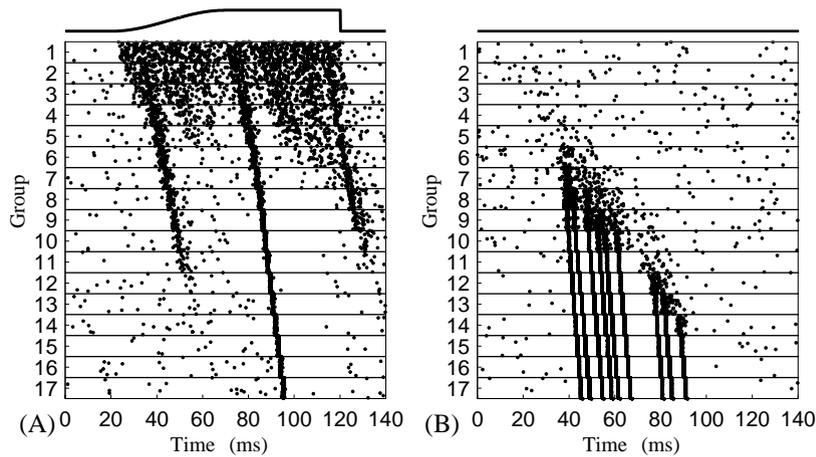


Fig. 1. Synchronous activity in synfire chains of group sizes $w = 100$ (A) and $w = 400$ (B) arising from asynchronous states. Each box represents the activity of a specific group. Each vertical position in a box is reserved for the spikes (marked by dots) of a particular neuron. (A) Synchronous activity following the injection of a slowly increasing current (curve) into the neurons of the first group. (B) Pulse packets developing from spontaneous discharges.

of a synfire chain is characterized by propagating volleys of synchronized spikes (e.g. Fig. 1A). Stable propagation of such “pulse packets” requires a minimal number of neurons per group [5]. The functionality of synfire chains [1] requires a clear separation between the excited state and the ground state, in which neurons independently fire at low rates: Pulse packets should not be evoked by random fluctuations of background activity. Though the synchronous state is well described [4], little is known about the transition from the asynchronous into the synchronous regime. Fig. 1A shows a network simulation in which this transition is initiated by injection of a slowly increasing subthreshold current, leading to an increase of firing rate in the stimulated first group. From this elevated asynchronous state, pulse packets self-organize in consecutive neuron groups. In contrast, no stimulus is applied in Fig. 1B. However, even though the spike rate in the first few groups is at ground state level, pulse packets spontaneously develop. Apart from the stimulus, the two cases (Fig. 1) differ in a single parameter: while neuron groups consist of $w = 100$ neurons in Fig. 1A, this value is increased to $w = 400$ in Fig. 1B. Obviously, there is an upper bound for group size above which synchronous activity is spontaneously ignited. In the following, we develop a rate model that provides a common framework for the two situations in Fig. 1 and allows us to predict the point of transition, leading from the asynchronous into the synchronous regime, in dependence of single neuron properties and background activity.

2. Methods

Analytical and numerical work is based on a leaky-integrate-and-fire neuron model with α -function-shaped synaptic currents [5]. Amplitudes of excitatory and inhibitory

post-synaptic potentials (PSPs) differ only in sign. Thus, mean μ_m and variance σ_m^2 of the membrane potential can be calculated as

$$\mu_m = (K_E \lambda_E - K_I \lambda_I) \int u(t) dt, \quad \sigma_m^2 = (K_E \lambda_E + K_I \lambda_I) \int u^2(t) dt, \quad (1)$$

where $u(t)$ denotes the PSP and λ_E the (Poisson) input rate arriving at K_E excitatory synapses, λ_I , K_I , respectively. With reset potential V_0 , spike threshold θ , and membrane time constant τ_m the output spike rate λ_{out} can be approximated by

$$\frac{1}{\lambda_{out}} = \tau_r + \tau_m \sqrt{\pi} \int_{(V_0 - \mu_m)/\sqrt{2}\sigma_m}^{(\theta - \mu_m)/\sqrt{2}\sigma_m} e^{x^2} [1 + \operatorname{erf}(x)] dx. \quad (2)$$

The r.h.s. is the sum of absolute refractory period τ_r and mean first-passage-time (e.g. [8]). Combining (1) and (2) yields a rate transmission function

$$\lambda_{out} = \Phi(K_E \lambda_E, K_I \lambda_I) \quad (3)$$

for stationary inputs. In a stable network state characterized by rates λ_E^* and λ_I^* each excitatory neuron reproduces λ_E^*

$$\lambda_E^* = \Phi(K_E \lambda_E^*, K_I \lambda_I^*), \quad (4)$$

inhibitory units λ_I^* , respectively. It has been shown that in random networks such attractor states can indeed exist (e.g. [2]). Here, we consider a given state $(\lambda_E^*, \lambda_I^*)$ fulfilling (4) as the ground state of the network. In an embedded synfire chain the total excitatory input of each neuron in group $i+1$ is composed of w channels arriving from the preceding group i firing at rates λ_i and contributions λ_E^* from the excitatory background. In a basic type of embedding the chain is assumed to represent a structure on top of a random network

$$\lambda_{i+1} = \Phi(w \lambda_i + K_E \lambda_E^*, K_I \lambda_I^*) \quad (\text{Model I}). \quad (5)$$

Thus, the total number of excitatory inputs of each neuron increases with w . In a more realistic model intra-chain connections are assumed to be taken from the embedding network

$$\lambda_{i+1} = \Phi(w \lambda_i + [K_E - w] \lambda_E^*, K_I \lambda_I^*) \quad (\text{Model II}). \quad (6)$$

Here, the total number of inputs remains constant. Eqs. (5) and (6) describe the relation between spike rates in consecutive groups in a stationary situation.

3. Results

The results of a stability analysis of iterative maps (5) and (6) with respect to w are summarized in the bifurcation diagrams in Fig. 2. For both embedding schemes the system exhibits a stable fixed point at low rates for small group sizes ($w < 130$). At moderate w an additional attractor at high rates is created. While the lower attractor in Model I is finally annihilated by collision with the unstable fixed point, bifurcation is transcritical in Model II. Thus, the requirement of a stable ground state in both cases implies an upper bound for w . This approach is only valid as long as all involved

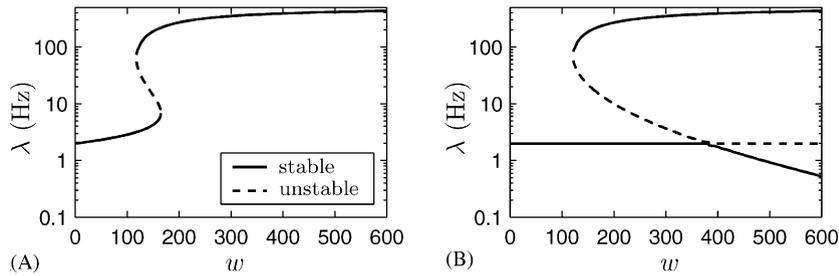


Fig. 2. Fixed points of stationary rate in a synfire chain as a function of group size w and rate perturbation λ (log-scaled). (A) Constant number of synapses from background (Model I). (B) Constant total number of inputs (Model II). Background activity $\lambda_E^* = 2$ Hz, $\lambda_I^* = 12.6$ Hz, with number of inputs $K = K_E + K_I = 20\,000$, $K_E/K_I = 0.88$. Leaky-integrate-and-fire model: $\theta - V_0 = 15$ mV, PSP amplitude: 0.14 mV, PSP rise time: 1.7 ms, membrane time constant $\tau_m = 10$ ms, membrane capacity $C = 250$ pF, absolute refractory time $\tau_r = 2$ ms (cf. [5]).

processes are stationary, i.e. as long as rates remain constant in time. The model must fail as soon as the system switches into the synchronous mode. To check the relevance of our considerations we perform a set of network simulations (Model II) in which stationary rate perturbations are applied to the neurons of the first group. For perturbations relaxing to the ground state in the rate model, the output rates of the 10th group are in good agreement with predictions. However, at a critical rate perturbation the system enters the synchronous regime where spike packets travel through the network. Spike rate obtained by averaging over time is no longer a useful measure. The measured rate of pulse packet occurrence in the 10th group is visualized in Fig. 3A as a function of rate perturbation λ and group size w . Fixed points of the rate model are shown superimposed. Panels (A), (D) and (E) refer to different background states (λ_E^*, λ_I^*). Inhibitory background rates λ_I^* were adjusted in order to fulfill the self-consistency condition (4). The three cases are distinguished by different membrane potential characteristics (1). Surprisingly, the transition from the asynchronous into the synchronous state coincides with the unstable fixed point of the rate model (cf. Fig. 3B and C). Furthermore, Fig. 3 reveals that the critical group size, at which the ground state loses its stability, decreases with increasing background rate. At high background rates the available range between the lower and the upper group size shrinks to zero (not shown), rendering background rate an additional bifurcation parameter.

4. Discussion

The findings summarized in Fig. 3 suggest that asynchronous stimulation of synfire activity is caused by an instability in rate dynamics. Note that the rate model correctly predicts the basin of attraction of the ground state. However, the nature of the high-rate regime differs dramatically from an asynchronous state. Ignition of synchronous activity in synfire chains does not necessarily require rate instability if correlations are large enough [4]. Therefore, we suggest that in our network model rate instability

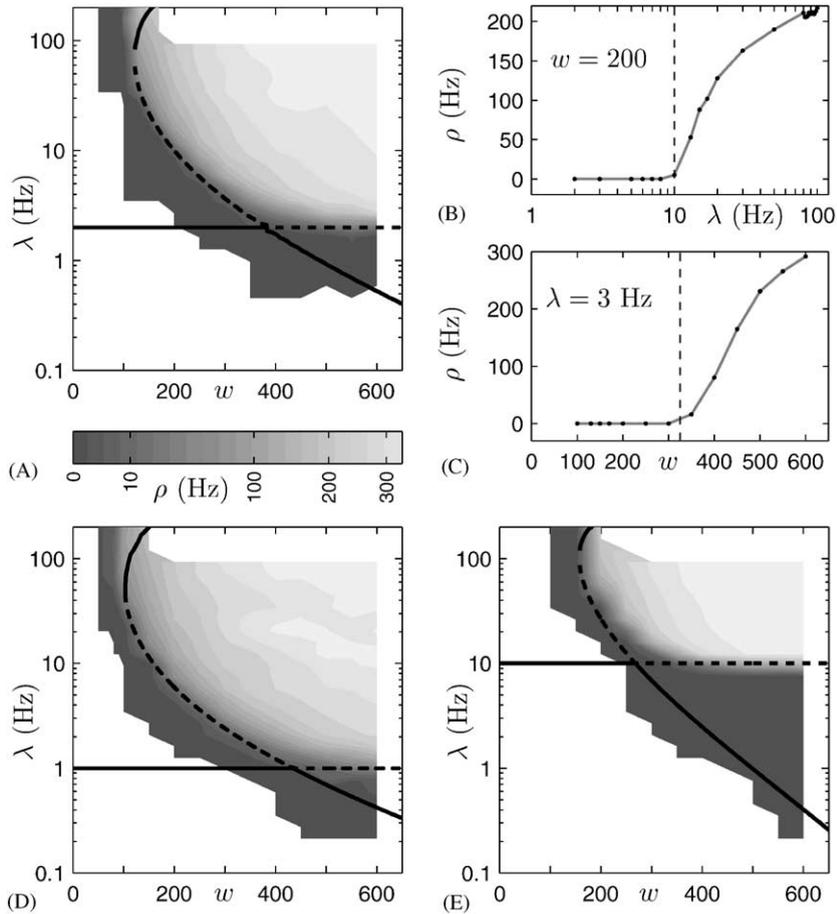


Fig. 3. Pulse packet rate ρ (gray-coded contours, measured in 10th group) as a function of group size w and rate perturbation λ (log-scaled) applied to the first group. Background activity: (A) $\lambda_E^* = 2$ Hz, $\lambda_I^* = 12.6$ Hz, (D) $\lambda_E^* = 1$ Hz, $\lambda_I^* = 4.8$ Hz, (E) $\lambda_E^* = 10$ Hz, $\lambda_I^* = 72.2$ Hz (other parameters as in Fig. 2). Stable (solid curves) and unstable fixed points (dashed curve) of the corresponding rate model (Model II) are superimposed. White area indicates regime in which no simulations were performed. (B) Vertical cross-section of (A) at $w = 200$. (C) Horizontal cross-section of (A) at $\lambda = 3$ Hz. In both panels simulation results (dots) are connected by gray lines, vertical dashed line indicates position of the unstable fixed point of the rate model.

occurs before correlations due to shared input are large enough to elicit synfire activity. Synchronous activity arises as the result of a rate induced increase of correlation: a rapid rate increase in successive groups (following rate instability) eventually leads to correlations large enough to ignite synfire activity. For parameters ensuring rate stability of the ground state correlations seem to be negligible. Stability of the asynchronous ground state imposes an upper bound on group size. In the present analysis we have assumed stationary background activity. Future work has to address feedback of

activity from the chain into the embedding network. Feedback to inhibitory populations may stabilize the systems ground state leading to a predominant role of correlations.

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