



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

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**Abstract**—We investigate the characteristics of reliability and synchronization of a neuronal network of delay-coupled integrate and fire neurons. Reliability and synchronization appears in separated regions of the phase space of 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.

## 1. 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]. It is known that independent phase oscillators can be synchronized by weak independent additive noise [3] but, the reliability is deteriorate when they are coupled [4]. 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 [5].

In neuronal system, it is known that noise play a positive role enhancing the response of the sensory system [6]. In the brain, the neurons are interconnected forming 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 [7].

Another important property associated to neural net-

works is the capability of its constituents to organize their response in a synchronous way [8]. Synchronization appears as a multi-scale phenomenon in the brain [9] and it is related, among other tasks, to information processing [10]. 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 [11], 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. 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.

## 2. 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:  $\dot{v}_i(t) = -\frac{1}{\tau_m}v_i(t) + \frac{1}{C_m}I_i(t)$ , 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 arriving from recurrent connections or from the external drive input. These spikes contributions are modeled as follows:  $I_i(t) = \frac{1}{N_c} \sum_j w_{ij} \sum_k f(t - t_j^k - D)$ , 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  $k$ th-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  $\alpha$ -function:  $f(t) = \frac{e}{\tau_\alpha} t e^{-t/\tau_\alpha}$ , where  $\tau_\alpha$  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 neu-

rons 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 sake of clarity, neurons receive the same independent fluctuating spike train in all trials. Simulation were done using the neuronal simulator package NEST [12].

## 2.1. 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 [13]. 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  $\Delta w$  given by [14]:  $\Delta w = \pm \lambda f_{\pm}(w) \times K(\Delta t)$  if  $\Delta t \geq 0$ . The temporal filter  $K(\Delta t) = \exp(-|\Delta t|/\tau)$  implements the spike-timing dependence of the learning. The time constant  $\tau$  determines the temporal extent of the learning window. The learning rate  $\lambda$  scales the magnitude of individual 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 [15]. In our simulations we used the typical parameter values:  $\tau = 20$  ms,  $\mu = 0.4$ ,  $\alpha = 1.05$  and  $\lambda = 0.005$ .

## 2.2. Measurement

To characterize both reliability and synchronization in the activity of our network, we consider the phase of each neuron defined as [16]:  $\phi_i(t) = 2\pi \frac{t - \tau_k}{\tau_{k+1} - \tau_k}$ , where  $\tau_k$  is the time of the  $k$ th 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:  $r_i(t) = \frac{1}{n} \sum_{k=1}^n \sin^2\left(\frac{\phi_i(t) - \phi_i^k(t)}{2}\right)$  being  $\phi_i^k(t)$  is the phase of the neuron  $i$  obtained in the  $k$ th realization starting from different initial conditions. The summation runs over  $n$  different realizations. A spatiotemporal average of  $r_i$ ,  $R = \lim_{T \rightarrow \infty} \frac{1}{T} \int_0^T \left(\frac{1}{N} \sum_{i=1}^N r_i\right) dt$ , 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 from 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 be-

tween 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,  $s_i(t) = \frac{1}{n_c(i)} \sum_{j \in n_c(i)} \sin^2\left(\frac{\phi_i(t) - \phi_j(t)}{2}\right)$  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,  $S = \lim_{T \rightarrow \infty} \frac{1}{T} \int_0^T \left(\frac{1}{N} \sum_{i=1}^N s_i\right) dt$ .

This measure quantifies the phase difference between the response pattern of each neuron in the network. Note that the 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 pattern we get  $S > 0$ .

## 3. Results

### 3.1. Reliability region

Our first goal is to determine if our neuronal network responds consistently when an external drive is applied.

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. 1. 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 (red area) at moderate coupling strengths and at high drive amplitudes.

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.

### 3.2. Synchronization region

We also determine the synchronization regions by computing the quantity  $S$ . Fig. 2 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 red (blue) color. As

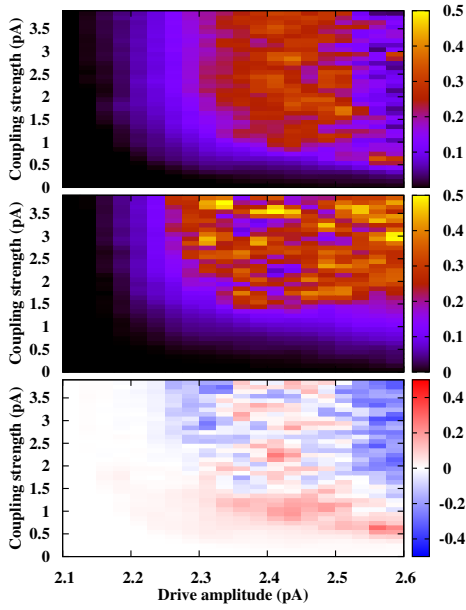


Figure 1: Reliability region determined by  $R$ . Perfect reliability is indicated by  $R = 0$  (black areas) while an unreliably response of the network correspond to  $R > 0$ . Upper panel: static synapses. Middle panel: nonlinear STDP is applied between excitatory connections. Bottom panel: difference between the two previous regions where an increase (decrease) of reliability is codified by red (blue) color.

it can be seen, we do not observe perfect synchronization in our simulations, being desynchronization (yellow area) 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. 3 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. 3. 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. 3).

### 3.3. 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  $R$

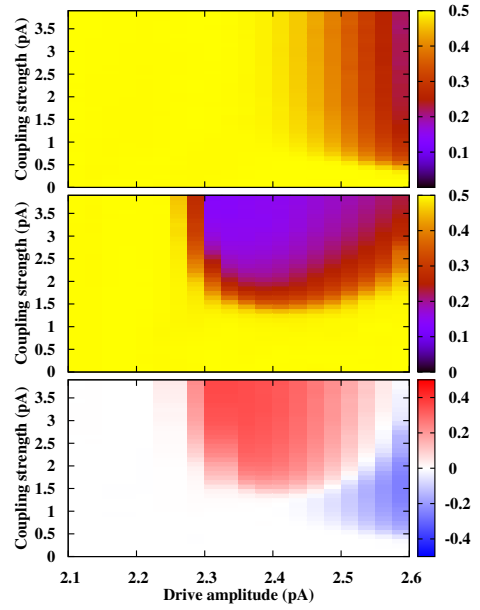


Figure 2: Synchronization region determined by  $S$ . Perfect synchronization is indicated by  $S = 0$  while an asynchronous response of the network correspond to  $S > 0$ . Upper panel: static synapses. Middle panel: nonlinear STDP is applied between excitatory connections. Bottom panel: difference between the two previous regions where an increase (decrease) of synchronization is codified by red (blue) color.

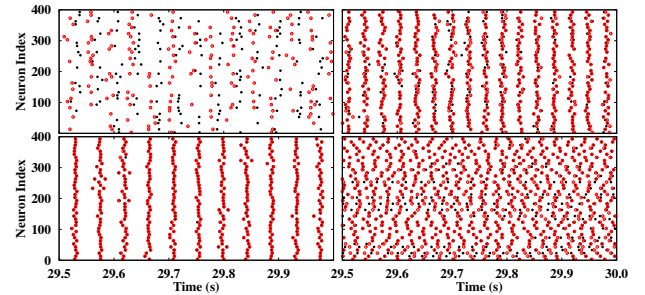


Figure 3: Raster plots for two simulation starting from two different initial conditions. Top (bottom) row correspond to a simulation without (with) STDP. Parameters used: left column,  $w = 3.0 pA$  and  $D_n = 2.35 pA$ ; right column,  $w = 1.0 pA$  and  $D_n = 2.6 pA$ . For visualizations purposes, only a fraction of the network is shown.

and  $S$  for different coupling and delay values. In Fig. 4 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.

Fig. 4 also 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

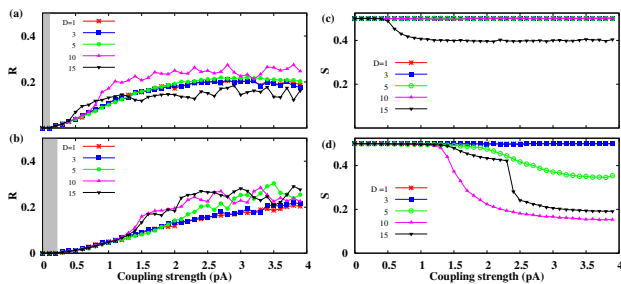


Figure 4: Dependence of  $R$  with the coupling and delay for (a) static synapses and (b) nonlinear STDP. Grey areas represent the regions of reliability. Synchronization parameter  $S$  as a function of the coupling and different values of the delay for (c) static synapses and (d) nonlinear STDP. The drive amplitude is  $D_n = 2.4$  pA

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 [17]. When plasticity is taken into account, the delay has a crucial role in the synchronization of the network (see Fig. 4d).

#### 4. 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 found that STDP has a modulatory effect in both the reliability and synchronization of the system. 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. These 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 as it has also recently been discussed [18].

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