High Conductance States in a Mean Field Cortical Network Model

Alexander Lerchner   Mandana Ahmadi   John Hertz

Nordita, Blegdamsvej 17, 2100 Copenhagen, Denmark

Abstract

Measured responses from visual cortical neurons show that spike times tend to be correlated rather than exactly Poisson distributed. Fano factors vary and are usually greater than 1, indicating a tendency toward spikes being clustered into bursts. We show that this behavior emerges naturally in a balanced cortical network model with random connectivity and conductance-based synapses. We employ mean field theory with correctly colored noise to describe temporal correlations in the neuronal activity. Our results illuminate the connection between two independent experimental findings: high conductance states of cortical neurons in their natural environment, and variable non-Poissonian spike statistics with Fano factors greater than 1.

Key words: synaptic conductances, response variability, cortical dynamics

1 Introduction

Neurons in primary visual cortex show a large increase in input conductance during visual activation: *in vivo* recordings (see, e.g., [1]) show that the conductance can rise to more than three times that of the resting state. Such *high conductance states* lead to faster neuronal dynamics than would be expected from the value of the passive membrane time constant, as pointed out by Shelley et al. [2]. Here we use mean field theory to study the firing statistics of a model network with balanced excitation and inhibition and observe consistently such high conductance states during stimulation.

In our study, we characterize the irregularity of firing by the Fano factor F, defined as the ratio of the variance of the spike count to its mean. For

temporally uncorrelated spike trains (i.e., Poisson processes) $F = 1$, while $F > 1$ indicates a tendency for spike clustering (bursts), and $F < 1$ indicates more regular firing with well-separated spikes. Observed Fano factors for spike trains of primary cortical neurons during stimulation are usually greater than 1 and vary over an entire order of magnitude (see, e.g., [3]). We find the same dynamics in our model and are able to pinpoint some relevant mechanisms: synaptic filtering leads to spike clustering in states of high conductance (thus $F > 1$), and Fano factors depend sensitively on variations in both threshold and synaptic time constants.

2 The Model

We investigate a cortical network model that exhibits self-consistently balanced excitation and inhibition. The model consists of two populations of neurons, an excitatory and an inhibitory one, with dilute random connectivity. The model neurons are governed by leaky integrate-and-fire subthreshold dynamics with conductance-based synapses. The membrane potential of neuron i in population a ($a = 1, 2$ for excitatory and inhibitory, respectively) obeys

$$\frac{du_a^i(t)}{dt} = -g_L u_a^i(t) - \sum_{b=0}^{2} \sum_{j=1}^{N_b} g_{ab}^{ij}(t)(u_a^i(t) - V_b). \tag{1}$$

The first sum runs over all populations b, including the excitatory input population representing input from the LGN and indexed by 0. The second sum runs over all neurons j in population b of size N_b. The reversal potential V_b for the excitatory inputs ($b = 0, 1$) is higher than the firing threshold, and the one for the inhibitory inputs (V_2) is below the reset value. The constant leakage conductance g_L is the inverse of the membrane time constant τ_m.

The time dependent conductance $g_{ab}^{ij}(t)$ from neuron j in population b to neuron i in population a is taken as

$$g_{ab}^{ij}(t) = \frac{g_{ab}^0}{\sqrt{K_b}} \sum_s \exp(-(t - t_s^j)/\tau_b)\Theta(t - t_s^j) \tag{2}$$

if there is a connection between those two neurons, otherwise zero. The sum runs over all spikes s emitted by neuron j, τ_b is the synaptic time constant for the synapse of type b (excitatory or inhibitory), and Θ is the Heaviside step function. K_b denotes the average number of presynaptic neurons in population b. We followed van Vreeswijk and Sompolinsky [4] in scaling the conductances

2

like $1/\sqrt{K_b}$ so that the fluctuations in the total conductance are of order 1, independent of network size and connectivity.

3 Mean Field Theory

We use mean field theory to reduce the full network problem to two neurons: one for each population, each receiving a Gaussian noisy input, the mean and covariance of which depend self-consistently on the firing statistics. This method is exact in the limit of large populations with homogeneous connection probabilities [5]. Here we consider stationary firing only, for simplicity. Then the time-dependent conductance described in (2) can be replaced by a realization of a Gaussian distributed random variable g_{ab} with mean

$$\langle g_{ab} \rangle = g_{ab}^0 \sqrt{K_b}\, r_b, \tag{3}$$

and covariance

$$\langle \delta g_{ab}(t)\, \delta g_{ab}(t') \rangle = (g_{ab}^0)^2 (1 - K_b/N_b)\, C_b(t - t'), \tag{4}$$

Here r_b is the firing rate of the presynaptic neuron b and $C_b(t - t')$ is the autocorrelation function of its synaptically-filtered spike trains. A simple approximation for the autocorrelation, analogous to that used by [6] and [7], is to take the firing to be temporally uncorrelated. The term $(1 - K_b/N_b)$ is a correction for the finite connection concentration K_b/N_b and can be derived using the methods of [8].

The self-consistent balance condition is obtained by setting the net current in (1) to zero when the membrane potential is at threshold θ_a and the conductances have their mean values (3). In the large K_b-limit, it reads

$$\sum_{b=0}^{2} g_{ab}^0 \sqrt{K_b}\, r_b\, (\theta_a - V_b) = 0. \tag{5}$$

The distribution of the variables g_{ab} can be calculated numerically using an iterative approach [9]. One starts with a guess based on the balance equation (5) for the means and the white-noise approximation for the covariances. One then generates a large sample of specific realizations of $g_{ab}(t)$, which are used to integrate (1) to generate a large sample of spike trains. The latter can then be used to calculate new estimates of the means and covariances by applying (3) and (4) and correcting the initial guesses, moving them toward the new values. These steps are repeated until convergence.
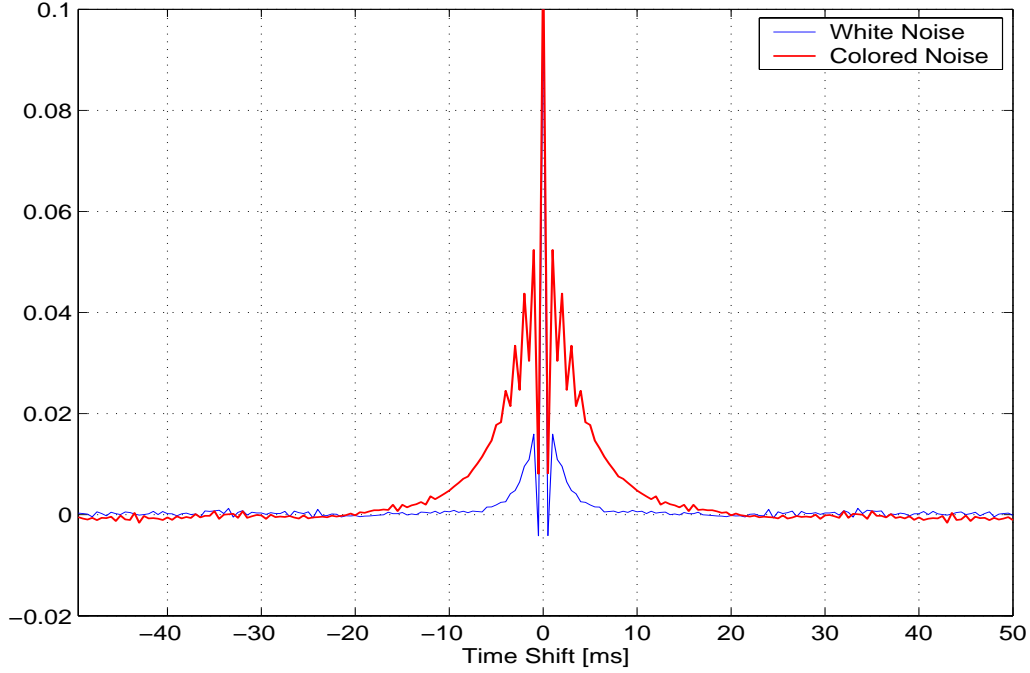
Fig. 1. Autocorrelation functions for white noise (blue) and colored noise (red). The white noise approximation underestimates the amount of temporal correlation in the neuronal firing.

4   Results

For the above-described model, we chose parameters corresponding to population sizes of 16,000 excitatory neurons and 4,000 inhibitory neurons, representing a small patch of layer IV cat visual cortex. The neurons were assumed to be connected randomly, with 10% connection probability between any two neurons. The firing threshold was fixed to 1, excitatory and inhibitory reversal potentials were set to $+14/3$ and $-2/3$, respectively, and the membrane time constant $\tau_m = g_L^{-1}$ was taken to be 10 ms. For the results presented here, the integration time step was 0.5 ms.

Fig. 1 illustrates the importance of coloring the noise produced by intra-cortical activity. The white noise approximation underestimates both the correlation times and the strength of the correlations in the neuron's firing: its autocorrelation (blue) is both narrower and weaker than the one for colored noise (red).

Fano factors vary systematically with both the distance between reset and threshold and the synaptic time constant τ_s. Non-zero synaptic time constants consistently produced Fano factors greater than 1. Varying the reset between 0.8 and 0.94 and τ_s between 2 and 6 ms resulted in values for F spanning an entire order of magnitude, from slightly above 1 to about 10 (see Fig. 2).
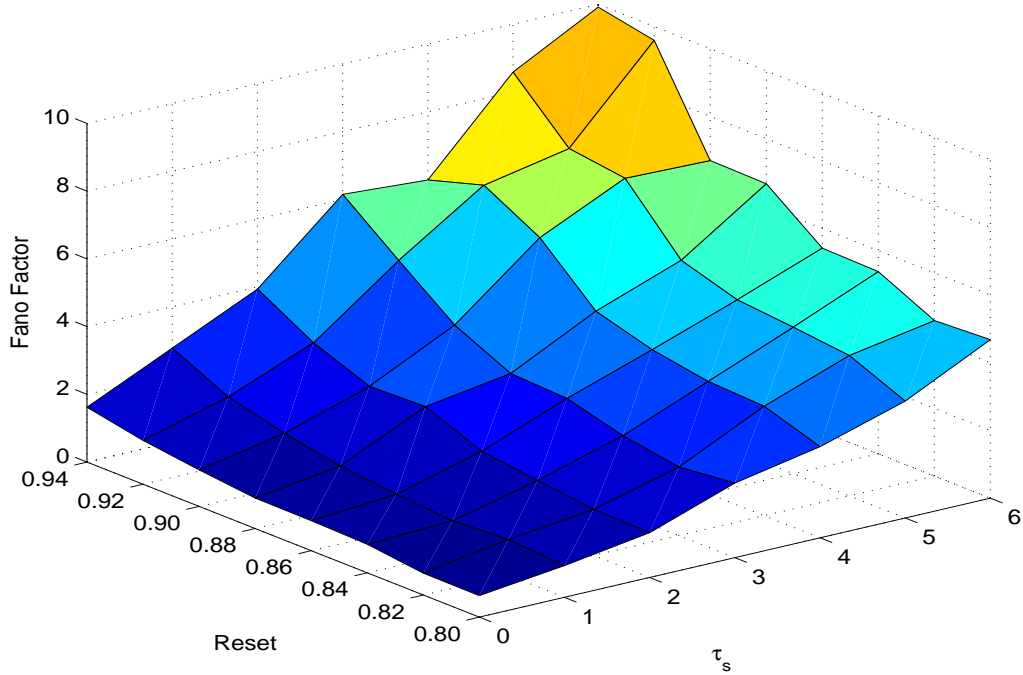
Fig. 2. Fano factors for a range of reset values and synaptic time constants τ_s. Longer synaptic time constants lead to increased clustering (bursts) of spikes, which is reflected in higher Fano factors.

5 Discussion

In all our simulations, we observed that the membrane potential changed on a considerably faster time scale than the membrane time constant $\tau_m = 10$ ms. This behavior is observed only if conductance-based synapses are included in the integrate-and-fire neuron model. To understand this phenomenon, it is convenient to follow Shelley et al. [2] and rewrite the equation for the membrane potential dynamics (1) in the following form:

$$\frac{du_a(t)}{dt} = -g_T(t)\left(u_a(t) - V_S(t)\right),\qquad(6)$$

with the *total conductance* $g_T(t) = g_L + \sum_b g_{ab}(t)$, and the *effective reversal potential* $V_S(t) = g_T(t)^{-1}\sum_b g_{ab}(t)V_b$. The membrane potential $u_a(t)$ follows the effective reversal potential with the input dependent *effective membrane time constant* $g_T(t)^{-1}$. The effective reversal potential changes on the time scale of the synaptic time constants, which are up to five times shorter than τ_m in our simulations. However, if the effective membrane time constant is shorter than the synaptic time constant (due to a large enough total conductance), then the neuron will fire repeatedly during intervals when $V_S(t)$ stays above threshold, as observed in our simulations.

5

In high conductance states, the firing statistics are strongly influenced by synaptic dynamics (see Fig. 2). This is in contrast with strictly current-based models, where the neuron reacts too slowly to reflect fast synaptic dynamics in its firing. Here, the synaptic filtering of arriving spikes leads to temporal correlations in $V_S(t)$ and thus to temporal correlations (in the form of spike clustering) in firing. These correlations, in turn, lead to further correlations in the input, producing still more strongly-correlated firing. For this reason, in mean field models with conductance based dynamics, coloring the noise is especially important in order to describe accurately the temporal correlation in firing statistics (see Fig. 1). We confirmed these considerations by running simulations without synaptic filtering ($\tau_s = 0$). As expected, intra-cortical activity became uncorrelated and the white noise approximation produced the same result as coloring the noise correctly. In that case, Fano factors stayed close to 1 (see Fig. 2), i.e, no tendency of spike clustering was observed.

Previous investigations showed that varying the distance between threshold and reset in balanced integrate-and-fire networks has a strong effect on the irregularity of the firing [10]. By including a conductance-based description of synapses, we were now able to show a strong effect of synaptic time constants on firing statistics, even if they are several times smaller than the passive membrane time constant: Synaptic filtering facilitates clustering of spikes in states of high conductance.

References

[1] L J Borg-Graham, C Monier, and Y Fregnac, *Nature* **393**:369-374 (1998).

[2] M Shelley, D McLaughlin, R Shapley, and J Wielaard, *J. Comput. Neurosci*, **13**:93-109 (2002).

[3] E D Gershon, M C Wiener, P E Latham and B J Richmond, *J Neurophysiol* **79**:1135-1144 (1998).

[4] C van Vreeswijk and H Sompolinsky, *Science* **274**:1724-1726 (1996), *Neural Comp* **10**:1321-1371 (1998).

[5] C Fulvi Mari, *Phys Rev Lett* **85**:210-213 (2000).

[6] D J Amit and N Brunel, *Cerebral Cortex* **7**:237-252 (1997).

[7] N Brunel, *J Comput Neurosci* **8**:183-208 (2000).

[8] R Kree and A Zippelius, *Phys Rev A* **36**:4421-4427 (1987).

[9] H Eisfeller and M Opper, *Phys Rev Lett* **68**:2094-2097 (1992)

[10] J Hertz, B J Richmond, and K Nilsen, *CNS 2002*, to be published in *Neurocomputing* (2003).