



Effects of Poisson noise in a IF model with STDP and spontaneous replay of periodic spatiotemporal patterns, in absence of cue stimulation

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ABSTRACT

We consider a network of leaky integrate and fire neurons, whose learning mechanism is based on the Spike-Timing-Dependent Plasticity. The spontaneous temporal dynamic of the system is studied, including its storage and replay properties, when a Poissonian noise is added to the post-synaptic potential of the units. The temporal patterns stored in the network are periodic spatiotemporal patterns of spikes. We observe that, even in absence of a cue stimulation, the spontaneous dynamics induced by the noise is a sort of intermittent replay of the patterns stored in the connectivity and a phase transition between a replay and non-replay regime exists at a critical value of the spiking threshold. We characterize this transition by measuring the order parameter and its fluctuations.

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1. Introduction

We study the effects of noise in the spontaneous collective dynamics of a network of N leaky Integrate and Fire (LIF) neurons, whose learning mechanism is based on the Spike-Timing-Dependent Plasticity (STDP). The temporal patterns we consider are periodic spike-timing sequences, whose features are encoded in the relative phase shifts between neurons' spikes. We review the storage and replay properties of such LIF networks whose connections come from a learning strategy based on STDP with P phase-coded patterns with random phases.

Then we focus on the effects of an independent Poissonian noise added to the post-synaptic potentials during spontaneous activity. In previous works (Scarpetta and Giacco, 2012; Scarpetta et al., 2010) we focused on the dynamics emerging as a consequence of a short cue stimulation, and we showed that in order to trigger spontaneous patterns of activity reminiscent of those stored during the learning stage, a few spikes with the right phase relationship are sufficient. Here we focus on the spontaneous dynamics without any external stimulus, and we show that a noisy signal added to the potentials may induce an intermittent replay of the stored patterns.

This spontaneous reactivation induced only by noise, is particularly relevant considering that relationship between spontaneous and evoked cortical activity during development is the object of many recent studies (Berkes et al., 2011; Han et al., 2008). Notably we study the phase-transition which appears in the noisy spontaneous dynamics of our model, in absence of external stimulation. We characterize the critical regime, at the transition between the region of spontaneous persistent replay and the region of no-replay. In this critical regime a short transient intermittent replay is initiated by noise. The replay lasts for a short time and after a while a new pattern may be transiently reactivated spontaneously. To characterize the spontaneous activity of the network, we evaluate the order parameter and its fluctuations as a function of spiking threshold of the coupled neurons. At a low spiking threshold the order parameter is high and fluctuations are low, while at the critical spiking threshold, where there is a transition between no-replay (high θ_{th}) and persistent replay (low θ_{th}), the order parameter's fluctuations are maximized, as expected for a continuous phase transition. Interestingly many recent experimental results, such as Tagliazucchi et al. (2012), suggest that resting brain spends most of the time near to the critical point of a second order phase transition. An important result of this paper is the study of the dynamical critical point and of the different dynamical regimes observed by changing the excitability parameters of the network.

The paper is organized as follows: in Section 2 we introduce the LIF neuronal model and the STDP learning rule used to design

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the connections, with a brief illustration of the evoked behavior (Section 2.1); in Section 3 we study the ability of the noise to induce the spontaneous recall of the pattern in absence of external stimulation, we introduce an order parameter, and we focus on the critical region; summary and discussion are outlined in Section 4.

2. The model

The spiking model has been introduced in Scarpetta and Giacco (2012), Scarpetta et al. (2010). We briefly review the model here. The single neuron model is a LIF. We use the Spike Response Model (SRM) formulation (Gerstner and Kistler, 2002; Gerstner et al., 1993) of the IF model. In this picture, the post-synaptic membrane potential of a neuron i is given by:

$$h_i(t) = \eta_i(t) + \sum_j J_{ij} \sum_{\hat{t}_j > \hat{t}_i} \epsilon(t - \hat{t}_j), \quad (1)$$

where $i = 1, \dots, N$, N being the numbers of units in the network, $\eta_i(t)$ is a Poisson noise, J_{ij} are the synaptic connections, $\epsilon(t)$ describes the response kernel to incoming spikes on neuron i , and the sum over \hat{t}_j runs over all pre-synaptic firing times following the last spike of neuron i . Namely, each pre-synaptic spike j , with arrival time \hat{t}_j , is supposed to add to the membrane potential a post-synaptic potential of the form $J_{ij}\epsilon(t - \hat{t}_j)$, where

$$\epsilon(t - \hat{t}_j) = K \left[\exp\left(-\frac{t - \hat{t}_j}{\tau_m}\right) - \exp\left(-\frac{t - \hat{t}_j}{\tau_s}\right) \right] \Theta(t - \hat{t}_j) \quad (2)$$

where τ_m is the membrane time constant (here 10 ms), τ_s is the synapse time constant (here 5 ms), Θ is the Heaviside step function, and K is a multiplicative constant chosen so that the maximum value of the kernel is 1. The sign of the synaptic connection J_{ij} sets the sign of the post-synaptic potential's change, so there's inhibition for negative J_{ij} and excitation for positive J_{ij} . When the membrane potential $h_i(t)$ exceeds the spiking threshold θ_{th}^i , a spike is scheduled, and the membrane potential is reset to the resting value zero.

We want to mimic the spontaneous activity of cortical networks in vitro, in the absence of external stimulation. There are many different possible causes of noise in the system. Here, we focus on the effects of Poisson noise, therefore $\eta_i(t)$ is modelled as

$$\eta_i(t) = J_{\text{noise}} \sum_{\hat{t}_{\text{noise}} > \hat{t}_i} \epsilon(t - \hat{t}_{\text{noise}}). \quad (3)$$

The times \hat{t}_{noise} are randomly extracted for each neuron i , and J_{noise} are random strengths, extracted independently for each neuron i and time \hat{t}_{noise} . The intervals between times \hat{t}_{noise} are extracted from a Poissonian distribution $P(\delta t) \propto e^{-\delta t/(N\tau_{\text{noise}})}$, while the strength J_{noise} is extracted from a Gaussian distribution with mean \bar{J}_{noise} and standard deviation $\sigma(J_{\text{noise}})$. This describes the noisy environment in which our network is embedded, in the absence of any external stimulation.

As shown in many raster plot of in vitro spontaneous dynamics with neuronal avalanches, there is often a small subset of units which has a higher spiking rate than the other units. These units with spontaneous higher spiking rate are modelled here as a subset of units with lower spiking threshold. These units with lower spiking threshold are therefore more sensitive to the Poissonian noise which acts on the membrane potentials of all the units of the network. If some of these low-threshold units belongs to one of the stored pattern and have consecutive phases in this pattern, then it may happen that these units are able to initiate a collective replay of the pattern. To check this hypothesis, therefore, we imagine that for each stored pattern there is a small subset of $Z = N/30$ units, with consecutive phases in the pattern, that have low spiking

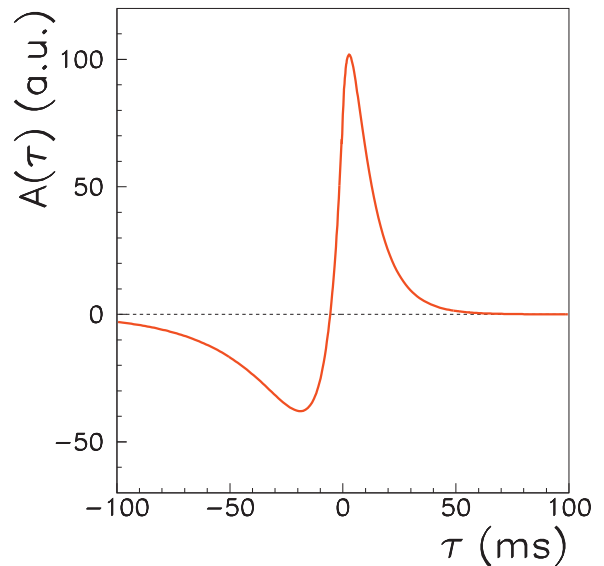


Fig. 1. Plot of the learning window $A(\tau)$ used in the learning rule to model STDP effects. The parameters of the function $A(\tau)$ are determined by fitting the experimental data reported in Bi and Poo (1998).

threshold θ_{th1} . These low threshold units will be more sensitive to noise, and their activation may eventually trigger the replay of the stored patterns. While the others $N - PZ$ units will have threshold θ_{th2} .

Numerical simulations of the dynamics are performed for a network with P stored patterns, where connections J_{ij} are determined via a learning rule previously introduced in Scarpetta and Giacco (2012), Scarpetta et al. (2010, 2011, 2001, 2002), Yoshioka et al. (2007). The connections values are frozen, and the collective dynamics is studied.

Therefore, following Scarpetta and Giacco (2012), the connections J_{ij} due to the learning of the periodic pattern μ is simply given by

$$J_{ij}^\mu = \sum_{n=-\infty}^{\infty} A(t_j^\mu - t_i^\mu + nT^\mu) = \sum_n A\left(\frac{\phi_j^\mu}{2\pi\nu^\mu} - \frac{\phi_i^\mu}{2\pi\nu^\mu} + \frac{n}{\nu^\mu}\right), \quad (4)$$

where t_j^μ (t_i^μ) is the spike time of unit j (i) in the pattern μ . The learning window $A(\tau = t - t')$ is the measure of the strength of synaptic change when a time delay τ occurs between pre and post-synaptic activity (Fig. 1). The stored patterns are defined as precise periodic sequence of spikes, i.e. spike-phase coded patterns, as the ones shown in Fig. 2, made up of one spike per cycle, and each spike has a phase ϕ_j^μ randomly chosen from a uniform distribution in $[0, 2\pi)$. The set of timing of spikes of unit j in pattern μ is $t_j^\mu + nT^\mu = (\phi_j^\mu)/(2\pi\nu^\mu) + n/\nu^\mu$, where $\nu^\mu = 1/T^\mu$ is the oscillation frequency of the neurons in the stored pattern. Thus, each pattern μ is represented through the frequency ν^μ and the specific phases of spike ϕ_j^μ of the neurons $j = 1, \dots, N$.

When multiple phase coded patterns are stored, the learned connections are simply the sum of the contributions from individual patterns, namely

$$J_{ij} = \sum_{\mu=1}^P J_{ij}^\mu. \quad (5)$$

As discussed in Scarpetta and Giacco (2012), the function $A(\tau)$ used satisfies the balance condition $\int_{-\infty}^{\infty} A(\tau) d\tau = 0$. This assures that in the connection matrix the summed excitation $(1/N) \sum_{i,j} J_{ij}$ and

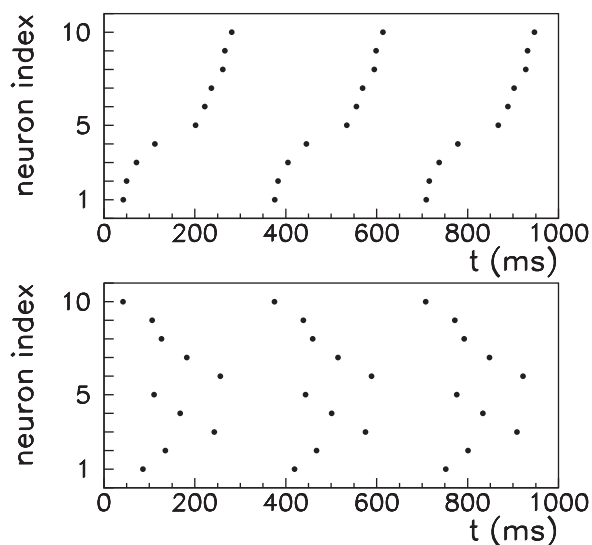


Fig. 2. Examples of two periodic spatiotemporal (phase-coded) patterns of spikes that are stored in our IF network. Only 10 units (randomly chosen) are shown.

the summed inhibition $(1/N)\sum_{i,j} J_{ij}$ are equal in the thermodynamic limit.

2.1. Emerging of collective patterns

The recurrent network with N LIF units, with connections fixed to the values calculated in Eq. (4) for different values of P is studied. Following Scarpetta and Giacco (2012), the response of the system to a cue external stimulation, in absence of noise, is illustrated in Fig. 3. A short cue with $M=300$ spikes with the proper phase relationship is able to induce the persistent replay of the stored pattern in a proper region of parameters, i.e. for low spiking thresholds. While at high threshold, such as in Fig. 3c, the cue stimulation only trigger a short transient replay, and at even higher threshold no activity is triggered by the stimulation.

In the regime of correct replay, shown in Fig. 3a and b, we check that if the partial cue is taken from pattern $\mu=2$, the neurons phase relationships recall the phase of pattern $\mu=2$ (uncorrelated with pattern $\mu=1$) (not shown).

Note that, after the short cue presentation, the retrieval dynamics has the same phase relationship among units as the stored pattern, but the replay may happen on a time scale different from the scale used to store the pattern, and the collective spontaneous dynamics is a time compressed (or dilated) replay of the stored pattern. The time scale of replay changes slightly with spiking threshold. In the example of Fig. 3a and b, the time scale of the retrieval dynamics is faster at lower threshold, and is different than the time scale used to learn the patterns. The time scale of replay activity also depends on ν^μ , as studied in Scarpetta and Giacco (2012). Here we focus on the case $\nu^\mu=3$ Hz because the corresponding time scale of the retrieval dynamics is such that the oscillations frequency is in the range of theta oscillations. The storage capacity, defined as the maximum number of encoded and successfully retrieved patterns, has been studied in Scarpetta and Giacco (2012) when the network respond to a short cue stimulation.

The storage capacity, as defined in Scarpetta and Giacco (2012), is shown as a function of the spiking threshold θ_{th} , in Fig. 4a, when $M=N/10$ spikes are used as cue, and $\nu^\mu=3$ Hz. For the proper values of threshold and for P lower than P_{max} , the evoked retrieval is successful (i.e. cue with a few spikes ($M=N/10$) is able to selectively activate the self-sustained replay of the stored pattern). We also show, for the region of correct evoked replay, the value of

the oscillation frequency of collective activity during the replay in Fig. 4b. At spiking threshold higher than a critical value θ_{th}^{crit} no persistent replay was possible for any value of P in response to the cue stimulation. Following results of Scarpetta and Giacco (2012), and Fig. 4, we estimate this critical point when $N=3000$, $\nu=3$ Hz to be about $\theta_{th}^{crit} \simeq 95$. At thresholds close to this critical value the network responds to cue with a transient activity that is a short replay of the stored pattern, but not with a persistent replay.

The critical regime, near the phase transition, is investigated here, but in the absence of any external cue stimulation ($M=0$). While in previous works (Scarpetta and Giacco, 2012; Scarpetta et al., 2010; Yoshioka et al., 2007) we studied the dynamics triggered by a short stimulation cue, in the following we investigate the spontaneous dynamics without any cue stimulation, in the presence of Poissonian noise only.

While in the region of persistent replay the evoked dynamics is robust wrt noise, in the region near the critical point the system is more sensitive to noise, therefore it is important to focus on effects of noise in this region in the absence of cue stimulation. Notably in this critical region it is the noise itself which may initiate a short replay, without any external trigger.

In the following therefore we study if a Poissonian noise, in a network with the proper connectivity as ours, is able to induce transient pattern replay, in the absence on any cue stimulation. This is motivated also by recent literature on the intriguing relationship between evoked and spontaneous cortical activity, and on the pattern replay observed in the post-task sleep. Indeed during sleep the reactivation of patterns stored in the connectivity is clearly not triggered by sensory stimulation but induced by noise itself spontaneously.

3. Effects of noise in the spontaneous critical regime, in absence of any cue stimulation

We investigate here if, even in absence of external cue stimulation, collective patterns of activity, reminiscent of stored patterns, emerge spontaneously, induced by noise. We therefore study the network spontaneous dynamics in the critical regime, in absence of any cue stimulation, in the presence of a Poissonian noise. We focus here on the critical behavior observed near the dynamical phase-transition, between the region of permanent replay and the region of no-replay. Figs. 5–7 show the spontaneous dynamics of a network of $N=3000$ units, $P=2$ patterns stored in the connectivity, and noise given by Eq. (3) with $\tau_{noise}=1$ ms, $\bar{J}_{noise}=0$, $\sigma(J_{noise})=5$, in the absence of external stimulation. A subset of $N_1=200$ units have a low spiking threshold $\theta_{th1}=26$ (to model the heterogeneity observed in vitro dynamics), and the other $N-N_1=2800$ units have $\theta_{th2}=80, 90, 105$, respectively, in Figs. 5–7. Different values of $\theta_{th1}=20, 22, 24, 26, 28, 30$ have been investigated, as well different values of noise variance, and the phenomena observed are similar but less pronounced. So we fix these values of $\theta_{th1}=26$, $\sigma(J_{noise})=5$ and we show the spontaneous behavior as a function of threshold of the majority of units θ_{th2} .

At lower threshold, $\theta_{th2}=80$ in Fig. 5 the collective replay of the pattern $\mu=1$, in absence of any cue stimulation, is triggered spontaneously and lasts for a very long time. The raster plot of the network dynamics is shown with a different sorting of units on the vertical axes, showing that pattern $\mu=1$ is replayed. The replay is initiated since the noisy units have triggered it, and the replay is permanent and very robust in this regime. Fig. 6 shows that at $\theta_{th2}=\theta_{th2}^c=90$, from time to time, there is a short transient replay of the patterns. Each replay event lasts for a limited interval of time and then fades away. In Fig. 6a, the units are sorted according to increasing values of stored phases in pattern $\mu=1$, while in Fig. 6b units are sorted according to $\mu=2$. When pattern $\mu=1$ is recalled,

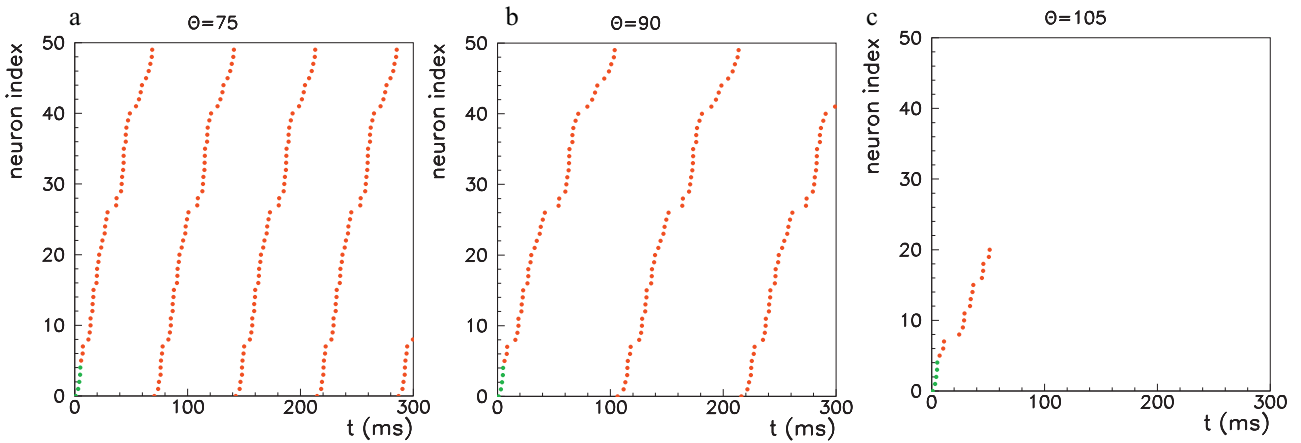


Fig. 3. Network dynamics at different values of spiking threshold θ_{th} . In these simulations a cue external stimulation (M spikes, shown in green) is used, and a single value of spiking threshold is used for all units of the network, and the noise is absent. At proper value of the spiking threshold the cue initiates a persistent retrieval of the spatiotemporal pattern, while at too high threshold the network is silent or with only a short transient retrieval. Example of selective successful evoked retrieval (a, b) and example of failure (c) are shown. The raster plot of 50 units (randomly chosen) is shown sorted on the vertical axis according to increasing values of phase ϕ_i^1 of the first stored pattern $\mu = 1$. The network has $N = 3000$ IF neurons, $\theta_{th} = 75, 90, 105$, respectively, in a, b and c. Connections are given by Eq. (5) with $P = 2$ stored patterns at $\nu^\mu = 3$ Hz.

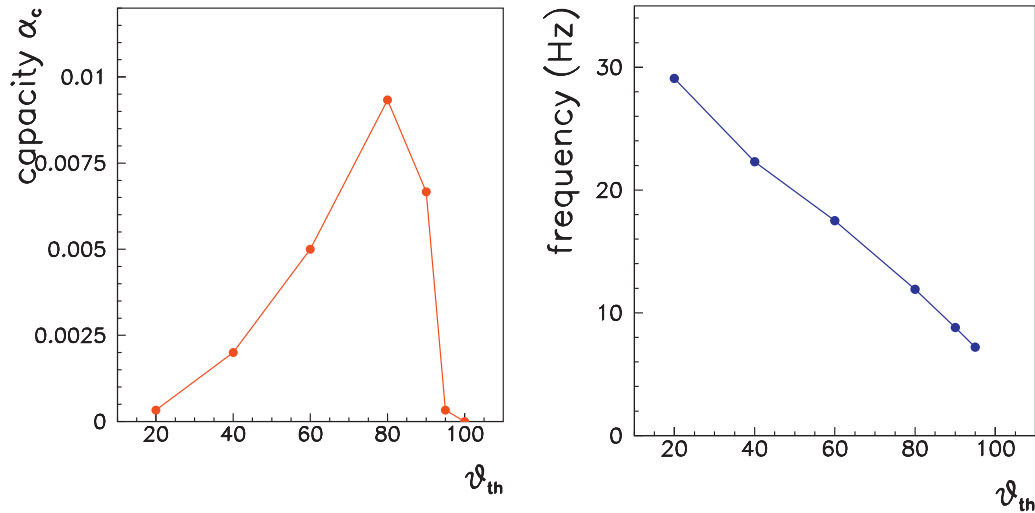


Fig. 4. (a) Storage capacity $\alpha^c = P_{max}/N$, defined as in Scarpetta and Giacco (2012), is shown at $\nu^\mu = 3$ Hz as a function of spiking threshold, when $M = N/10$ spikes are used as cue stimulation. As always in this paper the number of units is $N = 3000$. The figure shows that near $\theta_{th}^{crit} \sim 95$ there is a transition from a region of evoked persistent replay to a region of no-replay. (b) Frequency of the collective oscillations of the network dynamics during evoked replay, as a function of spiking threshold, for $P = P_{max}$.

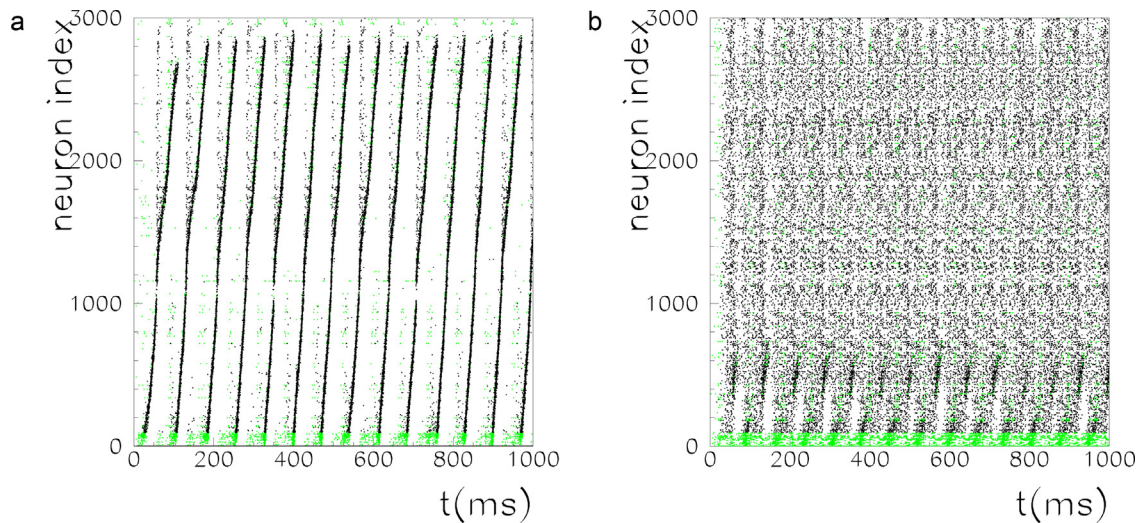


Fig. 5. Spontaneous dynamics, without any cue stimulation, in a noisy environment ($\tau_{noise} = 1$ ms, $\bar{J}_{noise} = 0$, $\sigma(J_{noise}) = 5$) with $\theta_{th2} = 80$, $\theta_{th1} = 26$, $N = 3000$, $\nu^\mu = 3$ Hz. Spikes are shown with units sorted on the vertical axes according to order of units in the first (a) or second (b) stored pattern. Units with threshold $\theta_{th1} = 26$ are shown in green, the other in black. Permanent replay of first pattern is observed, initiated by the noisy units (low threshold, more sensitive to noise).

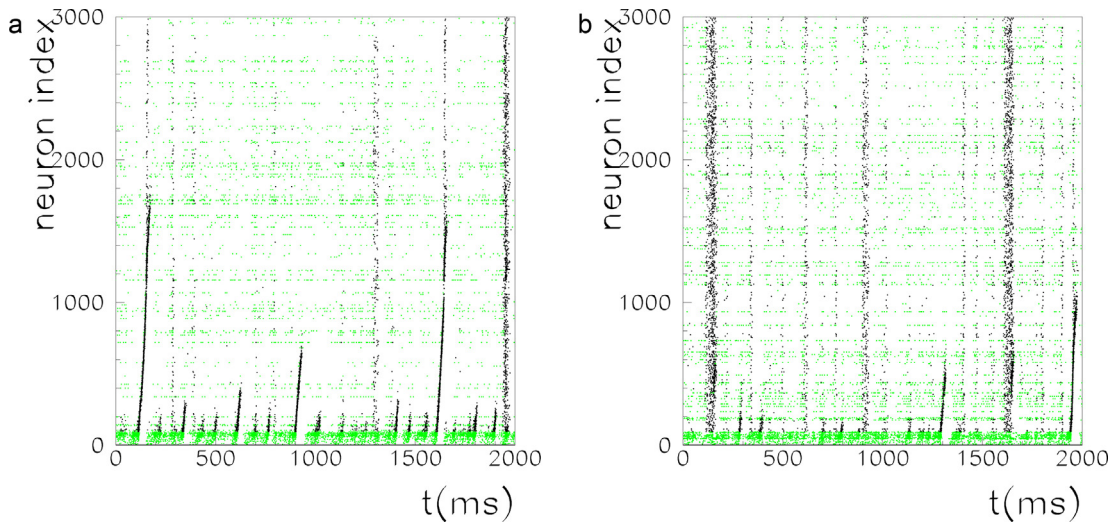


Fig. 6. Spontaneous dynamics without any cue stimulation in a noisy environment ($\tau_{noise} = 1$ ms, $\bar{J}_{noise} = 0$, $\sigma(J_{noise}) = 5$) with $\theta_{th2} = 90$, $\theta_{th1} = 26$, $N = 3000$, $\nu^\mu = 3$ Hz. Spikes are shown with units sorted on the vertical axes according to order of units in the first (a) or second (b) stored pattern. Units with threshold $\theta_{th1} = 26$ are shown in green, the other in black. Short transient replays of the two patterns are initiated, from time to time.

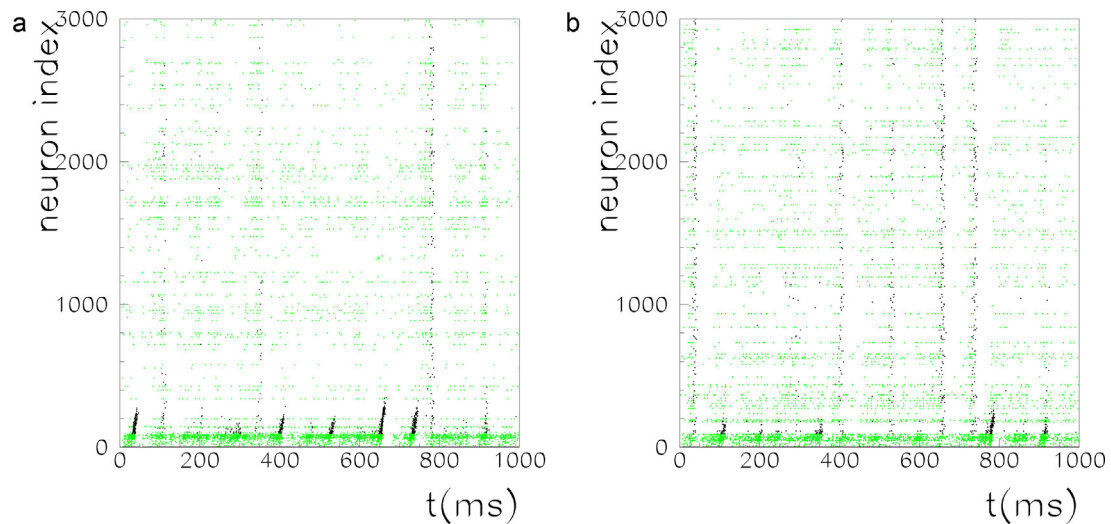


Fig. 7. Spontaneous dynamics without any cue stimulation in a noisy environment ($\tau_{noise} = 1$ ms, $\bar{J}_{noise} = 0$, $\sigma(J_{noise}) = 5$) with $\theta_{th2} = 105$, $\theta_{th1} = 26$, $N = 3000$, $\nu^\mu = 3$ Hz. Spikes are shown with units sorted on the vertical axes according to order of units in the first (a) or second (b) stored pattern. Units with threshold $\theta_{th1} = 26$ are shown in green, the other in black. No replay is observed.

a short sorted sequence of spikes appears in Fig. 6a, while when pattern $\mu = 2$ is retrieved, a short sorted sequence of spikes appears in Fig. 6b. At higher threshold, such as $\theta_{th2} = 105$ in Fig. 7 no replay is observed, and only noisy activity is observed. It is notably that, at intermediate value $\theta_{th2} = 90$ this intermittent replay is observed here, in absence of any external cue stimulation. We observe a sort of spontaneous reactivation of all stored patterns, as the one that seems to happen during sleep, useful for memory consolidation.

3.1. The critical point

In order to characterize this transition between a regime of spontaneous permanent retrieval (in the absence of cue stimulation) to a regime of no-retrieval, we measure the variance and the mean value $m^\mu(T^w)$ of the order parameter.

In analogy with the Hopfield model, we introduce an order parameter to estimate the overlap between the network collective activity during the spontaneous dynamics and the stored phase-coded pattern. This quantity is 1 when the phases ϕ_j of neurons j

coincides with the stored phases ϕ_j^μ , and is close to zero when the phases are uncorrelated with the stored ones.

Therefore, we consider the following time-dependent dot product $|M^\mu(t, T^w)| = \langle \xi(t) | \xi^\mu \rangle$ where ξ^μ is the vector having components $e^{i\phi_j^\mu}$, namely:

$$|M^\mu(t, T^w)| = \left| \frac{1}{N} \sum_{\substack{j=1, \dots, N \\ t < t_j^* < t + T^w}} e^{-i2\pi t_j^*/T^w} e^{i\phi_j^\mu} \right| \quad (6)$$

where t_j^* is the spike timing of neuron j during the spontaneous dynamics, and T^w is an estimation of the period of the collective spontaneous periodic dynamics.

Then, we consider the mean value of the order parameter:

$$m^\mu(T^w) = \frac{1}{\langle N_s \rangle} \langle |M(t, T^w)| \rangle \quad (7)$$

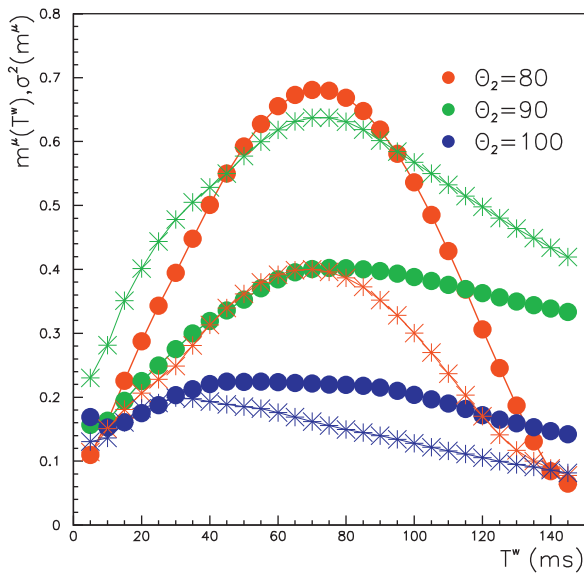


Fig. 8. Mean value $m(T^w)$ of the order parameter for pattern $\mu = 1$ (circles) and its fluctuations (stars) as a function of the chosen window T^w , for different θ_{th2} . $N = 3000$, $\theta_{th1} = 26$ and $\nu^\mu = 3$ Hz as in Figs. 5–7.

where the average $\langle \dots \rangle$ is done on the starting time t of the window, and $\langle N_s \rangle$ is the average number of spikes on a window of time T^w .

The fluctuations of the order parameter are defined by

$$\sigma^2(|M^\mu(t, T^w)|) = \frac{1}{\langle N_s \rangle^2} [\langle |M(t, T^w)|^2 \rangle - \langle |M(t, T^w)| \rangle^2]. \quad (8)$$

The order parameter $|M^\mu(T^w)|$, at the optimal time-window T^w , i.e. with T^w which maximizes $|M^\mu(T^w)|$, measures the similarity in the sequence of spiking neurons and in the phase lag between the spikes. This is a suitable choice especially when the replay of a spatio-temporal pattern has to be detected independently from the compression of the time scale. Note that if we have a spike train that is not periodic, we cannot define the period, however we can define the order parameter looking at the time-window T^w which maximizes $|M^\mu(T^w)|$.

In Fig. 8 stars are fluctuations while circles are the mean value $m^\mu(T^w)$, for three values of $\theta_{th2} = 80, 90, 100$, and different values of the time-window T^w . We simulate $\theta_{th1} = 20, 22, 24, 26, 28, 30$, and we plot results for $\theta_{th1} = 26$ (which is the value which gives higher order parameter) in Fig. 8. So we evaluate the mean value and the fluctuations of the order parameter for the value of T^w which maximizes it.

In Fig. 9 the mean value m^μ of order parameter and its fluctuations $\sigma^2(|M^\mu|)$ are shown as a function of spiking threshold θ_{th2} , when $\theta_{th1} = 26$ and for the optimal T^w . At low spiking threshold ($\theta_{th2} = 80$) m^μ is high and $\sigma^2(|M^\mu|)$ is low, indicating that, as shown in Fig. 5 the noise is able to initiate a successful retrieval (persistent replay) of the stored pattern. At high threshold ($\theta_{th2} = 100$) either the mean value and the fluctuations of the order parameter are low. At the critical point ($\theta_{th2} = 90$) between the two regimes, the fluctuations of the order parameter are maximized, as expected in a continuous phase transition.

The transition is then characterized by a dynamical order parameter, in terms of a dynamical phase transition, between two different dynamical behaviors (all in the absence of any external cue stimulation). A critical behavior, with maximization of fluctuation of order parameter at the critical threshold, is observed here as in continuous phase transitions. Notably recent results (Tagliazucchi et al., 2012) show, using large scale fMRI measures, that the brain spent most time near a critical point. Future works will focus on

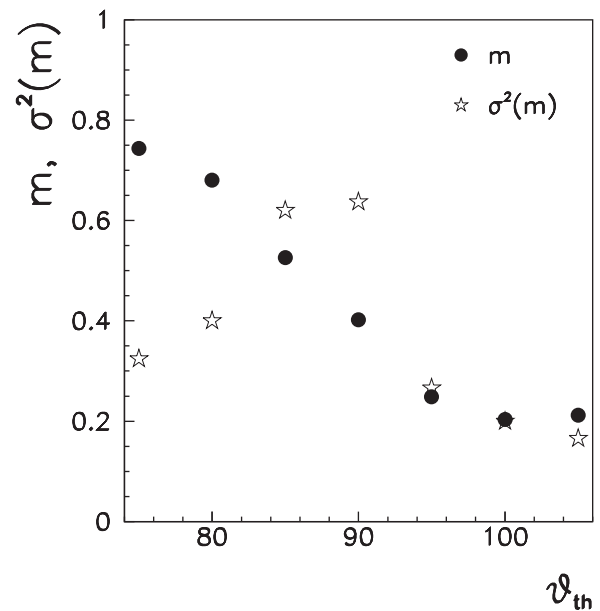


Fig. 9. Mean value $m(T^w)$ of the order parameter, at optimal T^w , and its fluctuations as a function of θ_{th2} , for $N = 3000$, $\theta_{th1} = 26$ and $\nu^\mu = 3$ Hz as in Figs. 5–7.

the spontaneous activity at the critical threshold from the point of view of neural avalanches.

4. Discussion

Here, using an STDP-based learning process (Scarpetta and Giacco, 2012; Scarpetta et al., 2011, 2011, 2009; STDP, 2008), we store in the connectivity of a LIF network, several spatiotemporal spike patterns, and we find that, depending on the excitability of the network, different working regimes are possible, with collective, transient or persistent, replay activity induced simply by noise. In our model not only the order of activation of the sequence is preserved, but also the precise phase relationship among units of the periodic spatiotemporal pattern.

While in the region of persistent replay the system is robust w.r.t. noise, as discussed in Scarpetta and Giacco (2012), in the region near the critical point the system is more sensitive to noise, as shown here. In the critical regime indeed, the different sequences stored in the connectivity may be reactivated transiently, from time to time, due to noise, and in absence of any cue stimulation.

We show that at the critical point the fluctuations of the order parameter are maximized, since the collective activity is made of different sequences of different lengths, which give rise to correlated activity on the top of a noisy uncorrelated activity.

Recently there is renewed interest in reverberatory activity (Lau and Bi, 2005) and in cortical spontaneous activity (Ringach, 2009; Pastalkova et al., 2008) whose spatiotemporal structure seems to reflect the underlying connectivity, which in turn may be the result of the past experience stored in the connectivity.

Similarity between spontaneous and evoked cortical activities has been shown to increase with age (Berkes et al., 2011), and with repetitive presentation of the stimulus (Han et al., 2008). Interestingly, in our IF model, in order to induce spontaneous patterns of activity reminiscent of those stored during the learning stage, a limited number of spikes with the right phase relationship are sufficient, and more importantly, even in absence of sensory stimulus, a noise with the right phase relationships is able to induce a pattern of activity reminiscent of a stored pattern. Therefore, by adapting the network connectivity to the phase-coded patterns observed during the learning mode, the network dynamics builds a

representation of the environment and then, during proper conditions, such as sleep or rest, the dynamical attractors corresponding to the stored patterns are transiently activated by noise.

Regarding place cells for example, a possible scenario is that, the pattern activated repeatedly during experience is stored in the connectivity, and then activated during sleep when the network is near critical point and noise is able to initiate short replay sequences, in absence of sensory stimulation. During exploration, when the animal visit adjacent place fields, the evoked activity of the place cells is a sequence of spikes with the consecutive activation of place cells, then also inside a single theta cycle the cells are activated in the right sequence. During sleep, in the absence of external inputs, the role of recurrent connections increases, probably due to an increase of excitability via neuromodulators or other mechanisms, and the spontaneous activity of the network shows temporarily short replay of stored patterns, probably initiated simply by the noise, as proposed in this work.

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