From the single neuron transfer function to the population dynamics

Maurizio Mattia and Paolo Del Giudice

Physics Laboratory, Istituto Superiore di Sanità at Roma, Italy

`mattia@ibmtera.iss.infn.it`

`paolo@ibmteo.iss.infn.it`

`http://neural.iss.infn.it`

February 9, 2001

Abstract

We develop a time-dependent population approach and a perturbative approximation to construct the evolution equations for the mean collective activity of a network of IF neurons, in the (extended) mean field framework.

The stability conditions for the collective activity are naturally and simply expressed in terms of the (slope of) single neuron, static transfer function.

The spectral analysis of the time-dependent collective activity is in good agreement with numerical simulations, and reveals modes ranging from high frequency oscillations, depending on spike transmission delays, which are responsible for departure from stability, in agreement with previous studies, to oscillations at a few Hertz, intrinsically related to the diffusion process describing the population dynamics, which do not contribute to the stability conditions.

The characteristic times of the latter, "slow" modes govern the transient response of the network, and we provide evidence of a remarkable agreement of the theoretical predictions with simulations.

The above reaction times again exhibit a simple dependence on the slope of the transfer function. We speculate on the possible relevance of these results for the change in the characteristic response time of a neural population during the learning process shaping the synaptic couplings and thereby affecting the slope of the transfer function.

Summary

The dynamic mean-field equations

In the diffusion approximation, the sub-threshold dynamics of the membrane depolarization V of a quite general class of IF neurons is given by [9]

$$\dot{V} = f(V) + \mu(V, t) + \sigma(V, t)\Gamma(t), \tag{1}$$

where the afferent current is described as a white noise with mean $\mu(V, t)$ and variance $\sigma^2(V, t)$ and $f(V)$ is a leakage term.

In an 'extended' mean field approach [3, 2] all the neurons in a homogeneous population are driven by a stochastic current with the same mean and variance, both depending on the recurrent and external emission rates (respectively ν and ν_{ext}), equal for all the cells: $\mu = \mu(V, \nu, \nu_{ext})$ and $\sigma^2 = \sigma^2(V, \nu, \nu_{ext})$.

The dynamics of the probability density function (p.d.f.) $p(v, t)$ of the depolarization is then described by a Fokker-Planck equation [7]

$$\partial_t p(v, t) = L p(v, t), \tag{2}$$

$$L(v, t) = -\partial_v [f(V) + \mu(V, t)] + \frac{1}{2} \partial_v^2 \sigma^2(v, t), \tag{3}$$

complemented by boundary conditions accounting for the realizations disappearing on the threshold and re-appearing at the reset potential [8, 1, 6, 4, 5].

Since L depends on μ and σ^2, it is an implicit function of the emission rate ν. The latter in turn expresses the flux of realizations crossing the threshold, or the fraction of neurons emitting spikes per unit time:

$$\nu(t) = -\frac{1}{2} \partial_v \sigma^2(v, t) \ p(v, t)\big|_{v=\theta}, \tag{4}$$

In stationary conditions ν is the inverse of the mean inter-spike interval, and for uncoupled neurons it also equals the single neuron transfer function $\Phi(\mu, \sigma^2)$:

$$\Phi(\mu, \sigma^2) = -\frac{1}{2} \sigma^2 \partial_v \ \phi_0(v, \mu, \sigma^2)\big|_{v=\theta}, \tag{5}$$

where $\phi_0(v, \mu, \sigma^2)$ is the zero eigenvalue eigenfunction of L, stationary solution of Eq. (2).

It is convenient to expand $p(v, t)$ in Eqs. (2) and (4) into the complete set of eigenfunctions ϕ_n of L [7, 6],

$$p(v, t) = \sum_n a_n(t) \phi_n(v, t) \tag{6}$$

which, recalling the implicit dependence on ν, implies:

$$\begin{aligned} \dot{a}_n &= \langle \psi_n | \partial_t p \rangle + \langle \partial_t \psi_n | p \rangle \\ &= \langle \psi_n | L p \rangle + \sum_m a_m \langle \dot{\nu} \, \partial_\nu \psi_n | \phi_m \rangle \\ &= \langle L^+ \psi_n | p \rangle + \dot{\nu} \sum_m a_m \langle \partial_\nu \psi_n | \phi_m \rangle, \end{aligned}$$

2

Where L^+ is the adjoint operator of L, ψ_n are its eigenfunctions and $\langle.|.\rangle$ is a suitable inner product. We single out the stationary mode to obtain the following "emission rate equation"

$$\begin{cases} \dot{\vec{a}} &= (\mathbf{\Lambda} + \mathbf{C}\dot{\nu})\,\vec{a} + \vec{c}\,\dot{\nu} \\ \nu &= \Phi + \vec{f}\cdot\vec{a} \end{cases}, \tag{7}$$

where f_n is the contribution to the flux due to the mode ϕ_n $(n \neq 0)$, $c_n = \langle\partial_\nu\,\psi_n|\phi_0\rangle$ and $C_{nm} = \langle\partial_\nu\,\psi_n|\phi_m\rangle$ are coupling terms, in that for uncoupled neurons μ and σ do not depend on the recurrent frequency ν, and $\partial_\nu\,\psi_n$ vanishes. $\mathbf{\Lambda}$ is the diagonal matrix of the common eigenvalues of L and L^+.

Stability, spectral analysis and transients

The system (7) has fixed points ν_0 given by the self-consistency equation [3, 2]

$$\begin{cases} \vec{a} &= 0 \\ \nu_0 &= \Phi(\nu_0) \end{cases}, \tag{8}$$

whose linear stability we assess using a perturbative approach. To this end we study the poles of the Laplace transform $\nu(s)$ of the linearized form of $\nu(t)$ in Eq. (7). The real and imaginary parts of these poles describe the characteristic times and the oscillatory properties of the collective activity $\nu(t)$.

Fig. 1 shows a subset of poles of $\nu(s)$ for an inhibitory population of linear IF neurons [5].

Such poles can be grouped in two classes. The first is related to the transmission delays ("transmission poles", red in Fig. 1), appearing only in coupled networks, approximately given by:

$$s_n^{(t)} \simeq \frac{1}{\delta}\ln|\Phi'| + i\,\frac{n\,\pi}{\delta}, \tag{9}$$

where n is any odd (even) integer for inhibitory (excitatory) populations, δ is the transmission delay and $\Phi' = \partial_\nu\Phi|_{\nu=\nu_0}$.

The fixed point becomes unstable when $\mathrm{Re}(s_n^{(t)}) > 0$ [8, 4], which happens exactly when

$$\Phi'(\nu_0) > 1, \tag{10}$$

for an excitatory population (as suggested in [3]). Stability of a weakly coupled inhibitory population requires $\Phi'(\nu_0) > -1$.

The "diffusion poles" $\{s_n^{(d)}\}$, (blue in Fig. 1) have negative real parts and do not contribute to the stability conditions. Far from instability $-1/\mathrm{Re}(s_n^{(d)})$ set the time scale of the transient of the network relaxation to the fixed point. For weak coupling, in a drift-dominated (supra-threshold) regime, $\{s_n^{(d)}\}$ are a perturbation of the eigenvalues λ_n of L; for the longest time scale:

$$s_1^{(d)} \simeq \lambda_1\left(1 + \frac{f_1\,c_1}{1 - \Phi' + \lambda_1\,\delta}\right). \tag{11}$$

It is worth noting how, despite the fact that there is no obvious *a priori* relation between the single neuron properties and characteristic times, and the dynamics of the collective activity, the single neuron transfer function Φ emerges in a
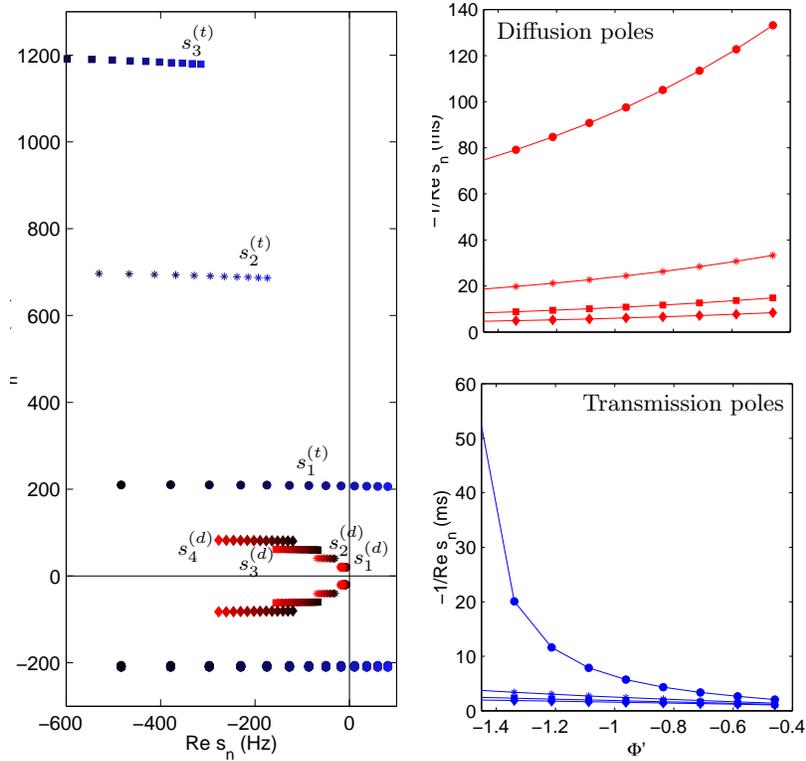
3

Figure 1: Left: poles distribution for recurrent inhibitory populations with different coupling strengths and, therefore, Φ'. Red: first 4 diffusion poles $(s_n^{(d)})$; blue: first 3 transmission poles $(s_n^{(t)})$ (poles are complex conjugate pairs). Right: Characteristic times vs Φ'.

leading role in determining both the stability of the system (via Eq. (10)), and the response times in Eq. (11).

The (stationary and transient) spectral content of $\nu(t)$ is embodied in the power spectrum $P(\omega)$, with $\omega_n^{(d,t)} \equiv \mathrm{Im}(s_n^{(d,t)})$. A non-trivial stationary power spectrum arises because of finite-size corrections to the mean field approximation: following [4], we assume that the N neurons are coherently affected by N-dependent fluctuations in the recurrent current, such that the spike emission process has Poisson statistics with parameter $N\nu(t)$.

The power spectrum of $\nu(t)$, subtracting the mean ν_0, is given by

$$P(\omega) = \frac{\nu_0/N}{\left| \left(e^{i\,\omega\,\delta} - \Phi' \right) - i\,\vec{f} \cdot \left(i\,\omega\,\mathbf{I} - \mathbf{\Lambda} \right)^{-1} \vec{c}\,\omega \right|^2} \tag{12}$$

where the numerator is the flat spectrum of the white noise approximating the finite-size fluctuations, vanishing for $N \to \infty$.

From the Figs. 2 it can be seen that: 1) both the characteristic times of the transient population response, and the frequency of the transient oscillations match well the predictions generated by the first diffusion poles; 2) the predicted
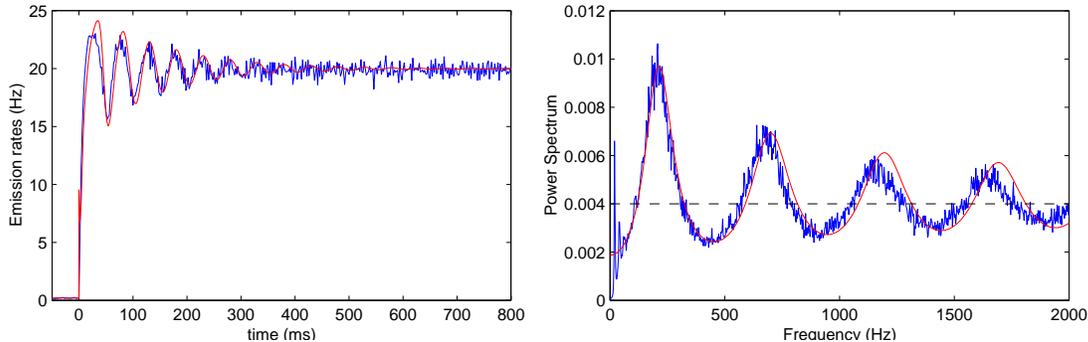
4

Figure 2: Simulations (blue) *vs* theory (red). Left: response to a step-wise stimulation. Right: power spectrum in stationary conditions. $P(\omega)$ is a superposition of Lorentzian distributions centred around ω_n, whose width is proportional to $-1/\mathrm{Re}(s_n)$. The dashed line in the plot on the right is the flat spectrum ν_0/N (see text).

power spectrum for the stationary population activity remarkably agrees with simulations; this is clearly seen in the figure for the high-ω, δ-related peaks, but we also note that the barely visible low-ω components of $P(\omega)$ actually match very well the above features of the transient.

Fig. 3 shows the theoretical predictions for the transient response of two excitatory populations, differing in the value of Φ'. It is seen that the larger Φ', the quicker the response. Φ' acts therefore as a "gain function" for the population response. Since Φ' is in the case at hand a monotonically increasing function of the synaptic couplings, we draw the tentative conclusion that in this situation the "learning" process entails a shortening of the population's reaction times to familiar stimuli (smaller latency).

References

[1] L. F. Abbot and Carl van Vreeswijk. Asynchronous states in networks of pulse-coupled oscillators. *Phys. Rev. E*, 48(2):1483–1490, 1993.

[2] Daniel J. Amit and Nicolas Brunel. Model of global spontaneous activity and local structured (learned) delay activity during delay periods in cerebral cortex. *Cerebral Cortex*, 7:237–252, 1997a.

[3] Daniel J. Amit and Misha Tsodyks. Quantitative study of attractor neural network retrieving at low spike rates: I. substrate–spikes, and neuronal gain. *Network*, 2:259, 1991.

[4] Nicolas Brunel and Vincent Hakim. Fast Global Oscillations in Netwoks of Integrate-and-Fire Neurons with Low Firing Rates. *Neural Computation*, 11:1621–1671, 1999.
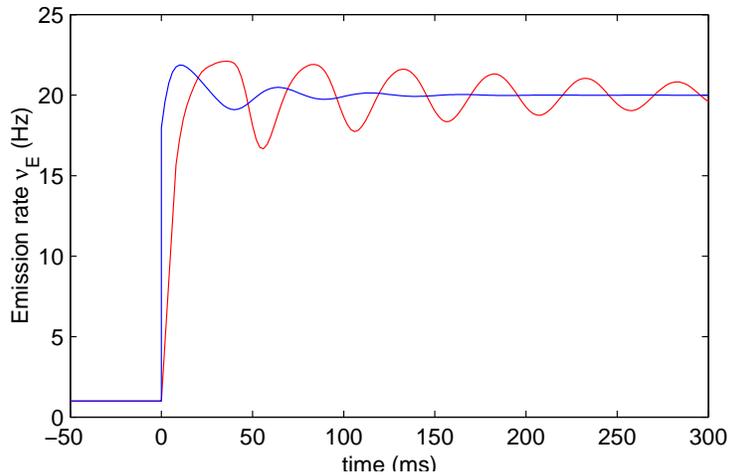
Figure 3: Transient response of two excitatory populations to a sudden increase in the external current: red, lower Φ'; blue, higher Φ'.

[5] Stefano Fusi and Maurizio Mattia. Collective Behavior of Networks with Linear (VLSI) Integrate-and-Fire Neurons. *Neural Computation*, 11(3):633–653, apr 1999.

[6] Bruce W. Knight, Dimitri Manin, and Lawrence Sirovich. Dynamical models of interacting neuron propulations in visual cortex. In E. C. Gerf, editor, *Proceedings of Symposium on Robotics and Cybernetics, Lille-France, July 9-12*, 1996.

[7] Hannes Risken. *The Fokker-Planck Equation: Methods of Solution and Applications*. Springer-Verlag, Berlin, 1984.

[8] Alessandro Treves. Mean-field analysis of neuronal spike dynamics. *Network*, 4:259–284, 1993.

[9] Henry C. Tuckwell. *Introduction to Theoretical Neurobiology*, volume 2. Cambridge University Press, 1988.