Computing with excitable systems in a noisy environment

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In this work we show that excitable units with biologically inspired couplings are capable of performing any logic operation in a noisy environment without synchronization.

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The brain is the most sophisticated information processing device that we know of. Neurons process analogic information that enters through the sensory system, transforming it into a sequence of pulses (action potentials) in order to relay it to other neurons. This is a dynamic process in which the time course is important (it is believed that, in certain cases, the information is encoded in the frequency of the signals [1]). Furthermore, it occurs in a noisy environment and in the absence of an external synchronizing clock [2]. It is not clear that the brain operates as a computer, yet the metaphor has proven to be useful (e.g., neural networks [3] and biologically inspired circuits [4]). Thus, the following question arises: *How can computations be performed out of an analogic input, without synchrony and in a noisy environment?* Using a biologically inspired synthetic model, we prove in this work that computability with neuronlike units in a noisy environment is possible, without external synchronization.

In a seminal work, McCulloch and Pitts showed that a synthetic neuron model could perform all the logic operations that an electronic computer does [5]. This approach requires an absolute coordination of the signals and a noise-free environment. In order to overcome some of these shortcomings, continuous time models have been developed in which the relevant variable is the average firing rate of the neurons (see, e.g., [1]). Neural networks built with chemical reactions in which the state of the units is represented by stationary states are similar to these average rate models. In particular, the program of showing computability with these networks has been successfully carried out by Ross and coworkers [6–8]. On the other hand, in the last few years, the extent to which average rate models are accurate representations of information coding in real neurons has been debated arguing that there is information contained in the sequence of spikes that is not captured by these averages [2,9]. To account for the richness of coding possibilities of spike trains, it is appropriate to work with continuous time models that are able to represent the actual spiking behavior, i.e., that describe in more detail the time course of the membrane potential [10,11]. These excitable units, coupled with biologically inspired connections, should be able to perform small frame averages in a dynamical way. This is the approach we follow in the present work.

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We present a synthetic model that includes (some of) the processes involved in the transmission of information in neurons in a dynamic way (i.e., the competition between the various processes selects the time scales that are relevant for the information processing and transmission). It is important to point out that noise produces intriguing effects in the dynamics of nonlinear systems, such as the introduction of new time scales [12]. This is particularly true in excitable systems [13–15], such as neurons. In spite of this, we do prove computability in our noisy model. In order to do so, we show that logic gates can be built in this way and that global consistency [16] is satisfied for an arbitrary long logic circuit, depending on the properties of the coupling.

We now introduce the model. We start with the simplest, but yet, generic model displaying a noisy excitable dynamics. Its evolution is given by

$$d\theta/dt = \mu_0 - \cos(\theta) + \xi(t), \tag{1}$$

where θ is an angular variable ($-\pi < \theta \leqslant \pi$) and $\xi(t)$ is (for simplicity) Gaussian white noise [$\langle \xi \rangle = 0$, $\langle \xi(t)\xi(t+\tau) \rangle = 2D\delta(\tau)$]. In the absence of noise ($\xi = 0$), this system is excitable for $\mu_0 < 1$ and presents oscillations for $\mu_0 > 1$. We associate the firing of an action potential with a complete turn in θ and θ to a dimensionless membrane potential at the soma. This equation is known as Adler's equation and also as VCON (voltage controlled oscillator neuron) [17]. It dynamically contains, in a pure way, the saddle node bifurcation within a limit cycle (Andronov bifurcation). Not only it can model excitable dynamics, but it is also known to be a canonical model, i.e., any other system at this bifurcation can be transformed to the VCON by an appropriate change of variables. All neuron models presenting what is known as class I excitability display this type of bifurcation. For each of these models it is possible to relate μ_0 to their original parameters. An example of this transformation for the Wilson-Cowan neural model can be found in [17]. Since we work with $\mu_0 \approx 1$, the potential at rest is $\theta \approx 0$ and the action potential corresponds to $\theta \approx \pi$. In the excitable regime ($\mu_0 < 1$), the presence of noise can trigger spontaneous firings. The interspike time distribution of this dynamics is wide. It presents a maximum [13] and an exponential tail [18]. Beyond $\mu_0 = 1$, the noise slightly widens the otherwise peaked interspike time distribution (see Fig. 1). The qualitative difference between these two distributions may be used to define a binary code.

Our logic gate consists of an excitable cell, coupled to other excitable cells operating at the excitable or oscillatory

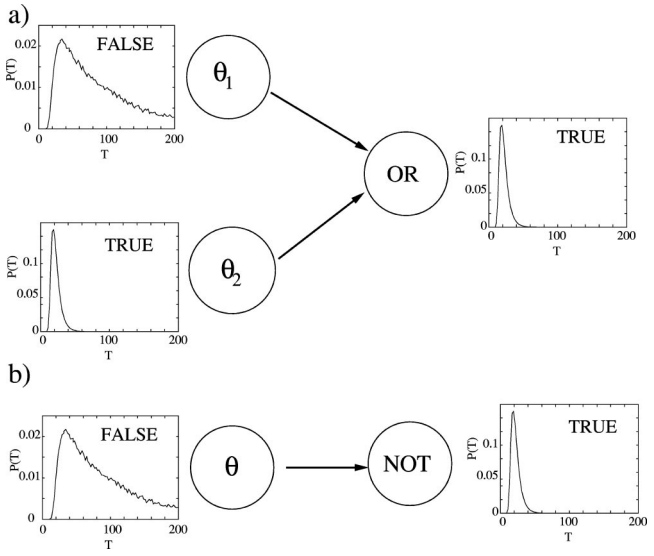

FIG. 1. Schematic diagram of (a) the OR gate. The logical state of the input cells [Eq. (2)] is given by the "effective parameter" $\mu=\mu_0+\gamma z$. A lower μ value corresponds to a wide interspike histogram and is associated with a false input. $P(T)$ is the probability density of the interspike time interval T. A higher μ value corresponds to a narrow interspike histogram and a true input. (b) The NOT gate. A false input gives a true output. All variables are dimensionless.

regimes. Therefore, the equation ruling the dynamics of the gate is similar to Eq. (1), with extra terms accounting for the couplings. In order to couple the excitable units, we draw inspiration from the synaptic connections among neurons. In most cases, these connections are mediated by the release of neurotransmitters, which, in turn, open ionic channels and change the dendritic potential of the postsynaptic neuron. At this point, the neuron adds spatially and temporally the inputs to a value that is passively conveyed to the soma, where eventually the action potential is fired. The variables needed to describe a simple model with these features are the density of neurotransmitters in the cleft, n, the dendritic potential z, and the density of open neurotransmitter-gated channels, N_o, all of which we take to be dimensionless. We assume that two neurotransmitter molecules A are needed to open one channel, and that each channel can exist in two states: open O and closed C. The simplest model for this process is given by the reaction step

$$2A+C\underset{k'}{\overset{k}{\rightleftharpoons}}O.$$

Assuming that the total density of channels is N and that the reaction occurs fast enough so that it relaxes on a short time scale towards its local equilibrium, then the density of open channels, N_o may be related to the total density of channels, N, and the density of neurotransmitters in the cleft, n, by $N_o=[n^2/(n^2+k_d)]N$, where $k_d\equiv k'/k$ is the dissociation constant. This dynamics has a similar effect to that of the enzyme reactions included in the chemical networks presented in [6–8]. Neurotransmitters are released into the synaptic cleft whenever an action potential occurs at the presynaptic neurons, and removed by enzymes, reuptake, and diffusion. Taking into account that the distribution of neurotransmitters reaches a rapid equilibrium with the channels, a minimal model for n can be written as

$$dn/dt=\frac{1}{\ell}\sum_{i=1}^{\ell}\Theta(\theta_i)-\alpha n, \tag{2}$$

where θ_i corresponds to the potentials of the presynaptic neurons (labeled by i), the sum runs over all the presynaptic inputs, α is the rate of neurotransmitter removal, and $\Theta(\theta_i)=\theta_i$ in the neighborhood of $\theta_i=\pi$ and zero otherwise. Therefore, the term $(1/\ell)\Sigma_{i=1}^{\ell}\Theta(\theta_i)$ acts as a source of neurotransmitters that is turned on whenever any of the presynaptic neurons spikes. Finally we need to model the dynamical behavior of the dendritic potential of the excitable cell acting as the gate, z. This potential changes due to (1) a gain term associated to the ionic currents that flow through the neurotransmitter-gated channels and (2) a loss term due to a leak current and to the opening of some voltage gated channels. In its simplest form, this can be written as

$$dz/dt=\frac{n^2}{n^2+k_d}K-\beta z, \tag{3}$$

where the constant K is positive (negative) for excitatory (inhibitory) synapses and involves both the total number of channels and the equilibrium potential of the ions that flow through these channels. In writing this we have assumed that z can be neglected in front of this equilibrium potential and that $z=0$ at rest. We have also assumed β to be constant for the values over which z varies. While we identify the inputs of the gate with the potentials at the soma of the presynaptic neurons, we identify the output of the gate with the potential of the soma of the postsynaptic neuron.

In order to couple the dynamics of the dendritic potential z, to that of the potential at the soma of the postsynaptic gate, θ, we write, instead of Eq. (1),

$$d\theta/dt=\mu_0+\gamma z-\cos(\theta)+\xi(t), \tag{4}$$

where the term γz represents the passive spreading of the potential from the dendrites into the soma. Notice that the effect of this term is to "rescale" the parameter μ_0. Namely, Eq. (4) is equivalent to Eq. (1) but with μ_0 replaced by $\mu_0+\gamma z$. Therefore, by changing the input γz, it is possible to change the behavior of the neuron from excitable to oscillatory and vice versa, and therefore, to change the output of the gate. We associate the "effective parameter" $\mu=\mu_0+\gamma z$ to the logic state of the neuron (the output of the gate).

We associate the two possible logic states ("true" and "false") to two regions in the μ parameter space. A true state corresponds to $\mu>\mu_T$ and a false one to $\mu<\mu_F$. The values of μ_T and μ_F are such that for most $\mu>\mu_T$ the neuron is in the oscillatory regime, while it is in the excitable one for all $\mu<\mu_F$. They are chosen, as we will explain, so as to guarantee the correct operation of the gate, even if many of them are sequentially nested (global consistency).

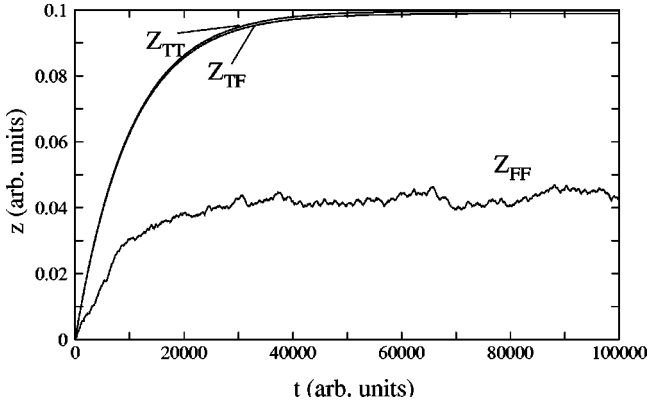

FIG. 2. Time evolution of the z variable of the OR gate ruled by Eqs. (2)–(4) with $\alpha=0.01$, $\beta=10^{-4}$, $K=10^{-5}$, and $k_d=0.233$ and three different inputs: false-false, true-false, and true-true. All variables are dimensionless.

We now show how to build an OR gate. Its operation is defined by Eqs. (2)–(4), with $\ell=2$ (i.e., two inputs). Equation (2) integrates the spikes of the inputs, reaching an asymptotic value that is roughly proportional to the sum of the average spiking rates of both inputs. Therefore, the density of neurotransmitters, n, approaches different mean values depending on the input types. However, since the fraction of open channels, $F_o \equiv n^2/(n^2+k_d)$, is a nonlinear saturating function of n, the asymptotic dendritic potential z, which is given by $F_o K/\beta$, may approach similar values for different sets of inputs, depending on the value of k_d. We choose k_d in such a way that almost all true-true and true-false inputs originate similar asymptotic values of $z(z_{TF} \approx z_{TT})$, which are in turn different from the values that the false-false inputs generate, z_{FF}. An example of this is shown in Fig. 2, in which the false (true) input corresponds to an evolution in the excitable (oscillatory) regime. In general, if the duration of each action potential, τ, at the input neurons is much smaller than the interspike time of the combined inputs, T, we may estimate the asymptotic value of n as $n \to \langle\Theta\rangle\tau \exp(\alpha T)/[\exp(\alpha T)-1]$, where $\langle\Theta\rangle\tau$ is the concentration of neurotransmitter released due to one external impulse. If $\alpha T_{FF} \gg 1$ while $\alpha T_{TF} \ll 1$, then $n_{FF} \approx \langle\Theta\rangle\tau$ and $n_{TF} \approx \langle\Theta\rangle\tau/\alpha T_{TF}$. Thus, given the form of F_o, a necessary condition for z_{TF} and z_{TT} to differ by less than 10%, and be different from z_{FF} is $3\alpha T_{TF} < \langle\Theta\rangle\tau/\sqrt{k_d} \leqslant 1$. This states a limit to global consistency in terms of the reaction rates of the channels dynamics. In real neurons several inputs arrive at each terminal and as many as 800 presynaptic potentials per second may be added to produce a postsynaptic potential [19]. Typical neurotransmitter removal occurs on very short time scales (on the order of some milliseconds [20]). Estimating $\alpha \sim 0.1$ ms^{-1} and $T_{TF} \sim 1$ ms, the above-mentioned constraint reads $0.3 < \langle\Theta\rangle\tau/\sqrt{k_d} \leqslant 1$, which is satisfied provided that the fraction of channels that open in response to one input spike is between 0.08 and 0.5.

Now we need to define the false and true regions. This is done by simultaneously adjusting the parameters μ_0, γ, μ_F, and μ_T in such a way that $\mu_0+\gamma z_{FF} < \mu_F$ for all z_{FF} values generated with inputs $\mu_1, \mu_2 < \mu_F$, and $\mu_0 + \gamma z_{TF} > \mu_T$ for all z_{TF} values generated with inputs $\mu_1 > \mu_T$ and $\mu_2 < \mu_F$. It is possible to do this because of the saturation effects that the couplings introduce, as we explained before. These requirements guarantee the global consistency for an arbitrarily long chain of logic gates. We illustrate this in Fig. 3, where we plot the logical state of the gate, $\mu=\mu_0+\gamma z$, as a function of the logical state of the inputs, μ_1, μ_2 as an example of satisfying these requirements. There we see that any input in the false-false region (region A) is mapped into the false region, i.e., $\mu(\mu_1,\mu_2) < \mu_F$, and that any input in the true-false or true-true region (region B) is mapped into the true region, i.e., $\mu(\mu_1,\mu_2) > \mu_T$. In this way, the output of the gate can be used as an input of another one and an arbitrarily long chain of logic gates can be implemented. This is equivalent to the following requirements: (a) in any chain of OR gates, the output is true if at least one of the cells is true; (b) in any chain of OR gates with only false inputs, the output is always false.

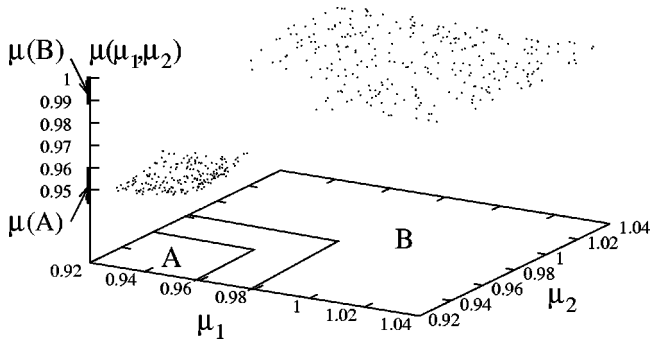

FIG. 3. The effective parameter $\mu=\mu_0+\gamma z$ of the OR gate given by Eqs. (2)–(4) with $\mu_0=0.949\,05$ and $\gamma=0.471\,01$, as a function of the parameter values of the inputs, μ_1, μ_2. We define two regions: A for both inputs $\mu_i < \mu_F = 0.96$, and B for at least one true input $\mu_i > \mu_T = 0.98$. Any input in A produces an output in the false region, $\mu < \mu_F$, and any input in B is mapped into the true region, $\mu > \mu_T$. All variables are dimensionless.

In order to implement all the logic operations we also need a gate that performs an inversion of the input. This can be achieved through a NOT gate, which is described by Eqs.

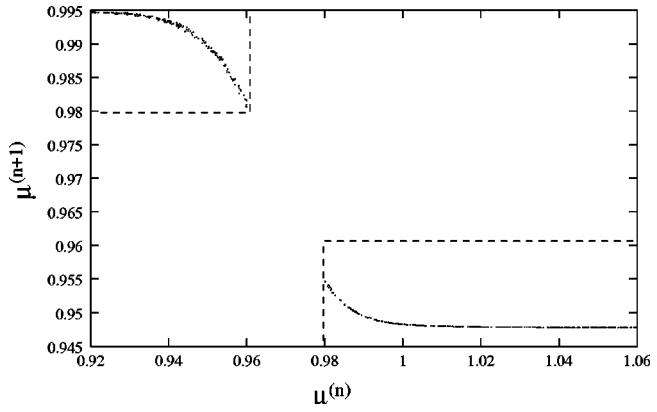

FIG. 4. The effective parameter $\mu^{(n+1)}$ of the NOT gate given by Eqs. (2)–(4) as a function of the parameter value of the input $\mu^{(n)}$. The false region ($\mu < \mu_F = 0.96$) is mapped into the true region ($\mu > \mu_T = 0.98$) and vice versa. All variables are dimensionless.

(2)–(4), with $\ell = 1$ (i.e., a unary operator). We used the same parameter values for Eqs. (2) and (3) as in the OR gate, but now the coupling is inhibitory ($K = -10^{-5}$). Therefore, a false input corresponds to a minimum negative asymptotic value of z and a true input to a negative z value of small absolute value. Since the difference between these asymptotic z values is similar to that of the OR gate ($z_{TF} - z_{FF}$), we can use the same value for the coupling parameter $\gamma = 0.471\,01$. The NOT gate acts as a one-dimensional map in parameter space μ, mapping the logical state of an excitable unit, $\mu^{(n)}$, to the next one $\mu^{(n+1)}$. In order to achieve global consistency we require that M_F (defined with the same μ_F as for the OR gate) be mapped into M_T and vice versa for an arbitrarily long chain of excitable units. In other words, we require that both regions are invariant after two iterations of the map. This can be done by a suitable choice of the parameter $\mu_0 = 0.994\,81$. In Fig. 4 we show a plot of the NOT gate acting as a map on the logical state space of the excitable units, μ.

In this way we show that excitable units with biologically inspired couplings are capable of performing any logic operation in a noisy environment without synchronization. To go beyond logic gates towards computability, it is necessary to implement memory devices. A natural direction for further work is to explore the construction of such units with our elements.

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