Chaos in Neuronal Networks with Balanced Excitatory and Inhibitory Activity

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Abstract

Neurons in the cortex of behaving animals show temporally irregular spiking patterns. The origin of this irregularity and its implications for neural processing, are unknown. In this paper the hypothesis that the temporal variability in the firing of a neuron results from an approximate balance between its excitatory and inhibitory inputs is investigated theoretically. It is shown that such a balance emerges naturally in large networks of excitatory and inhibitory neuronal populations which are sparsely connected by relatively strong synapses. The resulting state is characterized by strongly chaotic dynamics, even when the external inputs to the network are constant in time. Such a network exhibits linear response despite the highly non-linear dynamics of single neurons, and reacts to changing external stimuli on time-scales much smaller than the integration time constant of a single neuron.

Recent theoretical and experimental studies have focused on the source of the temporally irregular firing patterns of neurons in cortex, as examplified by their Poisson-like Inter-Spike Interval (ISI) histograms (1). Understanding the origin of this irregularity has important implications for elucidating the temporal components of the neuronal code in cortex. In vitro experiments in cortical slices show regular firing patterns when stimulated by a constant current, indicating that the irregular firing of neurons in the intact brain is due

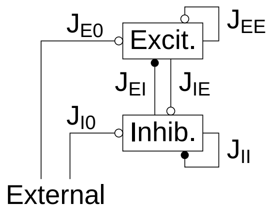

Figure 1: Schematic representation of the network architecture. Excitatory connections between populations are shown as open circles, inhibitory ones as filled circles.

to strong temporal fluctuations in their synaptic inputs (2). However the origin of the fluctuations of the synaptic inputs is not yet known. Furthermore, since a neuron in cortex makes thousands of synaptic contacts with other neurons, the fluctuations in the *total* synaptic input to a cell is expected to be relatively small even when individual synaptic inputs are strongly fluctuating (3). It was recently proposed that the timing of firing of cells in cortex is sensitive to the relatively small fluctuations in their total synaptic input because the excitatory inputs are largely cancelled by the inhibitory ones (4, 5). This intriguing hypothesis raises several questions: (i) What is the origin of the irregularity of individual synaptic inputs? (ii) How much fine-tuning of synaptic constants is required to ensure the balance between the total excitatory and inhibitory currents? (iii) What might be the functional benefits of generating synaptic currents which cancel each other? Several interesting studies (5) have investigated the balance hypothesis in network models, but whether a balance between excitation and inhibition can emerge without fine-tuning of network parameters remained an open question.

We have studied a simple network of N_E excitatory and N_I inhibitory neurons. Additional N_0 neurons from outside the network provide external excitatory inputs to the network neurons (Fig. 1). The model neurons are two-state units that update their state sequentially (6). The updated state of a neuron is active if the value of its input at the time of update exceeds its threshold, otherwise it is quiescent. Biologically, the inputs to a unit correspond to the synaptic currents impinging on a neuron, and the time between two consecutive updates of a unit represents the neuronal membrane time constant (approximately 10 *msec*).

An important aspect of the architecture is the random, sparse connectivity. On average, K excitatory, K inhibitory and K external neurons project to each neuron in the network. Although the average number of projections, K, is large, it is still much smaller than the total number of neurons in the subpopulations, N_E and N_I. Also important is the assumption that the individual connections are relatively strong, namely, that only $\sqrt{K}$ excitatory inputs are needed to cross the firing threshold (7). For example, each cell may receive about $K = 1000$ input currents of the order of $10.0pA$, while the threshold current is about $0.3nA$. Since the number of inputs that are shared by two cells is relatively small, the firing patterns of pairs of neurons are only weakly correlated. Hence, the input to a cell generated by the activity of its K presynaptic excitatory cells has a mean proportional to K and a relatively small fluctuating component, proportional to $\sqrt{K}$ (8). The same holds for the inhibitory input. Since we focus on the role of the network dynamics in generating the temporal irregularity we assume that the external input does not fluctuate. Thus, each cell receives a constant external excitatory input of order K. The mean synaptic inputs are also proportional to the firing rates of the presynaptic populations. Since the threshold is only of the order of $\sqrt{K}$ synaptic inputs, the total synaptic input to a cell will be overwhelmingly depolarizing or hyperpolarizing unless the activity of the excitatory and inhibitory populations dynamically adjust themselves so that the large total inhibitory input nearly cancels the large excitatory one (9). This generates a net synaptic input whose mean and fluctuations are both of the order of the threshold. The precise timing of crossing the threshold is determined by the fluctuations of the synaptic input, yielding a strongly irregular pattern of activity (Fig. 2A). This disorder is a signature of deterministic chaos. Its presence does not require external sources of noise. One of the remarkable features of the balanced network is the fact that although the single cell dynamics is highly nonlinear the population-averaged rates increase nearly linearly with the external input (Fig. 2B). This linear dependence results from the adjustments of these rates to maintain the balance between the total excitatory and inhibitory inputs to the cells (10). Thus, the balance of the inhibition and excitation is an emergent property of the network dynamics and does not require precise tuning of the network parameters.

The balanced state is characterized also by a broad distribution of (time-averaged) firing rates across the network. This distribution is the outcome of the different synaptic projections on each neuron as well as their different threshold levels (7).

Fig. 3A shows the analytical results of the distribution of rates in the

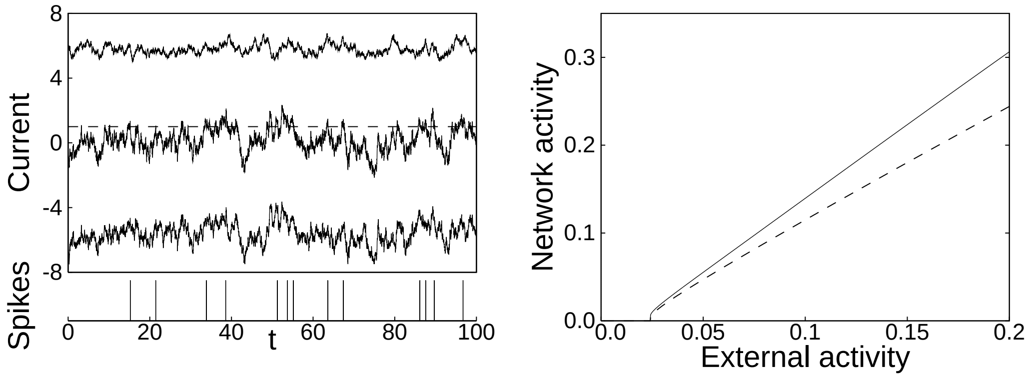

Figure 2: (**A**) Temporal structure of the inputs and activity of a single excitatory unit. The upper panel shows the total excitatory input consisting of external input and excitatory feedback (upper trance) and the total inhibitory input (lower trace) as well as the the net input (middle trace). The currents are shown in units of the threshold (dashed line). They were calculated by sampling from the Gassian statistics of the currents predicted by the theory (8). In the lower panel the times when the cell switches to the active state are indicated. The cell is set to the active state when a supra-threshold net input coincides with the update time of the cell (6). (**B**) The mean activity of the excitatory neurons (solid line) and the inhibitory ones (dashed line) as functions of the activity of the external units (10). The activities shown here and in the following figures, correspond to firing rates divided by their maximum value. Assuming a neuronal maximum rate of $1000Hz$ a mean activity of 0.1 corresponds to a firing rate of $100Hz$.
The following parameter values are used: $K = 1000$, $J_{E0} = J_{EE} = J_{IE} = 1.0$, $J_{I0} = 0.8$, $J_{EI} = -2.0$, $J_{II} = -1.8$, $\theta_E = 1.0$, $\theta_I = 0.8$ and $D = 0.3$. In (A) $m_0 = 0.08$ and $\tau = 0.9$.

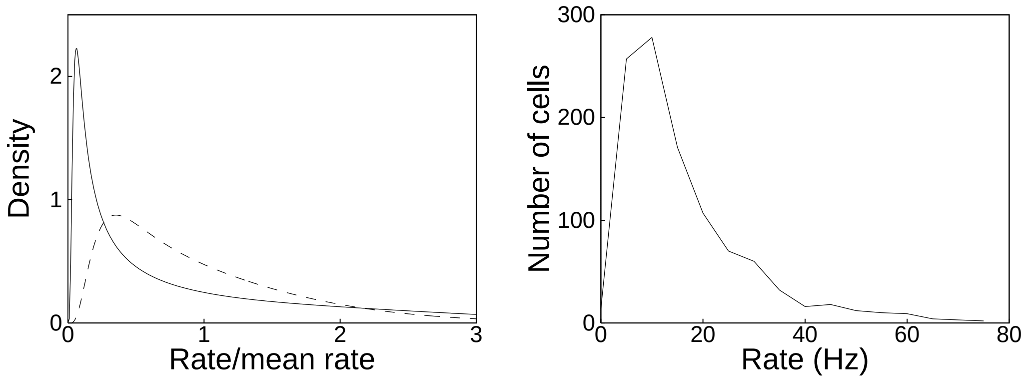

Figure 3: (**A**) The distribution of the rates of neurons in the excitatory population for different population-averaged rates. Solid line shows the distribution for $m_E = 0.01$; dashed line is for a higher mean rate ($m_E = 0.03$). The rate distribution is shown in terms of the local rates divided by the mean rate. Parameters are as in Fig. 2B. (**B**) The distribution of firing rates of neurons in the right prefrontal cortex of a monkey attending to a variety of stimuli (light source + sound) and executing simple reaching movements (11). The rates were overaged over the duration of events (stimuli or movements) that showed a significant response. The average rate is 15.8 Hz. Most cells fire at a lower rate, while a small fraction of the cells fire at much higher rates.

excitatory population for different values of mean rates. A prominent feature is the skewness of the distribution at low mean rates. Since in our model the temporal fluctuations are generated by the network activity itself, they are relatively small when the mean network activity is low. Hence only those neurons which have relatively low thresholds fire vigorously, the rest show activity levels which are much lower than the mean rate. This feature agrees well with experimentally obtained histograms of firing rates of neurons in the monkey prefrontal cortex (Fig. 3B) (11). Our analysis shows that increasing the external inputs to the network shifts the peak of the distribution to larger values but does not give rise to a bimodal distribution (Fig. 3A).

One possible functional advantage of the balanced state is the fact that the balanced network is very fast in tracking changes in the rate of the external input. The response time of the population rates is shorter than the time constant of single units by a factor of $1/\sqrt{K}$. An example of tracking a ramped external input, $m_0(t) = m_0 + v_0 t$ is shown in Fig. 4. For comparison, we also show the slow response of an unbalanced network of linear units with the same stationary rates and the same single unit time constants as

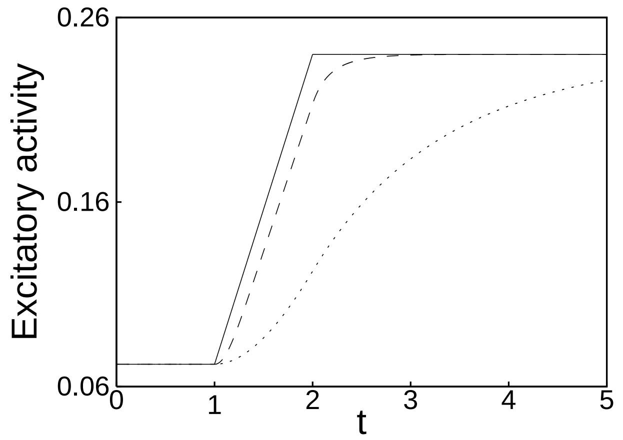

Figure 4: The average excitatory rate (dashed line) for an external drive that varies with time. The external drive is constant $m_0 = 0.06$ for $t < 1$, then increases linearly until $t = 2$ and thereafter remains constant at $m_0 = 0.16$. The solid line shows shows the evolution of the excitatory rate for a hypothetical network that tracks infinitely fast the external rate. The response of an unbalanced network of linear neurons is also shown (dotted line) (13). Parameters are the same as in Fig. 2A except for m_0.

our network (12). The ability of our network to react to changes in its environment on time scales that are much shorter than the update times of the individual neurons is a result of the combination of the large synaptic gain (of the order of $\sqrt{K}$) and the asynchronous nature of the dynamics. A change in the external input by a small amount over a small time increment generates a relatively large change in the synaptic inputs to the neurons in the network. As a result, those neurons that happen to be ready to update make a large change in their activity level. By successively recruiting different groups of neurons, the network population rates adapt fast to the changing input.

The chaotic nature of the balanced state is similar in many respects to the chaotic states of spin-glasses with random asymmetric connection matrices (13, 14). However, in spin-glasses, the balance between inhibition and excitation is automatically guaranteed for an arbitrary state of the network by the randomness of the signs of the connections. In the present networks, the sign of the connections is spatially organized, and the balance between excitation and inhibition is maintained by the network dynamics.

Cortical neurons and circuits are much more complex than the simple network we have studied here, but the mechanism proposed here can also account for the irregular spike trains observed in cortical cells. Indeed, the simplicity of our model suggests that irregular spiking is an emergent network property that does not necessarily depend on intricate cellular mechanisms. Other aspects of balanced networks such as broad skewed rate distributions and fast tracking are expected to hold also for more realistic models. Linear response of population activities will also hold provided that synaptic inputs are summed approximately linearly. Finally, the predicted chaotic activity of the balanced networks puts constraints on the utilization of precise temporal patterns of firing as neural codes.

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[3] The fluctuations in the total synaptic input can be large if the different individual inputs are strongly synchronized. Model networks with high degree of connectivity can display chaotic states characterized by strongly synchronized bursts of activity (15). Whether cortical networks exhibit such spatially coherent bursts under normal conditions is questionable.

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[6] The details of the dynamics are not essential. The simplest model for analytical study is one in which at each time step an updating neuron

is chosen at random. Qualitatively similar behavior exists if the neurons are updated sequentially in a fixed order. Another possibility is a smooth dynamic model for analog units, as in (13). These models differ primarily in the details of their short-time correlations. Time is scaled so that excitatory neurons are updated once per unit of time. Inhibitory units are updated every τ time units.

[7] The probability that a given excitatory (inhibitory) neuron projects to another given neuron is K/N_E (K/N_I). External neurons have a probability K/N_0 of connecting to a given cell in the network. All nonzero projections from cells of the lth population onto cells of the kth population have a strength J_{kl}. Here $k, l = 0, E, I$ denote the external, excitatory, and inhibitory populations, respectively. Inhomogeneities are modeled by distributing the thresholds of population k uniformly between a minimum $\theta_k \sqrt{K}$ and a maximum $(\theta_k + D)\sqrt{K}$.

[8] The total instantaneous input to a single neuron of population $k = E, I$ consists of weakly correlated fluctuating contributions. Therefore we can assume, for large K, that it has Gaussian statistics with a mean given by

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

and variance

$$\sigma_k^2 = \sqrt{K} \sum_{l=E,I} (J_{kl})^2 m_l(t). \tag{2}$$

The variable $0 \leq m_l(t) \leq 1$ denotes the unit activities averaged over all the units in the lth population. It represents the firing rate of the neuronal population relative to its maximal rate. A detailed analysis also yields the short-time correlations of the input which decay on time-scale of order unity. Note that the external input does not contribute to the fluctuations.

[9] To ensure that the saturated states ($m_l = 1$ or 0) are not stable the connection parameters J_{kl} must obey certain easily satisfied inequalities. They also ensure the existence of a balanced state. The stationary balanced state is stable provided that the inhibitory time constant τ is smaller than an upper bound τ_c. The value of τ_c ranges typically from 0.5 to 1.5.

[10] In the balanced state, u_k, Eq. (1), are roughly equal to the population-averaged thresholds $\theta_k \sqrt{K}$, yielding for the population activities m_E and $m - I$, the following linear relation to the external activity m_0

$$m_k = - \sum_{l=E,I} \mathbf{J}_{kl}^{-1} (J_{l0} m_0 - K^{-1/2} \theta_l). \tag{3}$$

Here $\mathbf{J}^{-1}$ is the inverse of the 2×2 matrix of connections J_{kl} between the two network populations. The activities are thresholded to zero when the above relations yield negative values.

[11] Unpublished data from M. Abeles, H. Bergman, and E. Vaadia.

[12] For comparison we consider a fully connected network of linear neurons where the coupling strengths between neurons in the network are equal to J_{kl}/K. These neurons integrate linearly their input with the same time constants as in the balanced network. The strengths of the synapses from cells outside of the network as well as the thresholds were chosen so that the stationary population rates of this network are the same as those for the balanced network.

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