Dynamical reservoir properties as network effects

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Abstract. It has been proposed that chaos can serve as a reservoir providing an infinite number of dynamical states [1, 2, 3, 4, 5]. These can be interpreted as different behaviors, search actions or computational states which are selectively adequate for different tasks. The high flexibility of chaotic regimes has been noted, as well as other advantages over regular regimes. However, the model neurons used to demonstrate these ideas could be criticized as lacking physical or biological realism. In the present paper we show that the same kind of rich behavior displayed by the toy models can be found with a more realistic neural model [6]. Furthermore, much of the complex behavior arises from network properties often overlooked in the literature.

1 Spatiotemporal neural chaos and its use

Following the discovery of putative chaotic regimes in electrical signals from the brain, and much scientific speculation as to the possible roles of chaos in cognition, actual computational models were proposed [1, 2, 3, 4, 5]. These models arguably explain some of what could be going on in the brain, but they also point to possible artificial devices taking advantage of the dynamical richness of chaos. To this end, a continuous-time setting is adopted and nonlinear network properties are investigated. Knowledge of general properties of nonlinear oscillators, as well as of generic networks, turns out to be very useful and can prompt a first approach to dynamical neural network modeling. This is the case of the references above, where e.g. Ginzburg-Landau and Rossler oscillators are meant to capture the essential oscillatory features of neurons. Particularly in Refs. [1, 2, 4], a full network setting is presented mimicking cortical architecture. Thus an actual spatiotemporal dynamics is unveiled, overcoming the limitations and criticism that result from working with single-unit or otherwise very small networks [4]. Unstable Periodic Orbits (UPOs) can be stabilized from within chaos, very fast and with minimum perturbation of the original system. The original chaotic attractor contains an infinite number of such dynamical modes, which could be stabilized at will according to the requirements of computational

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tasks. In Ref. [4], this is applied to the processing of spatiotemporal visual input patterns with different symmetries. The units (or "neurons") are topologically arranged in a network, and the simultaneous monitoring of their state variables reveals such spatiotemporal regimes as standing and rotating waves of different symmetries, or a complex mixture thereof.

2 Nonlinear oscillators: from out-of-the-box units to more realistic neurons

The mathematical models mentioned above face some criticism when comparisons are made with actual neurons. Neurons are not oscillators, even if certain cells can display autonomous rhythmic firing (a behavior we are not addressing here, but certainly nothing like an actual oscillator, especially if the membrane potential is the monitored variable). However, groups of neurons can show oscillating electrical activity, sustained by the exchange of excitation and inhibition. Neural coupling is far from the simple linear connectivity of diffusive type considered in Refs. [1, 2, 4] and other studies of networks of the reaction-diffusion type. Rather, neurons are connected via highly nonlinear transfer functions such as sigmoids. Finally, in real life there is an unavoidable delay in signal transmission between all neurons, which is usually not considered as an intrinsic property of the model networks. This includes the networks mentioned above.

Hence a more realistic model is sought. The purpose is to attain just the "right" level of biological or physical plausibility, while still having a manageable model for dynamical exploration. Although proposed in a different context, the model in Ref. [6] provides a good compromise. The individual unit is a slightly more complex version of the leaky integrator, and is also called the single-compartment neuron. Passive as well as active membrane properties are considered, along with highly nonlinear coupling and delays in signal transmission between neurons.

2.1 Deriving the neuron model

For lack of space, only an abbreviated account can be given here. Figure 1 illustrates the starting point: the electrical equivalent of the neural membrane.

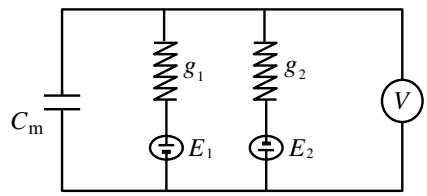

Fig. 1: Electrical equivalent of the neural membrane. See text for the details.

The state of the neuron is characterized by the membrane potential V. C_m is the membrane capacitance. E_n represents the ionic potential associated with

ion species n. The membrane conductance associated with species n is denoted g_n. A Resistive-Capacitive (RC) equation can be derived for the potential V:

$$C_{\mathrm{m}} \frac{dV}{dt} = -g_L(V - V_L) - g_1^c(V - E_1) - g_2^c(V - E_2) \ .$$

g_L is the resting conductance of the membrane, and V_L is its resting potential. The active part of the conductances, g_n^c for each species n, takes into account the opening or closing of ionic channels, depending on the level of synaptic excitation which arises through the coupling of neurons. Thus g_n^c is a sum of contributions from several terms $g_n^{(k \to i)}$ denoting the local conductance of ion species n at the synapse between neurons k and i. The different equilibrium potentials have the values $V_L = -60$ mV, $E_1 = 50$ mV, and $E_2 = -80$ mV. As with other parameters of the model, these values are suggested by electrophysiological experiments. The activation of channel g_1^c contributes to the increase of the membrane potential toward E_1, whereas the activation of g_2^c tends to decrease the membrane potential toward E_2. g_1^c and g_2^c are activated by excitatory and inhibitory presynaptic neurons, respectively. The synaptic conductances depend on the firing rate of the presynaptic neuron:

$$g_n^{(k \to i)}(t) \sim f_k(t - \tau) \ ,$$

where τ is the time-delay due to the finite speed of signal propagation. The firing frequency of the presynaptic neuron k saturates at a value $f_{\max}$, say, 100 Hz. We consider a sigmoidal transfer function between the membrane potential V_k and the firing frequency f_k:

$$f_k = f_{\max} \, F(V_k) \qquad\qquad F(V) = \frac{1}{1 + e^{-\alpha(V - V_c)}} \ .$$

By choosing particular parameter values α and V_c, a certain activation threshold is obtained such that the neuron is silent for lower values of the potential V. Past some higher value of V, the firing rate saturates. V_c is fixed at -25 mV. The α values are indicated in Section 2.2.

2.2 Connecting the neurons

In the isolated model neuron, the response of the membrane to perturbations from the resting state can be characterized by $\gamma = g_L/C_{\mathrm{m}}$, which is the inverse of the membrane's time-constant. The dynamics in this simple case is relaxatory. However, as several neurons are coupled together, new dynamical regimes may settle in, depending on details of the coupling and on the initial conditions of the population. One can observe multiple steady states, including global quiescence and global saturation, as well as a variety of oscillatory regimes for the electrical activity of the neurons. Although a single neuron, under the present model, does not oscillate, a coupled population may present oscillations due to the interplay of excitatory and inhibitory feedback through synaptic connections.

The variables of the dynamics are the instantaneous membrane potential of each neuron. A stationary state corresponds to the firing of action potentials

with a frequency constant in time. This frequency can be zero, or have some finite value. An oscillatory state, on the other hand, implies a time-modulation of the firing frequency.

Although there are many types of neurons, for the purpose of the modeling we divide them into two populations: one of excitatory neurons, with membrane potentials X_i, and another of inhibitory neurons, with membrane potentials Y_j. The dynamics of the coupled neuronal populations is described by

$$\begin{aligned}
\frac{dX_i}{dt} &= -\gamma(X_i - V_L) - (X_i - E_1)\sum_{k\neq i}\omega_{ki}^{(1)}\, F_X[X_k(t-\tau_{ki})] \\
&\quad - (X_i - E_2)\sum_{l\neq i}\omega_{li}^{(2)}\, F_Y[Y_l(t-\tau_{li})] \\
\frac{dY_j}{dt} &= -\gamma(Y_j - V_L) - (Y_j - E_1)\sum_{k\neq j}\omega_{kj}^{(3)}\, F_X[X_k(t-\tau_{kj})] \\
& i,k = 1,\ldots,N_{\rm ex}\ ,\ \ j,l = 1,\ldots,N_{\rm in}\ \ .
\end{aligned}$$

The network comprises $N_{\rm ex}$ excitatory neurons X_i, and $N_{\rm in}$ inhibitory neurons Y_j. The inverse of the membrane's time-constant takes the value $\gamma = 0.25$ msec^{-1}. τ_{ki} is the propagation delay between neurons k and i. This delay depends on the distance between the two neurons. Contrarily to previous versions of the model, here we consider different values of the slope α of the transfer function F, depending on whether the firing neuron is excitatory or inhibitory. We adopt the values $\alpha_X = 0.09$ mV^{-1} and $\alpha_Y = 0.2$ mV^{-1}. The synaptic weights ω characterize the efficiency of channel activation by the presynaptic neuron. They correspond to the coupling constants of the network. The weights $\omega_{ki}^{(1)}$, $\omega_{li}^{(2)}$, and $\omega_{kj}^{(3)}$ refer, respectively, to excitatory-to-excitatory, inhibitory-to-excitatory, and excitatory-to-inhibitory connections. We take these values as constant in time. Notice that there are no inhibitory-to-inhibitory connections.

The connectivity that we consider is of a local nature. For simplicity, only first-neighbor connections are implemented. Furthermore, we study networks that are invariant under translations in space, where the neurons are equally spaced. Therefore, in the X_i and Y_j equations one can drop the subscripts in the time-delays and synaptic weights: $\tau_{ki} = \tau$ and $\omega_{ki}^{(I)} = \omega^{(I)}$, where $I = 1, 2, 3$ designates the different types of interactions. The summations in the X_i and Y_j equations are to be performed with contributions only from presynaptic neurons in the immediate spatial vicinity of the postsynaptic neuron. This local pattern of connectivity may be more relevant for certain parts of the cortex than for others, but this discussion is out of the scope of the present paper.

2.3 Network topology

We have investigated the dynamical behavior of the above equations in different configurations, including the case of bi-dimensional networks with many excitatory and inhibitory neurons. However, for the purpose of this paper, we consider

only a 1-D spatial arrangement of a moderate number of neurons. Spatiotemporal chaotic solutions are sought, as well as the possibility of stabilizing these chaotic regimes into time-periodic orbits with diverse symmetries. Figure 2 shows the network topology.

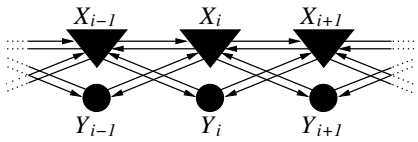

Fig. 2: Dynamical neural network. Excitatory neurons and inhibitory neurons are represented as triangles and circles, respectively. Connections $X_i \to X_{i\pm1}$ and $X_i \to Y_{i\pm1}$ are excitatory, whereas connections $Y_i \to X_{i\pm1}$ are inhibitory.

Here $N_{\text{ex}} = N_{\text{in}} = N$. Hence the total population size is $2N$. For the numerical simulations described below we take $N = 8$. The network has first-neighbor connectivity and the boundary conditions are of the zero-flux type. According to Section 2.2, we consider a spatially homogeneous network, thus $\omega_{ji}^{(I)} = \omega^{(I)}$ and $\tau_{ji} = \tau$. The weights of types (1) and (3) are fixed at $\omega^{(1)} = 3.15$ and $\omega^{(3)} = 2.5$ respectively. Parameters τ and $\omega^{(2)}$ can each have different values.

2.4 Dynamics: routes to spatiotemporal chaos

The network properties of connection topology and delay in signal transmission turn out to be crucial for the unfolding of a rich dynamics. It has been noted by several authors that the delay value can serve as a Hopf bifurcation parameter from stationary states into periodic oscillations. Moreover, it provides a route to chaos and a further increase in the chaotic attractor's dimension as its value is incremented. Both mechanisms were identified in our study of neural networks, thus confirming the importance of the delay. Here, we propose a somewhat different, albeit related, route. We fix $\tau = 1.8$ msec and vary the value of $\omega^{(2)}$, which weighs the amount of inhibitory feedback to the network.

Starting from $\omega^{(2)} = 17$ and taking successively lower values of $\omega^{(2)}$, while keeping all other parameters fixed as indicated above, we observe a sequence of bifurcations that occur for the neural system. For $16.05 < \omega^{(2)} < 17$ a stationary state is observed in which the excitatory (resp., the inhibitory) neurons share a common low membrane potential corresponding to a very low firing rate. At $\omega^{(2)} = 16.05$, a primary Hopf bifurcation occurs which destabilizes this stationary state giving rise to uniform oscillations of the network with a critical period of 13.76 msec. For lower values of $\omega^{(2)}$, the structure of these oscillations becomes increasingly complex. From $\omega^{(2)} = 1.69$ downwards, two new dynamical processes take place in conjugation: the network no longer oscillates homogeneously, and a cascade of period-doubling bifurcations is seen for the time-variation of any given neuron's membrane potential. The cascade accumulates for a value of $\omega^{(2)}$ close to 1.641. Past that point, spatiotemporal chaos is observed in a narrow but finite parameter range.

3 Chaos in the neural model

By fixing $\omega^{(2)} = 1.64$, we can investigate the resulting chaotic regime. Both the network average value of X and a profile of local deviations from this average have aperiodic temporal variation. The system shows an exponential divergence of initially nearby trajectories, which is characteristic of chaotic dynamics. The obtained behavior is conditioned by the moderate size of the network. The spatial correlation length is of the order of the system size. In a larger system, the observed regime would correspond to traveling waves of activity going rightward or leftward in a random fashion, and "riding" on a uniform profile that has itself an irregular temporal variation. In the present network, the waves are not fully developed. Chaos is associated with the destabilization of entire spatial modes. A partial spatial coherence is kept throughout the chaotic regime. This denotes the correlations that exist between neurons, caused by their coupling pattern. Temporally, the bulk part of the chaotic oscillations has a bimodal character, with a spindle-like higher frequency superimposed on the basic cycle. This is one example of rich dynamical behavior not found in networks of simple oscillators.

Further characterization of the spatiotemporal dynamics is not possible here due to space limitations, and is postponed to a later article. However, we note the important fact that the "reservoir" property is indeed found in the chaotic neural attractor. Moreover, several different behaviors in the form of UPOs can be identified and selectively stabilized via processes that are analogous to those employed with the toy models mentioned above.

It is demonstrated that a network of model neurons akin to leaky integrators, with physically plausible nonlinear connectivity and intrinsic delays in signal transmission, is capable of displaying a rich set of behaviors without the need of any significant parameter distortion from reference values. The model, which is amenable to electronic implementation, takes advantage of a fully time-continuous dynamics together with spatial distribution, thus providing an adequate framework for the dynamical computation paradigm that motivated this work.

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