Reliability and synchronization in a delay-coupled neuronal network with synaptic plasticity

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We investigate the characteristics of reliability and synchronization of a neuronal network of delay-coupled integrate and fire neurons. Reliability and synchronization appear in separated regions of the phase space of the parameters considered. The effect of including synaptic plasticity and different delay values between the connections are also considered. We found that plasticity strongly changes the characteristics of reliability and synchronization in the parameter space of the coupling strength and the drive amplitude for the neuronal network. We also found that delay does not affect the reliability of the network but has a determinant influence on the synchronization of the neurons.

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I. INTRODUCTION

Many nonlinear systems present the ability to repeat the same response to the same complex input signal even when starting from different initial conditions [1]. This ability, known as reliability or consistency, has been studied recently in different nonlinear systems [2–4]. It is known that independent phase oscillators can be synchronized by weak independent additive noise [5], but the reliability is deteriorate when they are coupled [6]. Understanding the reliability of dynamical systems is essential for information transmission and for the reproduction of spatiotemporal patterns in biological systems. Reliability tests could be applied in noninvasive diagnostic procedures to detect changes in system parameters due to aging, catastrophic events, or other system changes [7,8].

In a neuronal system, it is know that noise play a positive role enhancing the response of the sensory system [9–11]. The reliability of the firing sequence of a single neuron has also been studied demonstrating that a neuron that is repeatedly driven by a random drive signal can fire a consistent spike train with a high-temporal precision [1]. However, in the brain, the neurons are interconnected forming eventually complex neuronal networks. Understanding the response of neuronal networks to external stimulus is essential to unveil some functional features of such complex system as the brain. The reliability in neuronal response to a common input is related to many brain functions including perception, recognition, or visual working memory [12].

Another important property associated to neural networks is the capability of its constituents to organize their response in a synchronous way [13]. Synchronization appears as a multiscale phenomenon in the brain [14] and it is related, among other tasks, to information processing [15]. Thus, understanding the basic mechanisms underlying both reliability and synchronization has important implications for neuronal systems.

The concept of reliability has been interpreted as another formula of generalized synchronization [16,17], and it has been believed that the characteristics of reliability is similar to those of synchronization. However, no systematic investigation of the comparison between reliability and synchronization has been made. Here, the reliability and synchronization can be clearly distinguished from each other by using a network system. Reliability is the ability of the network to reproduce the same response when the network is repeatedly driven by an identical input signal, whereas synchronization is the ability for each neuron to show an identical temporal behavior when interacting on a network. It is very important to clarify the conditions for achieving reliability or synchronization that may be related to different information processing or functional roles in neuronal networks in the brain, as well as for other network dynamical systems.

In this paper we study the characteristics of reliability and synchronization in the response of a neuronal network to a repeated external stimulus. We characterize reliability by a measure that quantify the phase difference between sets of the response patterns for all the neurons that are repeatedly driven by the same external stimulus, when the dynamics of the neurons start from different initial conditions. On the contrary, synchronization is characterized by a measure that quantify the phase difference between the response pattern of each neuron in the network. We study the effect of including synaptic plasticity in the excitatory connections between the neurons and show how the characteristics of reliability and synchronization are affected by the synaptic plasticity. We also explore the role of the delay in the connections.

II. MODEL

We study a network composed of one thousand integrate-and-fire (IF) neurons delay-coupled through chemical synapses. The membrane potential $v_i(t)$ of neuron $i (i = 1,\dots,N)$ at its soma obeys the following equation:

$$\dot{v}_i(t) = -\frac{1}{\tau_m} v_i(t) + \frac{1}{C_m} I_i(t), \tag{1}$$

where $\tau_m = 10$ ms and $C_m = 250$ pF are the membrane time constant and capacitance, respectively. $I_i(t)$ is the synaptic current arriving at the soma and take into account all the spikes

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arriving from recurrent connections or from the external drive input. These spikes contributions are modeled as follows:

$$I_i(t) = \frac{1}{N_c}\sum_j w_{ij}\sum_k f\big(t - t_j^k - D\big), \quad (2)$$

where the first summation runs over different synapses with postsynaptic potential (PSP) amplitude w_{ij}, while the second sum extends over the spikes arriving at synapse j, at time $t = t_j^k + D$, where t_j^k is the emission time of kth spike at neuron j, and $D = 10$ ms is the transmission delay. The function $f(t)$ stands for the contribution of the incoming spikes and is represented as an α function:

$$f(t) = \frac{e}{\tau_\alpha} t e^{-t/\tau_\alpha}, \quad (3)$$

where τ_α is the rise time. Initially, we consider a homogeneous interaction between the neurons, i.e., $w_{ij} = w$. Our network is composed by 80% of neurons receiving excitatory connections and 20% receiving inhibitory connections. We interconnect them conforming a sparse network, with 10% of randomly chosen connections between the neurons. To keep balanced the network, the inhibitory synapses are four times stronger than the excitatory ones. As the external signal we assume an independent Poissonian spike train of amplitude D_n acting over each neuron. For the shake of clarity, neurons receive the same independent fluctuating spike train in all trials. Simulation were done using the neuronal simulator package NEST [18].

A. STDP synaptic rule

Spike Timing Dependent Plasticity (STDP) is a phenomenon related to the change in the synaptic weight w_{ij} between a pair of neurons sharing excitatory connections [19]. For a single pair of presynaptic and postsynaptic action potentials with time difference $\Delta t = t_{post} - t_{pre}$ STDP induces a change in the synaptic efficacy Δw given by [20]

$$\Delta w = \begin{cases} \lambda f_-(w)K(\Delta t) & \text{if } \Delta t \leqslant 0 \\ \lambda f_+(w)K(\Delta t) & \text{if } \Delta t > 0 \end{cases}.$$

The temporal filter $K(\Delta t) = \exp(- \mid \Delta t \mid \tau)$ implements the spike-timing dependence of the learning. The time constant τ determines the temporal extent of the learning window. The learning rate λ scales the magnitude of individuals weight changes. The temporal asymmetry of the learning is represented by the opposite signs of the weight changes for positive and negative time differences. The updating functions $f_+(w) = (1 - w)^\mu$ and $f_-(w) = \alpha w^\mu$ scale the synaptic changes and implement synaptic potentiation for $\Delta t > 0$, and depression otherwise [21]. In our simulations we used the typical parameter values: $\tau = 20$ ms, $\mu = 0.4$, $\alpha = 1.05$, and $\lambda = 0.005$.

B. Measurement

To characterize both reliability and synchronization in the activity of our network, we consider the phase of each neuron defined as [22]

$$\phi_i(t) = 2\pi \frac{t - \tau_k}{\tau_{k+1} - \tau_k}, \quad (4)$$

where τ_k is the time of the kth firing of the neuron i. To measure the reliability in the response of the network across different realizations we repeatedly drive each neuron with the same independent Poissonian spike train. We define the quantity: $r_i(t) = \frac{1}{n}\sum_{k=1}^n \sin^2(\frac{\phi_i(t)-\phi_i^k(t)}{2})$ being $\phi_i^k(t)$ is the phase of the neuron i obtained in the kth realization starting from different initial conditions. The summation runs over n different realizations. A spatiotemporal average of r_i,

$$R = \lim_{T\to\infty} \frac{1}{T}\int_0^T \left(\frac{1}{N}\sum_{i=1}^N r_i\right) dt, \quad (5)$$

measures the degree of reliability of the response of the system. The idea of this measure is to quantify the phase difference between sets of the response patterns of the network when the neurons are repeatedly driven by an identical external signal and their dynamics start form different initial conditions. Note that the phase difference is compared between the same neurons, but at different trials of the driving signals. For a consistent response of the system, the phase difference between the patterns is zero, giving a value of $R = 0$, while any inconsistent response of the system gives a phase difference larger than zero, resulting in values of $R > 0$.

To measure synchronization between the neurons, we use a similar index, $s_i(t) = \frac{1}{n_c(i)}\sum_{j\in n_c(i)} \sin^2(\frac{\phi_i(t)-\phi_j(t)}{2})$ where $\phi_j(t)$ is the phase of the neuron j and the summation runs now over the $n_c(i)$ connected neighbors of neuron i. We obtain a measure of the synchronization of the network in a particular realization by averaging over the neurons and over time,

$$S = \lim_{T\to\infty} \frac{1}{T}\int_0^T \left(\frac{1}{N}\sum_{i=1}^N s_i\right) dt. \quad (6)$$

This measure quantify the phase difference between the response pattern of each neurons in the network. Note that the

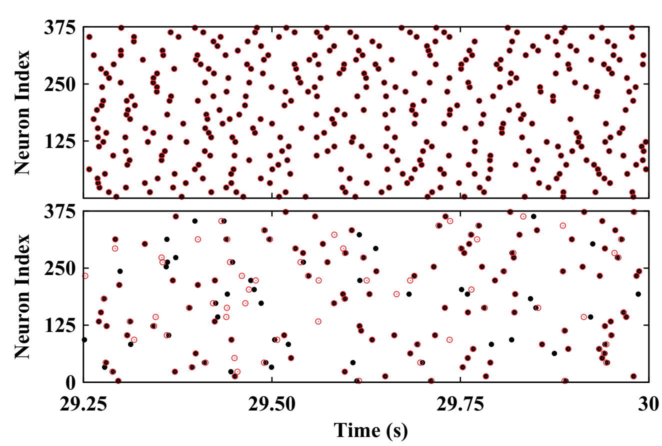

FIG. 1. (Color online) Raster plot of two simulation starting from different initial conditions (open circles and filled dots). The synaptic amplitudes are $w = 0.0$ pA (top) and $w = 1.5$ pA (bottom). The external signal amplitude is fixed to $D_n = 2.25$ pA. For a clear visualization, only a fraction of the neurons is shown.

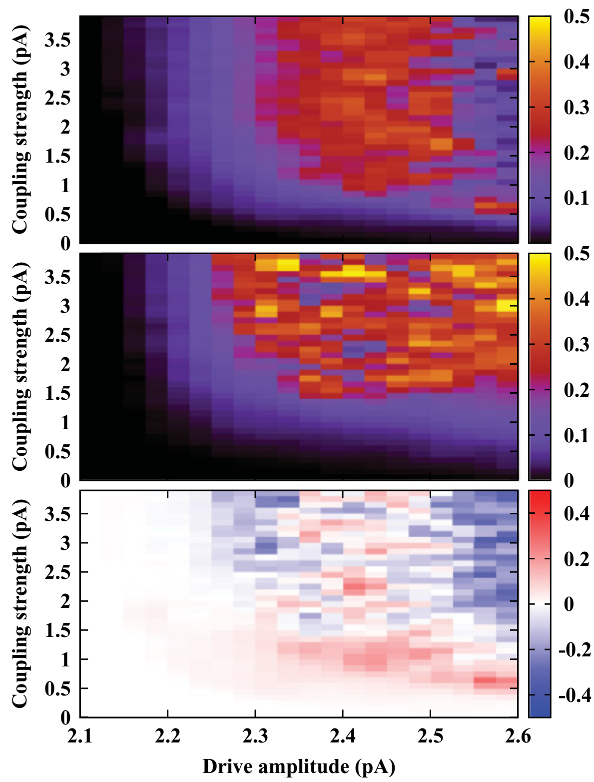

FIG. 2. (Color online) Reliability region determined by R. Perfect reliability is indicated by $R = 0$ (black areas) while an unreliably response of the network corresponds to $R > 0$. Upper panel: static synapses. Middle panel: nonlinear STDP is applied between excitatory connections. Bottom panel: difference between the two previous regions where an increase (decrease) of reliability is codified by a positive (negative) value.

phase difference is computed between the different neurons in the network during the same realization. When the network has a pattern response where the neurons fire in synchrony, this measure gives $S = 0$. On the contrary, for a desynchronous patterns we get $S > 0$.

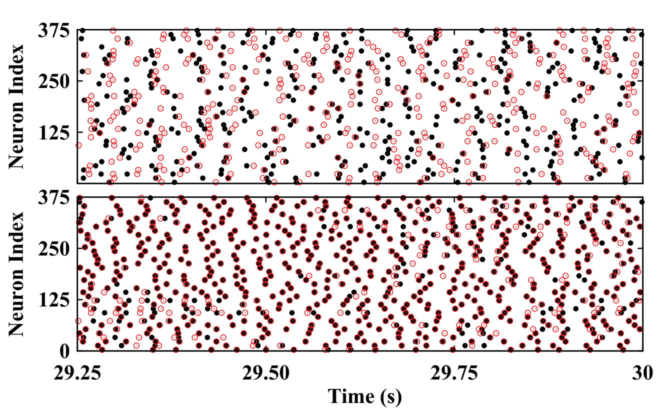

FIG. 3. (Color online) Raster plot of two simulations starting from different initial conditions. Top (bottom) panel corresponds to a simulation without (with) STDP. The parameters are $w = 1.1 pA$ and $D_n = 2.375 pA$. For a clear visualization, only a fraction of the network is shown.

III. RESULTS

A. Reliability region

Our first goal is to determine if our neuronal network responds consistently when an external drive is applied. To illustrate the scenario, Fig. 1 shows the raster plot of the activity of the network for different coupling strengths and a fixed value of the external drive amplitude. As it can be seen, the reliability of the network diminishes when the interaction between the neurons increases. It is also worth mentioning that the activity of the network is reduced due to an increase of the inhibition as the synaptic amplitude increases.

We compute the index R for different coupling intensities and drive signal strengths. The region where the system responds consistently is indicated as a black area in Fig. 2. The upper panel stands for the usual homogeneous static connections, i.e., $w_{ij} = w$. The middle panel shows the reliability regions when STDP is applied between excitatory connections. As it can be seen in the bottom panel, representing the difference between the two previous, the inclusion of the STDP increases the region of reliability at moderate coupling strengths and at high-drive amplitudes.

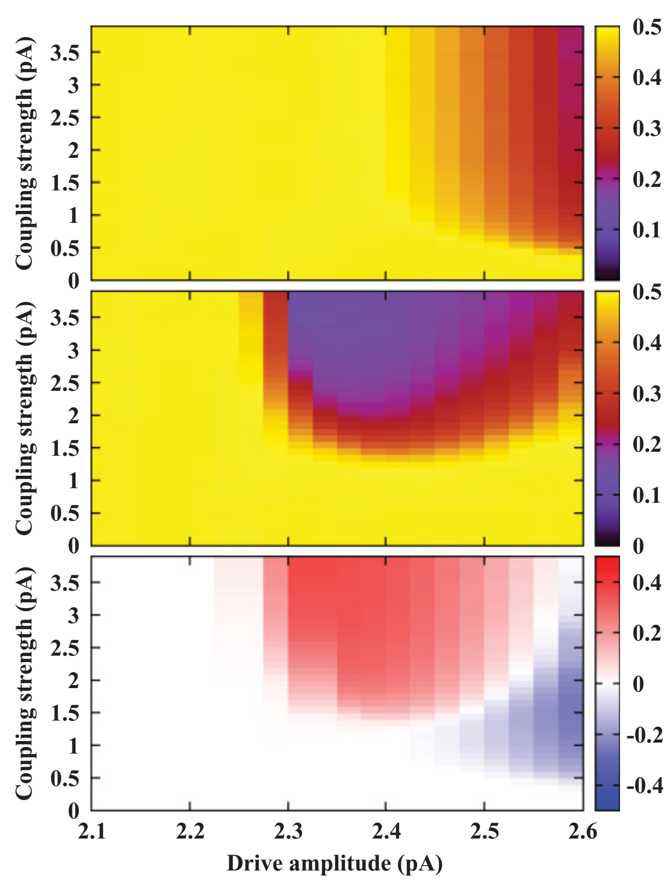

FIG. 4. (Color online) Synchronization region determined by S. Perfect synchronization is indicated by $S = 0$ while an asynchronous response of the network corresponds to $S > 0$. Upper panel: static synapses. Middle panel: nonlinear STDP is applied between excitatory connections. Bottom panel: difference between the two previous regions where an increase (decrease) of synchronization is codified by a positive (negative) value.

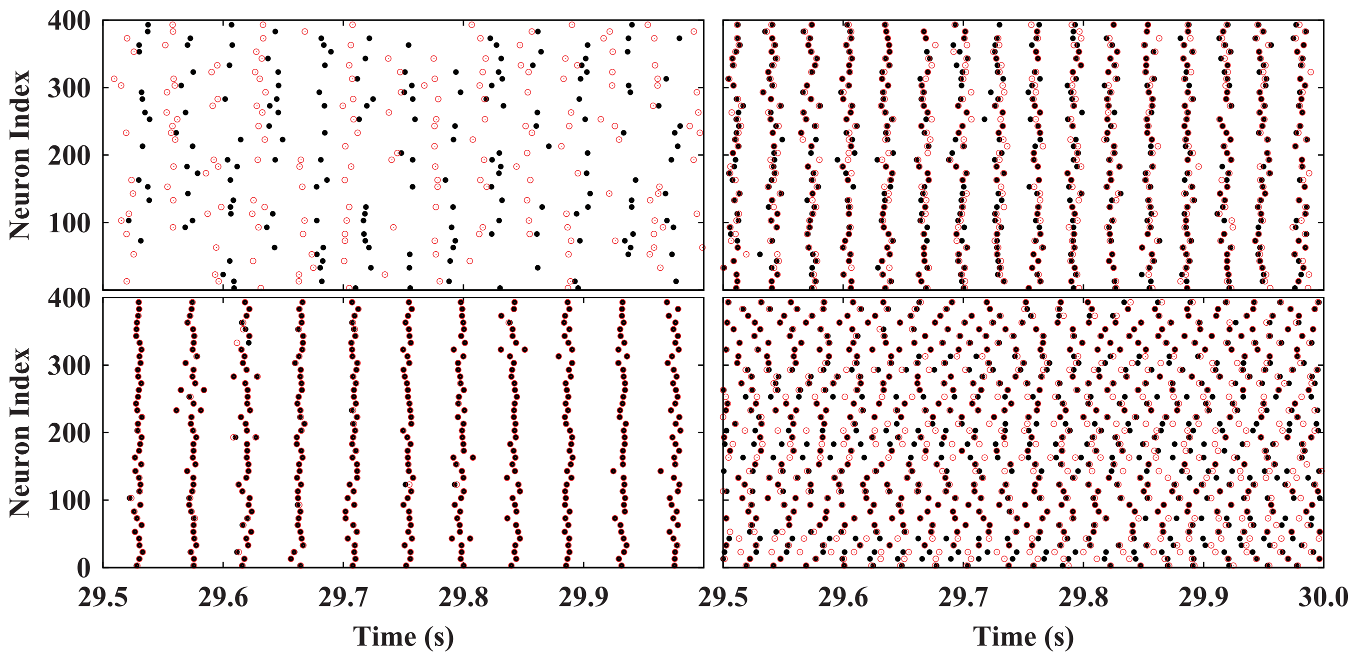

FIG. 5. (Color online) Raster plots for two simulation starting from two different initial conditions. Top (bottom) row corresponds to a simulation without (with) STDP. Parameters used: left column, $w = 3.0pA$ and $D_n = 2.35pA$; right column, $w = 1.0pA$ and $D_n = 2.6pA$. For visualizations purposes, only a fraction of the network is shown.

To illustrate what is the effect of the plasticity, Fig. 3 shows the raster plot of the network for the same coupling intensity and drive amplitude in both cases: without plasticity (upper panel) and when STDP is applied to excitatory synapses (lower panel). The inclusion of plasticity has two main effects: on one hand, there is an increase of the activity of the network due to the reinforcement of the excitatory weights. On the other hand, this increase of the activity leads to an enhancement of the reliability of the system. The neurons are now capable of reproducing the same pattern of activity even when the system starts from different initial conditions.

B. Synchronization region

We also determine the synchronization regions by computing the quantity S. Figure 4 shows, codified in colors, the values of the parameter S. The upper panel corresponds to the case of static conventional synapses while the middle row stands for simulations where the STDP is applied to the excitatory synapses. Perfect synchronization, i.e., a zero phase difference between the firing of the neurons, is codified by a value of $S = 0$ (black color) while any other state differing from perfect synchrony has a value $S > 0$. The bottom panel corresponds to the difference between the two regions. An increase (decrease) of the synchronization in the system is codified by a positive (negative) value. As it can be seen, we do not observe perfect synchronization in our simulations, being desynchronization (values of $S \sim 0.5$) predominant for static synapses. Only at high drive amplitudes a region where the parameter S is close to zero appears. On the contrary, the inclusion of STDP dramatically changes the scenario. At intermediates drive amplitudes and high coupling intensities, a large area of values of S close to zero appears indicating a region where the neurons fire more synchronously. To illustrate these results, Fig. 5 displays the raster plot of the network for different coupling strengths and drive amplitudes. The upper row corresponds to simulations with static synapses and the bottom row stands for simulations where the STDP is applied to the excitatory synapses. This figure corroborates the effect of the STDP. The reinforcement of the excitatory synapses leads to an increase of the activity of the network, and make the neurons to fire more synchronously as it can be seen in the left panel of Fig. 5. But plasticity can also have the opposite effect. At high drive amplitudes and moderates coupling strengths STDP diminishes drastically the synchrony of the network (see right panel of Fig. 5). In order to understand this effect, we plot in Fig. 6 the synaptic weights distribution for the cases presented in Fig. 5. For $w = 1.0pA$ and $D_n = 2.6pA$ STDP decreases the strength of the synapses (sharp distribution) with respect to the static synapses case, represented by a black line, yielding to

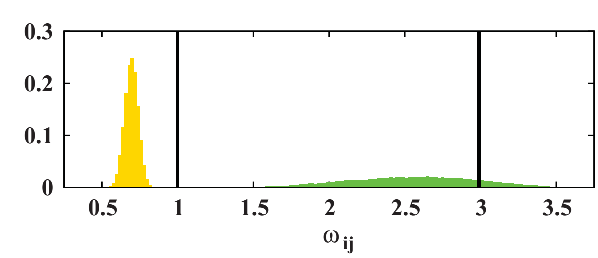

FIG. 6. (Color online) Distribution of the synaptic weights for two configurations. Broad distribution corresponds to $w = 3.0pA$ and $D_n = 2.35pA$. Sharp distribution corresponds to $w = 1.0pA$ and $D_n = 2.6pA$. The value of w in the absence of STDP is indicated by a black line in each case.

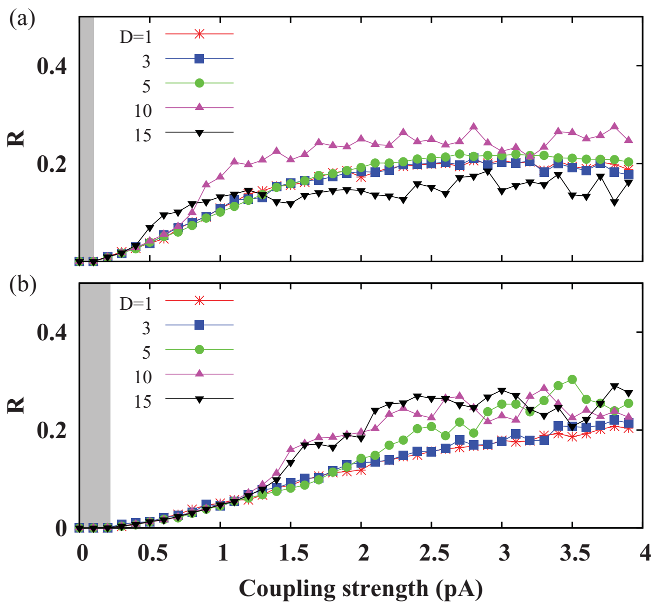

FIG. 7. (Color online) Dependence of R with the coupling and delay for (a) static synapses and (b) nonlinear STDP. Gray areas represent the regions of reliability. The drive amplitude is $D_n = 2.4pA$.

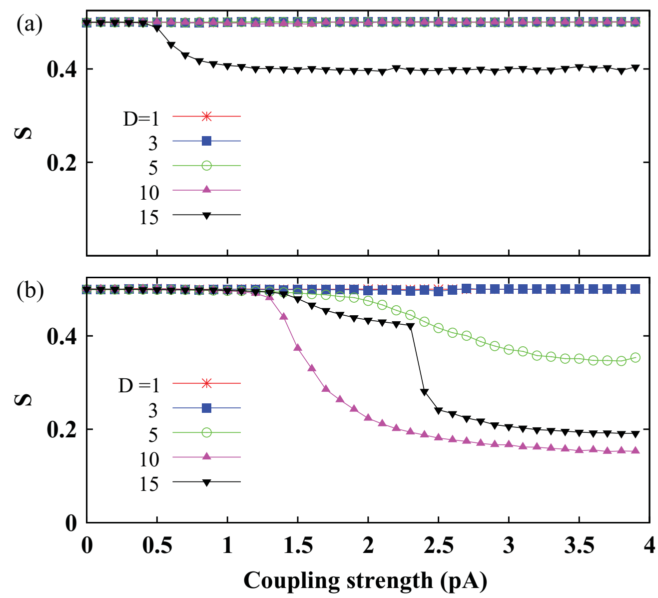

FIG. 8. (Color online) Synchronization parameter S as a function of the coupling and different values of the delay for (a) static synapses and (b) nonlinear STDP. The drive amplitude is $D_n = 2.4pA$.

a decrement of the synchrony of the network. For $w = 3.0pA$ and $D_n = 2.35pA$ (broad distribution) STDP enhance the synchrony of the network, although the distribution is much broad and the mean value is lower than the static synapse case, there is an increase of the strength of a significant fraction of the connections that it is associated with the enhancement of the synchronization in the network.

C. Dependence on the delay

Next, we explore how the conduction delay D affects the response of the network. We fix the drive amplitude D_n and compute the reliability and synchronization indexes R and S for different coupling and delay values. In Fig. 7 we show, as a function of the coupling intensity and for different delay values, the reliability parameter R. We observe that the delay does not affect the reliability or the enhancement of reliability in the network produced by STDP.

Figure 8 shows the synchronization index S as a function of the coupling intensity for different delay values. We observe, even in the absence of plasticity, whether the response of the network organizes in a synchronous manner depend on the delay value. This result is in accordance with other studies showing that the synchronization of a network of interacting neurons depend on the particular delay value of the connections [23–26]. When plasticity is taken into account, the delay has a crucial role in the synchronization of the network (see Fig. 8(b)).

IV. CONCLUSIONS

In summary, we have investigated the characteristics of reliability and synchronization of a network of interacting neurons described by the integrate-and-fire model. We have found that the system can respond consistently to an external driving stimulus and we have quantified the regions where reliability occurs by means of an order parameter based on the phase differences between the different pattern responses. Interestingly, we have found that synchronization appears in different region of the parameter space from the region for reliability, indicating that reliability and synchronization can be considered as different features for network systems. We have also studied the effect of synaptic plasticity induced by STDP rule between excitatory connections. We have found that STDP has a modulatory effect in both the reliability and synchronization of the system. For example, reliability is enhanced by STDP in the region of weak coupling strengths whereas it is suppressed by STDP when the drive amplitude is large. By contrast, synchronization is enhanced in the parameter region of moderate drive amplitudes and strong coupling while it is suppressed in the region of strong drive amplitude and weak coupling strength. We have found that the delay does not affect the reliability of the network. We also corroborate that the synchronization of the network depend on the particular value of the delay in the connections between neurons. Theses results suggest that synaptic plasticity has a crucial role for reliability of the response pattern of the network to an repeated external stimulus, as well as the synchronization of the response output between the neurons. The distinction between reliability and synchronization could be useful to analyze many driven network dynamical systems.

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