

In sensory systems, populations of neurons have to track rapidly fluctuating inputs. We investigate here how the dynamics of intrinsic current determine their ability to respond faithfully to such inputs.

We have studied the dynamics of the instantaneous firing rate of one neuron, or equivalently the dynamics of the population firing rate for a large population of uncorrelated noisy spiking neurons. In the linear approximation, an oscillatory input current at frequency f induces an oscillatory response of the firing rate, with an amplitude $A(f)$ and a phase shift $L(f)$. Knowledge of these two functions is important for two reasons: (1) it allows to determine the response of the population to arbitrary time-varying inputs, if the modulation of these inputs is not too large; in particular, the large frequency limit is interesting because it tells us how fast a population of neurons can respond to fast transient inputs; (2) together with synaptic characteristics, it determines whether a large recurrent network of cells settles in an asynchronous or synchronous state.

Previous analytical studies on the leaky integrate-and-fire (LIF) showed that when the noise is uncorrelated (white noise) the firing rate modulation amplitude $A(f)$ decreases as $1/\sqrt{f}$ with a phase lag $L(f)$ of 45 degrees. In contrast, when the noise is temporally correlated, the response modulation amplitude is finite and it follows the oscillations of the input with zero phase lag. In particular, if the noise is generated by synapses with time constants in physiological ranges (2-5 msec) a population of LIF neurons is able to follow fast temporal changes in its input instantaneously.

LIF neurons are purely passive integrators which fire "spikes" each time the membrane potential V reaches a fixed threshold. Therefore one can wonder whether the response properties of these neurons are representative of real neurons. As a matter of fact we have found in simulations that simple conductance-based model neurons behave differently. This is the case for instance of the Wang-Buzsaki (WB) model in which the modulation amplitude of the dynamical response decays like $A(f) \propto 1/f$ and has a phase lag $L(f)$ slightly larger than 90 degrees at high frequencies.

To clarify the origin of this qualitatively different behavior, we have studied analytically a family of models in which the dynamics of the neuron are still one-dimensional but which incorporate in a phenomenological way active properties of neurons and dynamics of spike firing.

First, we considered the 'quadratic' integrate-and-fire (QIF) neuron. In this model active properties are taken into account through a source term proportional to V^2 . Such a model can be shown to reproduce faithfully the dynamics of neurons with slowly varying inputs, near the onset of firing, provided that the latter occurs through a saddle-node bifurcation. Because of this quadratic term the neuron membrane potential diverges in a finite time. This divergence corresponds to the firing of an action potential. We have studied this model analytically and shown that for high frequencies the modulation amplitude of the response scales as $1/f^2$ and its phase, $L(f)$, converges to 180 degrees. Therefore, although this model

provides a more appropriate description of the neuronal dynamics (in particular of the spike) than the LIF model it behaves qualitatively different from neuronal models with more realistic dynamics.

This discrepancy is likely to be due to the fact that even in the QIF model the structure of the spiking dynamics is not well described, leading to discrepancies for high frequency modulation. To validate this intuition we considered a new model, the 'exponential' integrate-and-fire (EIF) neuron in which a simplified sodium current with an instantaneous exponential voltage-dependent activation is responsible for spike generation. This active current has the form $I_{act} = g_L \Delta_T \exp((V - V_T)/\Delta_T)$ where g_L is the leak conductance, the "threshold" V_T characterizes the values of the potential above which I_{act} increases sharply. The sharpness of this increase is determined by the parameter Δ_T . Note that the derivative of the I-V curve vanishes at $V = V_T$ and that the radius of curvature of this curve at V_T is proportional to Δ_T and is inversely proportional to the sharpness of the spike. In particular, in the limit $\Delta_T \rightarrow 0$, the EIF model becomes equivalent to the LIF model. Note also that the exponential form of the active current can be intuitively obtained from the sodium activation curve of conductance-based model. This is usually described by a Boltzmann function which is well fitted by an exponential near the spike onset.

For white as well as for correlated noise, we have shown analytically that, in the EIF model, $A(f)$ decreases as $1/f$ and $L(f)$ tends to 90 degrees for large f . Numerical simulations showed that, for the appropriate choice of the parameters, g_L , V_T and Δ_T , the stationary and dynamical properties of the EIF model matches very well those of the simulated WB model.

At large noise, the EIF firing rate dynamical response is a low pass filter, with a cutoff frequency that can be determined analytically. The cutoff frequency is given by the largest of two quantities: (i) the inverse of the membrane time constant (ii) a cutoff frequency proportional to the background firing rate, to Δ_T , and inversely proportional to the slope of the f-I curve.

Numerical simulations indicate that if the activation of the 'sodium' current (or the 'exponential' current in EIF model) is not instantaneous, the signal is slightly more attenuated than $1/f$. But, for realistic values of the activation kinetic (around 0.1ms), the EIF models gives still an accurate description of the dynamical response up to a few hundred Hz.

Finally, numerical simulations were performed on more complex conductance-based models, including an A-type current, a slow potassium current and a persistent sodium current. The asymptotic regime remains unchanged. This confirms that the high input frequency dynamics depends only on the fast sodium current leading to spike emission. Thus, the EIF model captures well the high input frequency behavior of any neuron with a Boltzmann type activation function of sodium currents.