Irregular Firing in Cortical Circuits with Inhibition/Excitation Balance

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Abstract

Cortical neurons in the intact brain show irregular spiking patterns. The origin of this irregularity is unknown. We study theoretically the hypothesis that this irregularity is due to approximate balance between the inhibitory and excitatory inputs into the cortical neurons. We model the cortical circuits by sparsely connected networks of inhibitory and excitatory neurons with relatively strong synapses. We show that a state with balanced excitatory and inhibitory inputs into the cells emerges without fine tuning of the parameters. The balanced state is characterized by strongly chaotic dynamics, even with constant external input. Despite the highly non-linear dynamics of single neurons, such networks respond linearly to external inputs and track changing stimuli on a time scale much smaller than the integration time constant of the neuron.

Recent theoretical and experimental studies have focused on the source of irregular firing in the brain [1]. In vitro experiments show regular firing patterns of cortical neurons when they are stimulated by constant current [2] implying that the irregular spiking in vivo is due to fluctuating synaptic currents. The origin of these fluctuations is not yet known. Usually it is assumed that the individual synaptic inputs into a cell are stochastic. However, it is not clear what is the origin of this stochasticity. A second question is why the fluctuations in the individual synaptic inputs are not averaged out in the summation over the large number of synapses that project to a cell.

One possibility is that the fluctuating inputs are synchronized and therefore strongly affect the postsynaptic cell's potential. Model networks with a high degree of connectivity can display synchronized irregular firing [3].

However, such models yield states with strongly synchronized bursts. It is questionable whether cortical networks display this kind of behavior.

A second possibility is that the fluctuations of the individual synaptic inputs remain effective because of cancellation between the mean excitatory and inhibitory currents [4]. Here we address the questions: Can networks with deterministic dynamics generate a highly irregular state with balanced inhibitory and excitatory currents and low levels of synchrony? How much fine tuning of the synaptic parameters in required to ensure this balance? What are the characteristics of this state and what are its functional implications?

To address these questions we consider a network of N_E excitatory and N_I inhibitory neurons [5]. The network also receives input from N_0 excitatory neurons outside of the network. We will use the subscripts E, I and 0 to denote the excitatory, inhibitory and external population, respectively. The connection are random but fixed in time. The probability that a neuron of the k-th population projects to a neuron of of population l is K/N_l, where K is the average number of synapses of each population that project to a cell. The synaptic strength of these projections is $J_{kl}/\sqrt{K}$. Here $k = E, I$ and $l = 0, E, I$. The parameters J_{k0} and J_{kE} are positive, while J_{kI} are negative.

The state of the neurons is described by a binary variable that denotes whether the neuron is active or quiescent. A neuron is active if its postsynaptic potential exceeds its threshold when the neuron is updated. Inhomogeneities between the neurons are modeled by choosing the thresholds of the neurons in population k from a uniform distribution between θ_k and $\theta_k + D$. The neurons are updated sequentially. A cell fires at its maximum rate if it is active every time it is updated. Excitatory neurons are updated once per time unit, inhibitory units every τ time units.

An important assumption of our model is that the total excitatory and inhibitory currents as well as the total current from outside of the network into a cell are large compared to the neuronal threshold. We model this by choosing thresholds θ_k that are of order 1 and assuming that the strength of individual synapses is of order $1/\sqrt{K}$ as stated above. Thus if $K = 1000$, roughly 30 excitatory inputs are needed to bring the neurons above threshold. We analyzed the properties of the network assuming a high degree of sparsity $K \ll N_k$.

To show that the stochastic nature of the firing is a property of the network, we assume a *constant* external input. We denote the input to the excitatory and inhibitory neurons as $J_{E0} m_0 \sqrt{K}$ and $J_{I0} m_0 \sqrt{K}$, respectively.

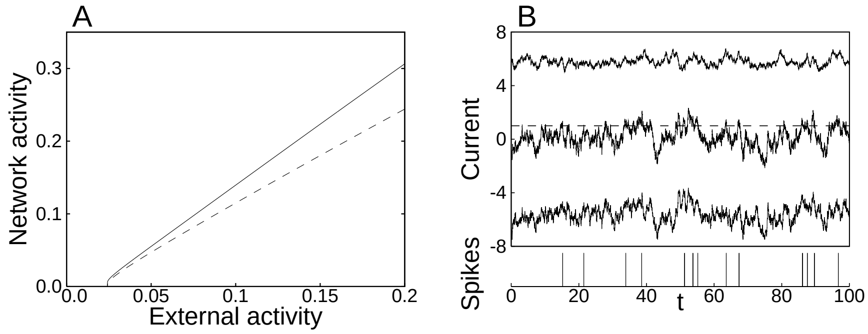

Figure 1: (A) Network rates as function of the input rates The excitatory rates (solid line) and the inhibitory rate (dashed line) are shown as function of the external rates. Above a minimum input that exceeds the threshold the network rates increase nearly linearly with in external rates. (B) Total excitatory input (upper trace), total inhibitory input (lower trace) and net input (middle trace) for a neuron in a large network with $K = 1000$. The inputs are shown in units of the threshold input (dashed line). In all figures we used $K = 1000$, $J_{E0} = J_{EE} = J_{IE} = 1$, $J_{I0} = 0.7$, $J_{EI} = -2.0$, $J_{II} = -1.7$, $\theta_E = 1.0$, $\theta_I = 0.7$, and $D = 0.3$.

Here m_0 is the mean rate of the input neurons.

We now outline the analysis of the stationary state of the network. If the external input is constant, $m_0(t) = m_0$, the network will settle into a stationary state in which the average rates of excitatory and inhibitory populations are constant, $m_k(t) = m_k$. Here m_k is the probability that a cell of population k updates to the active state.

In such a state a cell receive, on average, input from Km_k active cells in population k. Thus the average input, u_k, of cells in population k is given by

$$u_k = \sqrt{K} \left(\sum_{l=0,E,I} J_{kl} m_l \right). \tag{1}$$

Since the connectivity is sparse we can assume that the activity of the cells that project to a given cell are only weakly correlated. This means that the standard deviation of the input σ_k satisfies

$$\sigma_k^2 = \sum_{l=E,I} (J_{kl})^2 m_k. \tag{2}$$

Equations (1) and (2) imply that in general both the total excitatory and the total inhibitory synaptic input are of the order $\sqrt{K}$, while the fluctuations in these inputs are of order 1. To have stationary states in which the cells do not fire at their maximum rate or are completely quiescent, the net input has to be of the same order as the threshold. Thus, for large K, the total excitatory and inhibitory inputs have to nearly cancel each other. According to Eq. (1) this means that the network rates satisfy (to leading order in $1/\sqrt{K}$)

$$m_k = -\sum_{l=E,I} \mathbf{J}^{-1}_{kl} J_{l0} m_0. \tag{3}$$

Here $\mathbf{J}^{-1}$ is the inverse of the 2×2 matrix of connections J_{kl} between the network populations. The requirement that the network rates are positive leads to the constraint on the synaptic strengths $\sum_l \mathbf{J}^{-1}_{kl} J_{l0} < 0$.

The requirement that the total excitatory and inhibitory inputs cancel, leads according to Eq. (3) to a linear dependence of the network rates on the rate of the external input, even though the individual units do not have linear response characteristics. This linear dependence strictly holds only in the large K limit. However, Fig. 1A shows that this is also approximately true in networks with finite K. This figure shows the equilibrium rates as function of the input rate in a network with $K = 1000$. Figure 1B shows total excitatory, inhibitory and net input for a single neuron in the network. As explained, both the excitatory and inhibitory inputs are large compared to the threshold. However the average net input is below threshold. The fluctuations determine the precise timing of the threshold crossings, yielding a very irregular pattern of activity (lower panel) even though the external input does not fluctuate. This disorder is a signature of deterministic chaos.

In the balanced state different cells of the same population can have very different time averaged rates. Figure 2A shows the analytically determined rate distribution of the excitatory population. The rates have a broad unimodal distribution which is skewed and, for small m_k, extends up to $\sqrt{m_k}$. The distribution becomes more skewed as the average network rate decreases. There are two sources for this distribution of the rates. The first source is due to the randomness of the connectivity. This causes the number of projections from each population that cells receive to be different. The second source is the inhomogeneity in the thresholds. Since the fluctuations in the input become small when the rate is low, only those neurons that have the lowest thresholds have a relatively high probability that their input will exceed the threshold. These cells will fire at a rate that is much above the average rate, most other cells will fire at a rate that is significantly below average. In Fig. 2B we show experimental data for the distribution of rates in the right prefrontal cortex of a monkey that is attending to a stimulus

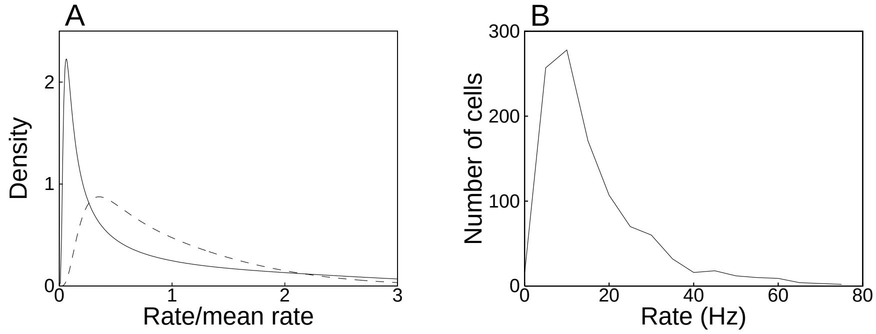

Figure 2: (A) Rate distribution for the excitatory population for different average rates. The external rates were adjusted so that the population rates are $m_E = 0.01$ (solid line) or $m_E = 0.03$ (dashed line). (B) Distribution of firing rates in the right prefrontal cortex of a monkey attending to a complex stimulus (light + sound) and executing a simple reaching movement. The rates were averaged over the duration of events that showed a significant increase in activity.

that consists of a sound and a light and executes a simple reaching movement [6]. The figure shows a broad unimodal distribution of the firing rates with most cells firing at a rate below the average rate and a small fraction of the neurons firing at much higher rate, in agreement with the theory.

We now address the potential the functional advantage of balanced networks. An important advantage of a balanced network is that it reacts on a short time scale to changes in the external input. This response is much faster than that for networks in which the excitatory and inhibitory inputs are of the same order as the neuronal threshold. This is shown in Fig. 3, which displays the response of the network to temporal changes in the external rate m_0. For comparison we also show the relatively slow response to this changing input in a model with threshold linear units, with synaptic strengths of order $1/K$. In both models the units have the same time constants and stationary rates.

Our network's ability to rapidly track changes in external inputs results from a combination of a large synaptic gain (of order $\sqrt{K}$) and the sequential updating. Because of the large synaptic gain a small change in the external rates results in a large change in the synaptic input, so that at a given time the cells that happen to be ready to update make a large change in their activity. Successive recruitment of groups of neurons leads to a rapid adjustment of the population rate to changes in input.

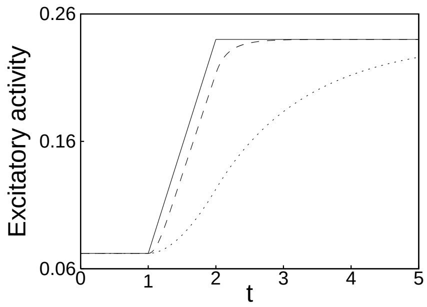

Figure 3: Comparison of the speed with which a balanced network and a network without balancing track changes the external rate. Between $t = 1.0$ and $t = 2.0$ the external rate is increased uniformly, after that it is kept constant again. The solid line shows the activity of a hypothetical network that tracks changes in the external rates infinitly fast. A balanced network (dashed line) tracks the external rates much faster than a network without balancing (dotted line).

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