

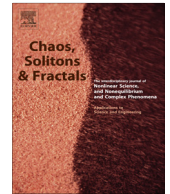


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Stable chaos in fluctuation driven neural circuits

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ABSTRACT

We study the dynamical stability of pulse coupled networks of leaky integrate-and-fire neurons against infinitesimal and finite perturbations. In particular, we compare mean versus fluctuations driven networks, the former (latter) is realized by considering purely excitatory (inhibitory) sparse neural circuits. In the excitatory case the instabilities of the system can be completely captured by an usual linear stability (Lyapunov) analysis, whereas the inhibitory networks can display the coexistence of linear and nonlinear instabilities. The nonlinear effects are associated to finite amplitude instabilities, which have been characterized in terms of suitable indicators. For inhibitory coupling one observes a transition from chaotic to non chaotic dynamics by decreasing the pulse-width. For sufficiently fast synapses the system, despite showing an erratic evolution, is linearly stable, thus representing a prototypical example of *stable chaos*.

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1. Introduction

It is known that cortical neurons *in vivo* present a high discharge variability, even if stimulated by current injection, in comparison with neurons *in vitro* [1,2]. In particular, these differences are peculiar of pyramidal neurons, while inter-neurons reveal a high neuronal firing variability in both settings [3]. This variability is usually measured in terms of the coefficient of variation CV of the single neuron inter-spike interval (ISI), defined as the normalized standard deviation of the ISI, i.e. $CV = STD(ISI)/\langle ISI \rangle$ [4]. For cortical pyramidal neurons $CV \approx 1.0$ *in vivo* [1] and $CV < 0.3$ *in vitro* [2], while for cortical inter-neurons $CV \approx 1.0 - 1.2$ [3] in both settings. The variability of the spike emissions *in vivo* resembles a stochastic (Poissonian) process (where $CV = 1$), however the neural dynamics features cannot be accounted by simple stochastic models [1]. These phenomena can be instead modeled by considering a deterministically balanced network, where inhibitory

and excitatory activity on average compensate one another [5–8]. Despite the many papers devoted in the last two decades to this subject, it is still unclear which is the dynamical phenomenon responsible for the observed irregular dynamics [9–12].

A few authors pointed out the possibility that *stable chaos* [13] could be intimately related to the dynamical behavior of balanced states [14–19]. Stable chaos is a dynamical regime characterized by linear stability (i.e. the maximal Lyapunov exponent is negative), yet displaying an erratic behavior over time scales diverging exponentially with the system size. Stable chaos has been discovered in arrays of diffusively coupled discontinuous maps [20] and later observed also in inhibitory neural networks [14]. This phenomenon is due to the prevalence of nonlinear instabilities over the linear (stable) evolution of the system. This leads in diffusively coupled systems to propagation of information (driven by nonlinear effects) and in diluted inhibitory networks to abrupt changes in the firing order of the neurons [13].

Clear evidences of stable chaos have been reported in inhibitory δ -coupled networks by considering conductance based models [14] as well as current based models with

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time delay [15–18]. In particular, these analyses focused on the characterization of the time needed for the transient irregular dynamics to relax to the final stable state, the authors convincingly show that these transients diverge exponentially with the system size, a key feature of stable chaos. Furthermore, in [16,17] it has been shown that, considering time extended post-synaptic pulses, a transition from stable to regular chaos is present, where fluctuation driven dynamics is apparently maintained [17].

In this paper, we would like to compare the dynamics of a balanced network, whose dynamics is driven by fluctuations in the synaptic inputs, with neural networks composed of tonically firing neurons. Similar comparisons have been performed in some previous studies [21,22], however here we would like to focus on the role of nonlinear instabilities and in particular on indicators capable of measuring finite amplitude instabilities in such networks. The effect of finite perturbations is relevant from the view point of neuroscience, where the analysis is usually performed at the level of spike trains, and a *minimal* perturbation corresponds to the removal or addition of a spike. This kind of perturbations can produce a detectable modification of the firing rate *in vivo* in the rat barrel cortex [23]. This has been reported as the first experimental demonstration of the sensitivity of an intact network to perturbations *in vivo*, or equivalently of an erratic behavior in neural circuits. However, it is unclear whether this sensitivity should be associated to linear or nonlinear effects. In particular the authors in [23] considered a network composed of excitatory and inhibitory neurons, where an extra spike in the excitatory network is soon compensated by an extra spike in the inhibitory network, indicating a sort of balance in the activity of the studied neural circuit. The ability of a perturbed balanced network to restore rapidly the steady firing rate has been also discussed in [19] for a minimal model. Furthermore, Zillmer et al. [16] have shown that a finite perturbation in a stable regime can cause a divergence of the trajectories.

These latter numerical studies, together with the fact that the addition of an extra spike is clearly a finite perturbation from the point of view of dynamical systems, strongly demand for further experimental investigations to clarify whether the erratic behavior reported in [23] is due to infinitesimal or finite amplitude instabilities.

Even though all these findings are congruent with the nature of stable chaos [13], it must be noted that a careful characterization of this regime in neural networks in terms of finite amplitude indicators is still lacking. The only previous study examining this aspect in some detail concerns a purely inhibitory recurrent Leaky Integrate-and-Fire (LIF) neural network with an external excitatory drive, which can sustain balanced activity [19]. Starting from this analysis, which was limited to δ -pulses, we have considered an extension of the model to finite width pulses. Furthermore, we have characterized the linearized evolution via usual Lyapunov exponents and the nonlinear effects in terms of the response of the system to finite perturbations. This analysis has been performed by employing previously introduced indicators such as Finite Size Lyapunov Exponents (FSLEs) [24] or the probability that a finite perturbation can be (exponentially) expanded [19], and new indicators capable of capturing nonlinear instabilities.

The paper is organized as follows: Section 2 is devoted to the introduction of the neural network model used through this paper, together with the indicators characterizing linear and nonlinear instabilities. Section 3 presents a comparative study of the linear and nonlinear stability analysis with emphasis on the influence of the pulse-width and the size of the network on the dynamical behavior. Finally, in Section 4 we discuss our results with respect to the existing literature and we report possible future developments of our research.

2. Model and methods

We will consider a network of N Leaky Integrate-and-Fire (LIF) neurons, where the membrane potential v_i of the i th neuron evolves as

$$\dot{v}_i(t) = a - v_i(t) + I_i(t) \quad i = 1, \dots, N, \quad (1)$$

where $a > 1$ is the supra-threshold neuronal excitability, and I_i represents the synaptic current due to the pre-synaptic neurons projecting on the neuron i . Whenever a cell reaches the threshold value $v_{th} = 1$ a pulse is emitted instantaneously towards all the post-synaptic neurons, and its potential is reset to $v_r = 0$. The synaptic current $I_i(t) = gE_i$ is the superposition of the pre-synaptic pulses $s(t)$ received by the neuron i with synaptic strength g , therefore the expression of the field E_i reads as

$$E_i(t) = \frac{1}{K^\gamma} \sum_{j \neq i} \sum_{n|t_n < t} C_{ij} \Theta(t - t_n) s(t - t_n). \quad (2)$$

Here the sum extends to all the spikes emitted in the past in the network, $\Theta(t - t_n)$ is the Heaviside function and the parameter γ controls the scaling of the normalization factor with the number K of pre-synaptic neurons. Proper normalization ensures homeostatic synaptic inputs [25,26]. The elements of the $N \times N$ connectivity matrix C_{ij} are one (zero) in presence (absence) of a connection from the pre-synaptic j th neuron to the post-synaptic i th one. In this paper we limit our analysis to random sparse networks, where each neuron receives exactly K pre-synaptic connections and this number remains fixed for any system size N . The model appearing in Eqs. (1) and (2) is adimensional, the transformation to physical units is discussed in Appendix A.

Following [5], we assume that the pulses are α -functions, $s(t) = \alpha^2 t \exp(-\alpha t)$, in this case the dynamical evolution of the fields $E_i(t)$ is ruled by the following second order differential equation (ODE):

$$\ddot{E}_i(t) + 2\alpha\dot{E}_i(t) + \alpha^2 E_i(t) = \frac{\alpha^2}{K^\gamma} \sum_{j \neq i} \sum_{n|t_n < t} C_{ij} \delta(t - t_n), \quad (3)$$

which can be conveniently rewritten as two first order ODEs, as

$$\dot{E}_i = P_i - \alpha E_i, \quad \dot{P}_i = -\alpha P_i + \frac{\alpha^2}{K^\gamma} \sum_{j \neq i} \sum_{n|t_n < t} C_{ij} \delta(t - t_n), \quad (4)$$

by introducing the auxiliary field $P_i = \dot{E}_i - \alpha E_i$.

Eqs. (1) and (4) can be exactly integrated from the time $t = t_n$, just after the deliver of the n th pulse, to time $t = t_{n+1}$

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