

Irregular Collective Behavior of Heterogeneous Neural Networks

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(Received 10 June 2010; published 7 October 2010)

We investigate a network of integrate-and-fire neurons characterized by a distribution of spiking frequencies. Upon increasing the coupling strength, the model exhibits a transition from an asynchronous regime to a nontrivial collective behavior. Numerical simulations of large systems indicate that, at variance with the Kuramoto model, (i) the macroscopic dynamics stays irregular and (ii) the microscopic (single-neuron) evolution is linearly stable.

DOI: 10.1103/PhysRevLett.105.158104

PACS numbers: 87.19.lj, 05.45.Xt, 87.19.lm

The investigation of networks of oscillators can provide new insight into the basic mechanism which underlies brain functioning. In particular, the spontaneous onset of a collective dynamics is an intriguing phenomenon that can contribute to information transmission across different brain areas. Given the large number N of neurons (oscillators) present in a real brain, it is tempting to adopt a statistical-mechanics point of view and thereby investigate the behavior for $N \rightarrow \infty$ (the so-called thermodynamic limit). Three main setups are typically invoked [1]: (i) sparse networks, characterized by a fixed number of synaptic connections; (ii) networks where excitatory and inhibitory inputs balance on average [2]; (iii) massively connected networks, where the number of links is proportional to N . In the first two cases, the spiking activity is naturally accompanied by statistical fluctuations due to either the finite number of input signals or the closeness to the firing threshold. This behavior is coherent with the experimental evidence of an irregular background activity in the cerebral cortex [3].

In this Letter, we numerically show that an irregular microscopic and macroscopic dynamics can generically arise also in an inhibitory, globally coupled network. More precisely, we consider a heterogeneous network of pulse-coupled integrate-and-fire (IF) neurons [1], each characterized by a different bare spiking frequency. This setup is similar to that of the Kuramoto model (KM) [4], where each single oscillator is identified by a phase variable ϕ . The analogy is so tight that it has even been shown that the pulse-coupling mechanism characterizing IF neurons reduces, in the weak coupling limit, to that of the KM, the only difference being that the coupling function is not purely sinusoidal [5]. It is therefore quite important to clarify to what extent a network of IF neurons reproduces the KM scenario for stronger coupling strengths, especially by recalling that the KM is often invoked while testing new ideas on the control of synchronization within neural contexts [6]. A similar setup, in the presence of excitatory connections, was analyzed in Ref. [7], where the effect of heterogeneity on the stability of the fully synchronous

regime was investigated. Finally, in order to make the model closer to a realistic setup, we include delay to account for the finite propagation time of the electric pulses.

Our strategy consists in studying the macroscopic collective dynamics in the large N limit, for different values of the coupling strength g . In the KM, above a critical value of the coupling strength, a subset of the oscillators mutually synchronize, as signaled by a nonzero value of the order parameter $\rho = |\sum_{j=1}^N e^{i\phi_j}/N|$. In this Letter we show that IF neurons give rise to a similar but substantially different scenario. First of all, the second largest Lyapunov exponent is always negative [8], implying that the evolution must eventually converge to a periodic orbit. On the other hand, the study of relatively small networks shows that the time needed to approach a periodic orbit is exponentially long with the system size, implying that the “transient” extends over increasingly longer time scales. In other words, this is an instance of *stable chaos* [9], a phenomenon already observed in disordered networks of pulse coupled oscillators [10–12] and whose generality in inhibitory networks has been addressed in [11].

A second difference is that, at variance with the KM, the coupling contributes also to slowing down the spiking activity of the single neurons (a somehow similar mechanism operates in ensembles of cold atoms [13]) and drives a subset of neurons below the firing threshold—a phenomenon reminiscent of oscillator death [14]. However, the most striking difference concerns the above-threshold regime, as the overall neural activity is not *simply* periodically modulated, but exhibits irregular, seemingly chaotic, oscillations (still in the presence of a negative “microscopic” second Lyapunov exponent). Nothing of this type has been observed in the corresponding setup of a KM with delayed coupling [15].

The evolution equations for the N membrane potentials v_i write,

$$\dot{v}_i = a_i - v_i - \frac{g}{N} \sum_{n|t_n < t} S_{i,l(n)} \delta(t - t_n - t_d) \quad (1)$$

where all variables are expressed in adimensional units. When v_i reaches the threshold $v_i = 1$, it is instantaneously reset to the value $v_i = 0$, while a spike is emitted (and received with a delay t_d). The network is assumed to be heterogeneous, in that different neurons are exposed to different suprathreshold currents a_i ; $(v_0)_i = 1/\ln[a_i/(a_i - 1)]$ is the bare spiking frequency. $S_{i,l}$ denotes the connectivity matrix and the sum in Eq. (1) runs over the spikes received by the neuron i . Finally, the coupling strength g is our control parameter: the negative sign in front of last term in the r.h.s. means that we assume inhibitory coupling. Notice also that the same last term does not only couple the oscillators but modifies also their frequency.

All the simulations reported in this Letter refer to a *globally coupled* network, i.e. $S_{i,l} = 1$ for any i, l , but we have verified that the introduction of additional disorder (by randomly removing a fixed fraction of connections) does not substantially modify the overall scenario. The delay is set everywhere equal to $t_d = 0.1$, while the currents a_i are randomly and uniformly distributed in the interval $[1.2, 2.8]$. These parameter values are consistent with those selected in Ref. [12], where they have been chosen on the basis of biological motivations. In order to investigate the collective behavior, it is necessary to introduce a suitable order parameter [16]. We do so by coarse graining the spiking activity, *dressing* each spike with a finite width and thereby constructing a smooth effective field E . If we assume the pulse shape, $p(t) := \alpha^2 t \exp(-\alpha t)$ ($t > 0$), the corresponding field E can be generated by integrating the equation,

$$\ddot{E} + 2\alpha\dot{E} + \alpha^2 E = \frac{\alpha^2}{N} \sum_{n|t_n < t} \delta(t - t_n - t_d). \quad (2)$$

This procedure is often used to determine the field actually seen by the single neurons [17]; here it is just a strategy to construct a meaningful order parameter, that is defined as the standard deviation σ of E ($\sigma^2 = \langle E^2 \rangle_t - \langle E \rangle_t^2$, where $\langle \cdot \rangle_t$ denotes a time average). We choose $\alpha = 20$, a value that corresponds to sufficiently broad pulses to get rid of the statistical fluctuations, but not so large as to wash out the time evolution. As long as the asymptotic regime is an asynchronous state characterized by a constant activity, σ is zero in the infinite N limit, while any form of collective dynamics gives rise to a nonzero σ . This is precisely what is seen in Fig. 1, where σ is plotted versus the coupling strength g for different network sizes. Below $g_c \approx 0.5$, σ is quite small and appears to decrease as $1/\sqrt{N}$ with the system size (see the left inset), indicating that the deviation from zero is a finite-size effect. Above g_c , σ starts to grow and is independent of the system size, suggesting the onset of some form of synchronization (the right inset contains an instance of the field evolution for $g = 5$). Superficially, this scenario is reminiscent of the synchronization transition observed in the KM. In the

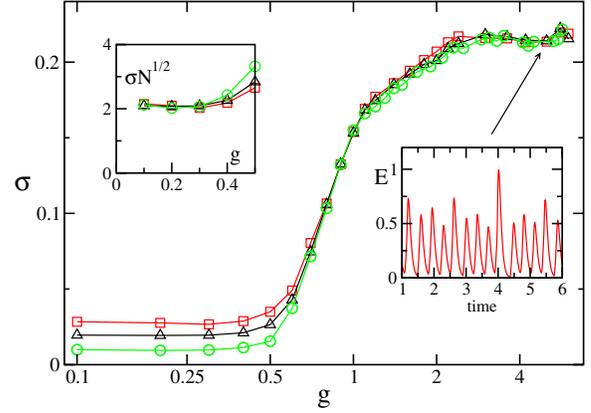


FIG. 1 (color online). Standard deviation, σ , of the effective field E as a function of the coupling strength g for $N = 5750$, (red) squares, $N = 11\,500$, (black) triangles, and $N = 46\,000$, (green) circles. The upper inset contains the rescaled standard deviation. The lower inset contains an instance of the time evolution of E for $g = 5$ and $N = 5750$.

following we show that there are several conceptually relevant differences. The first difference concerns the microscopic (single-neuron) behavior. The maximum Lyapunov exponent, λ , of the Poincaré map (to get rid of the first zero Lyapunov exponent) is negative both below and above the transition and does not depend on N for large system sizes [18]. Altogether, the stable microscopic dynamics observed in this setup contrasts with the weakly unstable dynamics observed in the KM, where the maximum Lyapunov exponent is positive, though scales as $1/N$ [19]. On the other hand, the transient time T_r needed for a generic trajectory to converge to some periodic orbit grows exponentially with N . This is illustrated in Fig. 2, where the average \bar{T}_r (over more than 100 realizations of the disorder) is plotted for different coupling strengths. There, one can also appreciate that the exponential growth

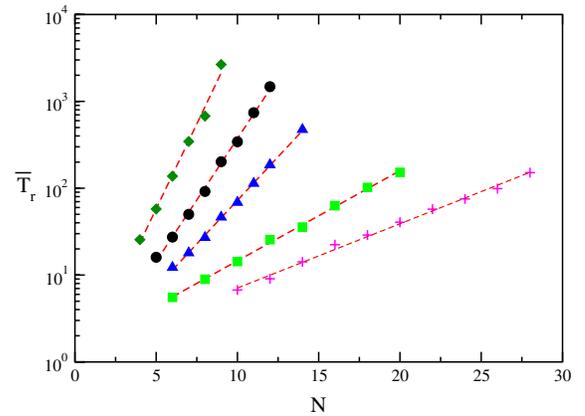


FIG. 2 (color online). Average transient length \bar{T}_r as a function of N for $g = 0.3, 0.7, 1.3, 3$, and 5 (diamonds, circles, triangles, squares, and plusses, respectively). The (red) dashed lines are exponential fits.

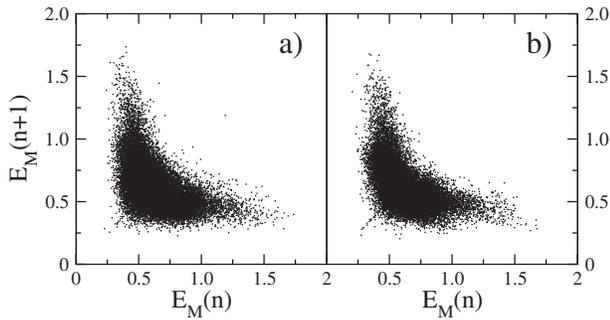


FIG. 3. Return maps for the maxima of the effective field E when $g = 5$ for $N = 11\,500$ (a) and $N = 46\,000$ (b).

rate decreases systematically with increasing g . Therefore, for large N , the relevant dynamical regime is represented by the transient dynamics, rather than by the periodic orbit approached over astronomical time scales. This *stable chaos* scenario was first observed in the absence of delay [10] for networks of identical oscillators, when disorder in the connectivity matrix is included. Its occurrence in the presence of delay depends crucially on the balance between the amplitude of the effective disorder in the connections and the stability of clustered states. Whenever local fluctuations decrease with N , the transient length does not only stop growing exponentially, but even decreases, since generic trajectories rapidly approach one of the clustered states [20]. At variance with the previously considered setups [11,12], the disorder induced by the heterogeneity of the currents, survives in the thermodynamic limit. Accordingly, the exponential growth of the transient length is expected to persist for arbitrarily large N even in the absence of disorder in the connections. In fact, we find no evidence of a convergence towards more coherent states.

The standard deviation σ allows identifying the very existence of collective fluctuations, but does not tell us anything about their dynamical character. Up to $g \approx 2$, simulations performed for increasing N suggest that the field E behaves periodically in the thermodynamic limit. On the other hand, the right inset in Fig. 1, which refers to $g = 5$, reveals a rather irregular behavior still for $N = 46\,000$. A more accurate analysis is however necessary before making any claim. As a first test, we construct a return map by plotting the $(n + 1)$ -st maximum $E_M(n + 1)$ of the field versus the previous one. In Fig. 3, we see that the points in the Poincaré section fill a broad and almost the same area for both $N = 11\,500$ and $46\,000$. Such features consistently indicate that the collective dynamics is characterized by complex oscillations.

Next, we characterize the collective motion by computing the Fourier power spectrum $S(\nu)$ of the field E . The spectra reported in Fig. 4 reveal several broad peaks whose width does not appear to decrease for increasing N . This confirms that the irregularity of the collective dynamics persists in networks of arbitrary size and therefore

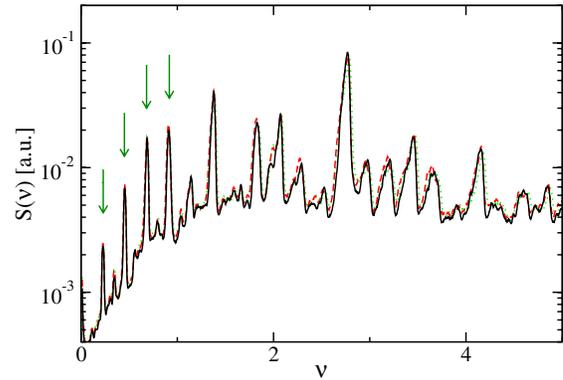


FIG. 4 (color online). Power spectrum $S(\nu)$ of the effective field for $N = 5750$, (dotted line) $11\,500$ (dashed line) and $46\,000$ (solid line). The spectra have been obtained by Fourier transforming a signal of temporal length $\approx 49\,300$. The arrows point to the frequencies identified in Fig. 5.

differs from the periodic oscillations reported, e.g., in Refs. [21,22].

In order to shed further light on the system evolution, we have analyzed the single-neuron behavior too. In Fig. 5, the spiking frequency ν (defined as the inverse of the average interspike interval—ISI) of the single neurons is plotted versus the bare frequency $\nu_0 \in [0.558, 2.26]$ (again for $g = 5$). The effective frequency is systematically smaller than ν_0 ; this is because the inhibitory coupling lessens the neural activity. In fact, inhibition is so strong, as to bring the least active neurons below threshold: neurons with $\nu_0 < \approx 1.56$ do not fire at all, and thus do not actively contribute to the network dynamics: they are just slaved by the other degrees of freedom.

The appearance of plateaux (the widest ones corresponding to harmonics of the frequency $\nu = 0.23$) reveals that neurons with similar bare frequencies lock together, as it is naturally expected for periodically forced oscillators

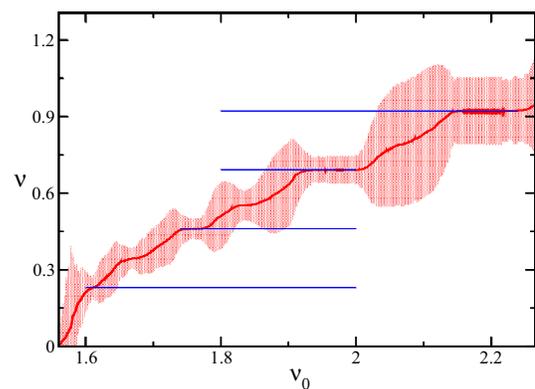


FIG. 5 (color online). Average spiking frequency of the oscillators as a function of the bare frequency (ranging in the interval $[0.558, 2.26]$), for $g = 5$ and $N = 46\,000$ neurons (red solid line). The thin horizontal lines are located at multiples of $\nu = 0.23$. The shaded area identifies the region covered by frequency fluctuations (see the text for further details).

(see the phenomenon of Arnold tongues). However, in this case, the forcing field is not periodic: the shaded region around the curve $\nu(\nu_0)$ highlights the fluctuations of the spiking frequency (half of the vertical width correspond to 3 standard deviations of ν). We have verified that such a width does not vanish upon increasing N , while the neurons within the same plateau are frequency locked but not phase locked. It is tempting to trace back the irregular collective motion to the presence of neurons that are nearly at threshold, whose activity is quite sporadic. However, we have verified that the overall evolution is almost unchanged when such neurons (and those which do not spike at all) are removed from the outset. The appearance of discretized frequencies has been observed also in chaotic delay coupled oscillators [23].

All of our numerical simulations suggest that the irregularity of the collective dynamics persists for $N \rightarrow \infty$. It is important to realize that this scenario is *a priori* legitimate, since the dynamics is ruled, in the thermodynamic limit, by a suitable nonlinear functional equation. In this case, the relevant object is the probability density $P(\nu, \nu_0, t)$ for the membrane potential of the neurons, whose bare spiking frequency lies in the interval $[\nu_0, \nu_0 + d\nu_0]$ to belong to the interval $[\nu, \nu + d\nu]$ at time t . As functional equations involve infinitely many degrees of freedom, one can, in principle, expect an arbitrary degree of dynamical complexity. In models such as the networks considered in [2], the corresponding probability density is a Gaussian and it is therefore described by just two variables. As a result, in that context one cannot observe anything more complex than periodic oscillations. In the standard KM it has been proved that not even periodic oscillations can arise; a periodic collective motion can be observed only by invoking a more complicate nonlinear dependence on the order parameter [24]. On the other hand, it has been conjectured that the collective dynamics is infinite dimensional in globally coupled logistic maps [25]. The presence of many active modes appears to be associated to the singular structure of the invariant measure, which, in the context of this Letter, has a further reason to be so because of the lack of microscopic chaos.

Altogether, we have shown that heterogeneity may induce irregular collective oscillations even in *simple* networks of one-dimensional phase oscillators. This mechanism may contribute to the background irregular activity observed in the cerebral cortex. Characterizing this behavior and understanding the conditions for its onset remains an open problem.

We wish to thank A. Torcini, Th. Kreuz, and S. Olmi for enlightening discussions. We acknowledge financial support from the CNR project “Dinamiche cooperative in strutture quasi uni-dimensionali.”

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