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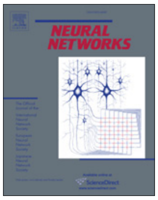

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Deterministic neural dynamics transmitted through neural networks

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ABSTRACT

Precise spatiotemporal sequences of neuronal discharges (*i.e.*, intervals between epochs repeating more often than expected by chance), have been observed in a large set of experimental electrophysiological recordings. Sensitivity to temporal information, by itself, does not demonstrate that dynamics embedded in spike trains can be transmitted through a neural network. This study analyzes how synaptic transmission through three archetypical types of neurons (regular-spiking, thalamo-cortical and resonator), simulated by a simple spiking model, can affect the transmission of precise timings generated by a nonlinear deterministic system (*i.e.*, the Zaslavskii mapping in the present study). The results show that cells with subthreshold oscillations (resonators) are very sensitive to stochastic inputs, and are not a good candidate for transmitting temporally coded information. Thalamo-cortical neurons may transmit very well temporal patterns in the absence of background activity, but jitter accumulates along the synaptic chain. Conversely, we observed that cortical regular-spiking neurons can propagate filtered temporal information in a reliable way through the network, and with high temporal accuracy. We discuss the results in the general framework of neural dynamics and brain theories.

1. Introduction

Action potentials (*spikes*) generated by neurons propagate to neuronal appendices, where voltage-triggered molecular processes produce a signal that is transmitted to other neurons. The combination of several inputs is necessary in order to provoke the generation of an action potential in the post-synaptic neuron, and propagate a pattern of activity further into a neural network. A large set of experimental techniques allow the monitoring of neuronal molecular processes at the synaptic level (Chong, Gough, & Ray, 2002). However, it is the study of the sequence of the exact timings of occurrence–the *epochs*–of the spikes, referred to as *spike train*, that is likely to represent the most adequate way to investigate information processing of neural activity (Abeles, 1991; Rieke, Warland, Bialek, & de Ruyter van Steveninck, 1997; Segundo, Stiber, & Vibert, 1995; Villa, 2000). The dynamics of the membrane potential of a nervous cell are nonlinear (Hille, 2001) and the spike train of a neuron can be considered as a nonlinear dynamic filter of the afferent spike trains (Segundo, 2003). With these premises, the question arises whether precise temporal information conveyed to a neuron may be somehow transmitted through a neural network, without losing its original content. Recurrent temporal patterns of spikes, often referred to as precise firing sequences, consist of occurrences of higher order spike intervals with high temporal accuracy (in the order of few milliseconds), repeating more often than expected by chance (Abeles & Gerstein, 1988; Dayhoff & Gerstein, 1983; Prut et al., 1998; Tetko & Villa, 2001b; Villa & Abeles, 1990). Such temporal patterns of spikes have been observed in a large set of experimental preparations, and have been shown to be associated to sensorimotor and cognitive processes (Shmiel et al., 2005; Villa, 2005; Villa, Tetko, Hyland, & Najem, 1999). Several hypotheses have been drawn to explain such temporal accuracy in experimental preparations. Synfire chains are feed-forward neural networks formed by chains of diverging/converging layers, that exhibit complex spatio-temporal patterns of firing (Abeles, 1991). Such a pattern is characterized by volleys of near-synchronous spikes, which propagate along a sequence of pools of neurons (Diesmann & Gewaltig, 1999). If one stimulates the first pool of a chain, without necessarily respecting strict synchronous timing, a synfire wave will be triggered if a threshold level of activity is reached, and from then on, reliably propagate down the chain. From a complementary viewpoint, deterministic chaotic activity has been revealed experimentally in

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spike trains (Celletti & Villa, 1996a, 1996b; Mpitsos, 1989; Rapp, Zimmerman, Albano, Deguzman, & Greenbaun, 1985) and previous theoretical studies, showed that precise sequences of points could be detected in time series generated by deterministic nonlinear dynamical systems (Tetko & Villa, 1997). Then, it has been suggested that precise temporal patterns of spikes may contain the information of underlying generative dynamics, regardless of their relative rarity (Asai & Villa, 2007). The present study addresses, in particular, the question whether a temporal sequence of spikes, with embedded information associated to a specific deterministic nonlinear dynamics, can be transmitted reliably through a simple neural network, as a natural extension of our preliminary study (Asai, Yokoi, & Villa, 2007). The diversity of neural models existing in the literature does not allow us to analyze here an exhaustive list, but we limit the present study to a simple model that can simulate three representative neural types, *i.e.* thalamo-cortical, cortical regular-spiking, and cortical with subthreshold oscillations (Izhikevich, 2004). In this study we tested a deterministic time series associated with the Zaslavskii chaotic attractor against Poissonian and Gaussian stochastic time series.

2. Method

2.1. Single neuron model

In this study we selected a simple spiking neuron (Izhikevich, 2003), that can reproduce several known types of neuronal dynamics. The model of a given neuron i receiving n inputs from j pre-synaptic neurons is defined as follows;

$$\frac{dv_i}{dt} = 0.04v_i^2 + 5v_i + 140 - u_i + I_i^{bg} + \sum_{j=1}^{n} I_{ij}^{syn} \qquad (1)$$

$$\frac{du_i}{dt} = a(bv_i - u_i),$$

with the auxiliary after-spike resetting

$$\text{if } v \geq v_{\text{critical}}, \quad \text{then } \begin{cases} v \leftarrow c \\ u \leftarrow u + d \end{cases} \qquad (2)$$

where time t is expressed in milliseconds (ms), v is the neuronal membrane potential in millivolts (mV), u is a membrane recovery variable (in arbitrary units), giving negative feedback to v, I_j^{syn}, is the input synaptic current from the jth pre-synaptic neuron, and I^{bg} is the input current due to the background activity. The model keeps continuous dynamics but it also generates neural discharges to make it comparable to other nonlinear leaky-integrate and fire models (Scott, 2002). Then, the critical value defined by v_{critical} mV, is not exactly a threshold for generating spikes, but it corresponds to a cut-off peak of the action potentials. The state variables v and u, are reset with values given by parameters c and d, respectively, if the membrane potential reaches v_{critical}. The time scale and sensitivity of the recovery variable u, to the subthreshold fluctuation of the membrane potential are controlled by parameters a and b. In this study we kept $v_{\text{critical}} = +30$ mV constant. The output spike train, *i.e.* the time series of neuronal discharges, is defined by the sequence of epochs when $v = v_{\text{critical}}$. Three different neuron types were considered in this study according, to the literature (Izhikevich, 2004): (i) a thalamo-cortical (TC) neuron characterized by parameters $a = 0.02, b = 0.25, c = -65, d = 2$; (ii) a neocortical regular-spiking (RS) neuron characterized by parameters $a = 0.02, b = 0.2, c = -65, d = 8$; (iii) a neuron type characterized by its sustained subthreshold oscillatory dynamics of the membrane potential (Izhikevich, 2001; Rinzel & Ermentrout, 1989) called resonator (RZ), with parameters $a = 0.1, b = 0.26, c = -65, d = 2$. Let us denote I^{syn} the input synaptic current, defined as

$$I^{syn} = -A^{syn} g^{syn} (v - V^{syn}), \qquad (3)$$

where V^{syn} is the synaptic reversal potential, set to 0 in this study; g^{syn} is the post synaptic conductance and A^{syn} is an intensity of the synaptic transmission. The g^{syn} post synaptic conductance is represented by the following alpha function

$$g^{syn} = C_0 \frac{e^{-\tilde{t}/\tau_1} - e^{-\tilde{t}/\tau_2}}{\tau_1 - \tau_2}, \qquad (4)$$

where $\tilde{t}$ is interval between the last pre-synaptic neuron's discharge and current time; τ_1 and τ_2 are time constants given by 0.2 and 2 ms, respectively, and C_0 is a coefficient used to normalize the maximum amplitude of g^{syn} to 1. In addition to specific inputs, let us assume that each neuron receives multiple inputs called *background activity*, whose current is denoted I^{bg}. We assume that I^{bg} is defined likewise I^{syn} (Eq. (3)), with a different intensity of the transmission, denoted by A^{bg}. The parameters A^{syn} and A^{bg} were tuned for each neuronal model, such that a single pulse of the specific pre-synaptic input can evoke a spike in the post-synaptic cell, if the membrane potential is at rest. Conversely, a single pulse of background activity cannot evoke an output spike, but a subthreshold excitatory post-synaptic potential. The values of (A^{syn}, A^{bg}) were set to $(0.033, 0.032)$, $(0.15, 0.14)$ and $(0.018, 0.017)$ for TC, RS, and RZ, respectively. We also used $A^{bg} = 0$ as a control case, meaning the absence of background activity. The phase diagrams of Fig. 1 show the trajectories of the dynamics leading to the generation of an action potential for each neuronal type. It is shown that the system (Eq. (1)) has two equilibrium points, which are intersection between $v-$ and u-nullclines. The leftmost equilibrium point is stable, and corresponds to the resting state of the membrane. The rightmost equilibrium point is a saddle point. The state point must go beyond the right side of the stable manifold of the saddle point, in order to evoke a neural discharge, otherwise the state point returns to the stable fixed point with a small loop. If the neuron receives a depolarizing input current, the v-nullcline is pushed up, and the two equilibrium points disappear by a saddle-node bifurcation, and the state point moves towards the right on the phase plane. In the case of TC and RZ models A^{syn} and A^{bg} were set smaller than for RS. With these parameters the relative position of the resting membrane equilibrium points for TC and RZ are near to the bottom of the v-nullcline, such that a small input current is enough to move the state point out of the equilibrium, and generate an action potential. In the case of RS a larger input current is required to generate a spike, as illustrated in Fig. 1, with the equilibrium point located relatively on the hillside of the v-nullcline. Notice that the equilibrium point for RZ type at the resting state is a stable spiral, leading to oscillatory subthreshold membrane potential, while it is a stable node for TC and RS.

2.2. Simple neural network model

We considered a small neural network composed by 3 identical types of spiking neurons, connected serially in a forward direction, as illustrated by Fig. 2. Each cell received only one specific input, in addition to an independent background activity. Cell #1 received an external temporally organized input (I_1^{syn}) and projected to Cell #2. Cell #2 received an input from Cell #1 and Cell #3 received an input from Cell #2. I_1^{syn} represents a synaptic current induced by an input spike train, generated by a dynamical system (see next section). I_2^{syn} and I_3^{syn} are the synaptic currents corresponding to the afferences from the $(i-1)$th neuron. We considered three different network models, composed by either neuronal types (TC, RS or RZ).