



The spread of rate and correlation in stationary cortical networks

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Abstract

The analysis of the spatial and temporal structure of spike cross-correlation in experimental data is an important tool in the exploration of cortical processing. Recent theoretical studies investigated the impact of correlation between afferents on the spike rate of single neurons and the effect of input correlation on the output correlation of pairs of neurons. Here, this knowledge is combined to a model simultaneously describing the spatial propagation of rate and correlation, allowing for an interpretation of its constituents in terms of network activity. The application to an embedded feed-forward network provides insight into the mechanisms stabilizing its asynchronous mode.

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Keywords: Rate model; Cross-correlation; Integrate-and-fire; Synfire chain

1. Introduction

Equilibrated activity states in models of cortical networks are often described in terms of firing rate or related measures. It has been shown (e.g. Refs. [5,7]) that the transmission of firing rates by a single neuron is modulated by temporal relationships between its afferents. Correlations between converging inputs generally affect the magnitude of post-synaptic current fluctuations. Since spiking is driven by both mean and variance of the membrane potential the output rate is not only determined by the firing rate of the inputs but also by the degree of correlation. Depending on the network architecture the sets of afferents of two different neurons exhibit a

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certain overlap. These common input channels induce correlations between the total inputs of the two neurons depending on the size of the overlap, the afferent firing rates, and on correlations inside each set of afferents. As shown e.g. in Ref. [7] such common input correlations are to some degree transmitted by the neuron pair. In summary, there is a complex interplay between firing rates and correlations. Therefore, it appears questionable whether pure rate models can reveal a realistic picture of network dynamics. In the present study we attempt to construct a model describing both variables simultaneously. While rate transmission is treated analytically, the dependence of output correlation on input rate and input correlation is obtained by two-neuron simulations. As an example application we investigate to what extent the rate propagation in a feed-forward network is distorted if correlations are taken into account.

2. Rate transmission

Both analytics and numerics are based on a leaky-integrate-and-fire neuron model with α -function shaped synaptic currents [3]. Since amplitudes of post-synaptic potentials $h(t)$ (PSPs) are chosen to be small compared to the distance ϑ between reset potential and spike threshold, membrane potential dynamics can be considered as a diffusion process. In this framework the output rate λ_{out} is approximately determined by the mean μ and variance σ^2 of the stationary membrane potential distribution (e.g. Ref. [4]). Because of the linearity of the subthreshold dynamics, μ and σ can be calculated by linear filter theory, using $h(t)$ as the systems impulse response. This way the statistical properties of the superposition $X = \sum_{i \in \mathcal{A}} x_i$ of all processes x_i arriving from the set \mathcal{A} of afferents can be easily mapped onto those of the membrane potential. Here, we assume each process x_i to be stationary Poisson with rate λ_i . Hence, the mean weighted number of spikes $\langle X \rangle$ in a time interval Δt is given by $\sum_{i \in \mathcal{A}} g_i \lambda_i \Delta t$. For simplicity, the synaptic weights g_i are considered to be completely determined by the pre-synaptic neuron. Denoting the coefficient of correlation between processes x_i and x_j by r_{ij} , the variance of X is given by

$$\text{Var}[X] = \sum_i g_i^2 \lambda_i \Delta t + \sum_{i \neq j} r_{ij} g_i g_j \sqrt{\lambda_i \lambda_j} \Delta t. \quad (1)$$

Thus, the output rate λ_{out} of a neuron depends on both the rates λ_i of all its afferents *and* the correlations r_{ij} between all afferent pairs. The dependence of the output rate λ_{out} on the rate Λ_E of the total excitatory input is shown in Fig. 1A for a fixed Poisson inhibitory input. The curves refer to different variance-to-mean ratios F (Fano factors) of the excitatory input process. The solid line represents the Poisson case ($F = 1$). An increase in variance, e.g. due to correlations between the input channels, raises the probability of reaching spike threshold at lower mean membrane potentials. Hence, the output rate starts rising at lower Λ_E (dashed curve: $F = 2$, dotted curve: $F = 3$).

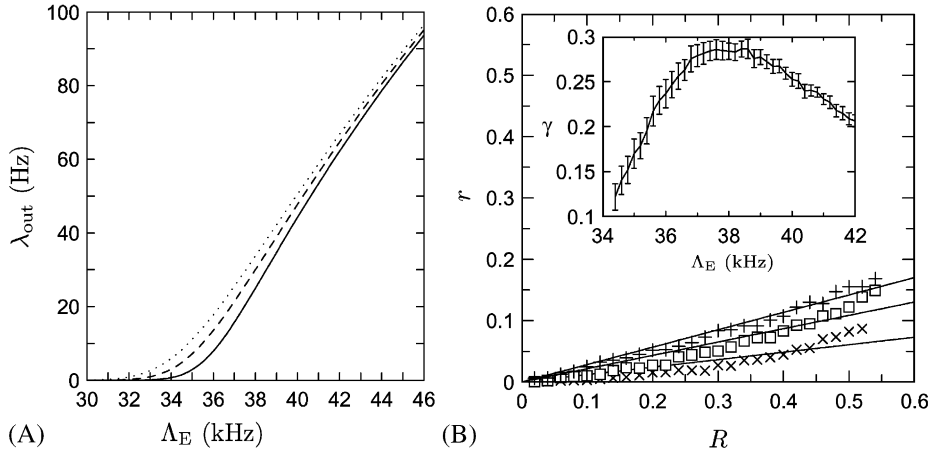


Fig. 1. (A) Response rate λ_{out} as a function of excitatory input rate A_E for different Fano factors $F = 1$ (Poisson, solid curve), $F = 2$ (dashed) and $F = 3$ (dotted). Inhibitory input is a Poisson process with a fixed rate $A_I = 30.24$ kHz. (B) Measured output correlation r (10,000 spikes/neuron) depending on input correlation R for three different excitatory Poissonian inputs with rates $A_E = 34.4$ kHz (\times), 36 kHz (\square) and 39 kHz ($+$). The inset summarizes the result of the linear regression $r = \gamma \cdot R$ (error bars indicate 95% confidence interval). $A_I = 30.24$ kHz, $\vartheta = 15$ mV, $\tau_m = 10$ ms, $\tau_{\text{ref}} = 2$ ms, membrane capacity: 250 pF, PSP amplitude: 0.14 mV, PSP rise time: 1.7 ms, correlation width $\Delta\tau = 5.1$ ms.

3. Correlation transmission

Given the sets $\mathcal{A}_k, \mathcal{A}_l$ of afferent channels of two different neurons k and l , we define the set \mathcal{C}_{kl} of “common inputs” as the intersection $\mathcal{A}_k \cap \mathcal{A}_l$. We call the complements $\mathcal{B}_{kl} := \mathcal{A}_k \setminus \mathcal{C}_{kl}$ the sets of “background” processes. The total input processes $X_{k/l}$ can now be subdivided into a common and a background fraction: $X_{k/l} = C_{kl} + B_{kl/lk}$ (with $C_{kl} := \sum_{i \in \mathcal{C}_{kl}} x_i$ and $B_{kl/lk} := \sum_{i \in \mathcal{B}_{kl/lk}} x_i$). The coefficient of correlation R_{kl} between X_k and X_l is given by

$$R_{kl} = \frac{\text{Cov}[X_k, X_l]}{\sqrt{\text{Var}[X_k] \text{Var}[X_l]}} = \frac{\text{Var}[C_{kl}]}{\text{Var}[C_{kl}] + \text{Var}[B_{kl}]} \quad (2)$$

For reasons of clarity, here we assumed that the three processes C_{kl}, B_{kl} and B_{lk} are pairwise independent and that the backgrounds are statistically equivalent, i.e. $\text{Var}[B_{kl}] = \text{Var}[B_{lk}]$. The degree of correlation induced by common input is thus determined by the ratio of the variances of the total common and background process. As shown in Eq. (1) these variances in turn depend on the rates and correlations inside the afferent populations.

Since the dynamics of our model neuron is completely deterministic, the input correlations $R_{kl} = 0$ and 1 are mapped 1:1 to the output correlation r_{kl} , independently of the statistics of the individual inputs. It is tempting to assume that this is true for all values of R_{kl} . However, several studies revealed that the gain of correlation is in general rather low and is modulated by the mean and variance of the input processes [6,7]. With the

help of two-neuron simulations we measured the correlation transmission $R_{kl} \mapsto r_{kl}$ and its dependence on afferent firing rates. Here, both neurons k and l receive stationary Poisson inputs from a common excitatory channel C of rate Λ^C and individual background channels $B_{k/l}$. The latter are formed by superpositions of excitatory and inhibitory processes $B_{k/l}^E$ and $B_{k/l}^I$. Their spike rates Λ_E^B and Λ_I^B are chosen to be identical for both neurons. Excitatory and inhibitory synaptic weights differ only in sign. Under these conditions Eq. (2) reads $R = \Lambda^C / (\Lambda^C + \Lambda_E^B + \Lambda_I^B)$. Therefore, the degree of input correlation can be tuned by adjusting the rates. Focussing on the dependence of the correlation transmission on the total excitatory input rate $\Lambda_E = \Lambda^C + \Lambda_E^B$ the inhibitory input rate $\Lambda_I = \Lambda_I^B$ is kept constant. Simulations are performed on a temporal grid of 0.1ms resolution. Fig. 1B shows the measured output correlations r as a function of the input correlation R . At low input correlations R the output r is well approximated by the linear relation $r = \gamma \cdot R$. The inset in Fig. 1B shows the dependence of the fitted slope γ on the excitatory input rate Λ_E . Results are consistent with those of former studies [6,7]. It has to be emphasized that the maximum correlation gain $\gamma_{\max} < 0.3$ is small in the observed range. The findings in Ref. [7] revealed that correlation transmission is enhanced by increasing the magnitude of fluctuations of the stimuli. Our analysis is restricted to Poisson inputs with δ -type cross-correlations.

4. Application to feed-forward networks

In the following example we show how the simultaneous transmission of rate and correlation yields a model describing the spatial propagation of stationary spiking activity in a synfire chain [1]. The common input C_i of two neurons a and b in the $(i+1)$ th layer of a complete synfire chain consists of the w channels $c_{i,j}$ ($j \in \{1, 2, \dots, w\}$) from the preceding group i (see Fig. 2A). In addition, a and b receive independent

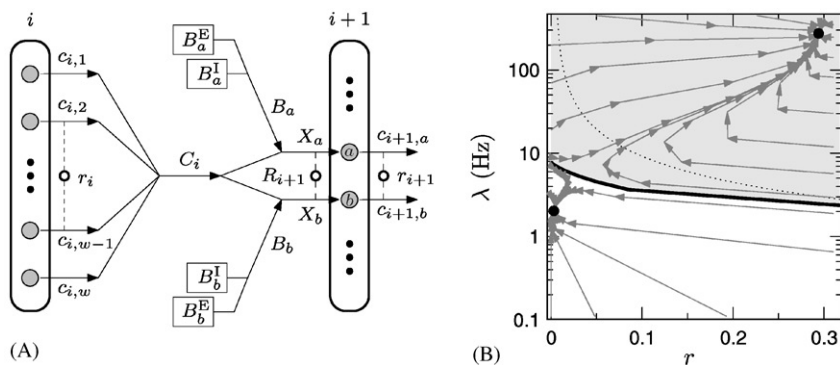


Fig. 2. (A) Synfire link, (B) (λ, r) -phase-space of a synfire chain of group size $w=200$ (log-scaled ordinate). Gray trajectories indicate the spatial evolution from several initial conditions λ_0, r_0 . Black dots mark the positions of the two attractors. Their basins meet at the separatrix (thick black curve). States below the dotted curve correspond to excitatory inputs with Fano factors $F < 2$ (parameters as in Fig. 1).

background inputs $B_{a/b}^E$ and $B_{a/b}^I$. Keeping the total number of excitatory synapses fixed at K_E and the number of inhibitory synapses at K_I mean and variance of the resulting input processes $X_{a/b}$ are given by

$$\begin{aligned}\langle X_{a/b} \rangle &= [(K_E - w)\lambda_E^* + w\lambda_i - K_I\lambda_i^*]\Delta t, \\ \text{Var}[X_{a/b}] &= [(K_E - w)\lambda_E^* + (1 + r_i[w - 1])w\lambda_i + K_I\lambda_i^*]\Delta t,\end{aligned}\quad (3)$$

Here, λ_E^* and λ_I^* denote the firing rates of the background neurons and λ_i those of the neurons in the i th layer. r_i is the coefficient of correlation between each pair of neurons in that group. Intra-chain connections are purely excitatory. Again, each individual process is assumed to be Poissonian. The resulting input correlation is

$$R_{i+1}(\lambda_i, r_i) = \left[1 + \frac{(K_E - w)\lambda_E^* + K_I\lambda_i^*}{w\lambda_i(1 + r_i[w - 1])} \right]^{-1}. \quad (4)$$

Using the approach presented in Section 2 and the simulation results for the correlation transmission an iterative map $(\lambda_i, r_i)_w \mapsto (\lambda_{i+1}, r_{i+1})_w$ can be constructed which simultaneously describes the propagation of firing rates and correlations along the chain. A typical result is shown in Fig. 2B. The phase portrait illustrates the spatial evolution of λ and r for several initial conditions λ_0, r_0 (gray trajectories). The map reveals two attractors (black dots): one at a low rate of about 2 Hz and a correlation of almost zero (we call this the “ground state” [8]) and one at large rates and higher correlations (gray area marks its basin of attraction). The thick black line shows the position of the separatrix. Its near horizontal shape is typical for the investigated system and arises as a result of the low correlation gain. This finding explains the results of a former study [8] which revealed that the transition from the asynchronous into the synchronous regime is well determined by a pure rate model ($r=0$). In our network model the stability of the ground state is barely affected by correlation perturbations and maintained for a reasonable range of group sizes w (however, cf. [2]). Due to the restrictions on Poisson processes our model is valid only at low rates and correlations. As a rough estimate for deviations from the Poisson assumption we considered the Fano factors $F(\lambda, r)$ of the total excitatory input process in the different regions of the (λ, r) -space (Fig. 2B).

5. Discussion

In the present study we analyzed the interplay between spike rates and correlations. Transmission characteristics serve as ingredients for a general framework to explore stationary states in cortical networks. Due to the requirement of Poissonian spike count statistics the scope of this framework is restricted to low rates and correlations. Since cross-correlations exhibit finite temporal widths the reduction to a single integrated quantity—the coefficient of correlation—constitutes an important constraint of the present work. In addition, higher-order correlations, e.g. those enforced by pairwise correlations, may play an important role in network dynamics. The present study exclusively incorporates pairwise correlations. As suggested by the example, the

designed theory is nevertheless applicable to certain network structures and produces reasonable results.

Acknowledgements

We acknowledge stimulating discussions with M. Abeles, Y. Aviel, M. Herrmann, A. Kuhn, and C. Mehring.

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