Stochastic Amplification of Fluctuations in Neural Networks

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The cerebral cortex exhibits complex patterns of oscillations even in the absence of external stimuli. Deciphering its nature, structure and function are challenging tasks. Cortical local field potentials are bistable and can fluctuate spontaneously between a quiescent (Down) and an active (Up) state, generating slow δ oscillations (also known as Up-and-Down States). Experimental evidence shows that spontaneous high oscillations (in the $\beta - \gamma$ band) emerge within Up states[1]; remarkably, similar oscillations do not appear in Down states. Moreover, this rhythm within Up states seems to be a collective phenomenon given that individual neurons do not lock to it. Our conclusion, supported by both theory and simulations, is that the collective phenomenon of "stochastic amplification of fluctuations" –previously described in other contexts such as Ecology[2] and Epidemiology– explains in an elegant manner, beyond model-dependent details, all this intriguing phenomenology described above[4].

One of the simplest model for Up and Down states describes the local field potential of the network, v, whose dynamics are regulated by a variable u, the synaptic utility, which measures the level of depression of the synaptic resources[3]:

$$\dot{v} = -\frac{v - V_r}{\tau} + \frac{w_{in}\mu u f(v)}{\tau}$$
$$\dot{u} = \frac{1-u}{\tau_R} - \mu u f(v), \qquad (1)$$

where τ and τ_R are the characteristic times of voltage leakage and synaptic recovery, respectively, w_{in} is the amplitude of internal inputs, V_r is the resting potential, and μ is the release fraction indicating the efficiency of synapses; the firing rate function, f, is assumed to depend on v as $f(v) = \alpha(v - T)$ if $v \geq T$, where T is a threshold value, and $f(v) = 0$.

This model presents two fixed points, which correspond to a high-activity level (Up state) and other quiescent (Down state). Adding noise to this equations, the system can switch between the two states.

To analyze fluctuations around a fixed point (v^*, u^*) of the deterministic dynamics, a standard linear stability analysis can be performed. Defining $x = v - v^*$ and $y = u - u^*$, one can linearize the deterministic part of the dynamics, writing the Jacobian matrix A, evaluated at every fixed point for the dynamics presented in equation 1. Also, we compute the power spectra of fluctuations of x and y, which both have a peak at

$$\omega_0 \simeq \sqrt{\det A - (\mathrm{Tr}A)^2/2}, \qquad (2)$$

A simple analysis of the characteristics of A which give a peak in the power spectrum (positive argument of the square root) reveals that A must have complex eigenvalues; in other words, the relaxation towards the stable fixed point should be in the form of damped oscillations (spiral trajectories) with a not too small damping frequency. Noise "kicks" the system away from the fixed point, and amplifies predominantly some frequency which –surprisingly enough– turns out to be *different* from the characteristic frequency of the deterministic damped oscillations. This is the mechanism of *stochastic amplification of fluctuations*.

Now, we can understand why this peak appears in the Up state but not in the Down: for the first one, eqs. 1 are strongly coupled –because of the high value of the firing rate f–, and eigenvalues turn out to be complex; for the Down state, the firing rate f is almost zero, equations 1 are essentially independent and eigenvalues become real.

The same analysis can be performed in other models of Up-and-Down dynamics (as excitation-inhibition models), but the arguments remain the same. Also, the mechanism only applies for variables describing the mean-field level, whose values oscillate around one (or more) fixed points. In the case of neurons, their microscopic values are integrating and spiking all the time, so we cannot observe the same peak at this level. In other words, stochastic amplification has to be viewed as a collective phenomenon.

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