Columbia University Medical Center

Modeling Firing Rate Dynamics

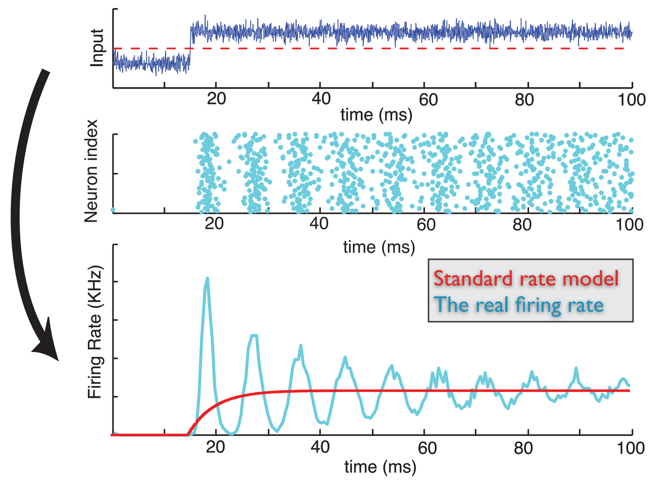
Evan S. Schaffer & L.F. Abbott

Swartz Center for Theoretical Neuroscience, Dept. of Neuroscience, Columbia University

think : theory
Center for Theoretical Neuroscience

The goal: from spikes to firing rate

Schematic: Can we predict the firing rate of a neuron as a *simple function* of an arbitrary *time-varying input*?



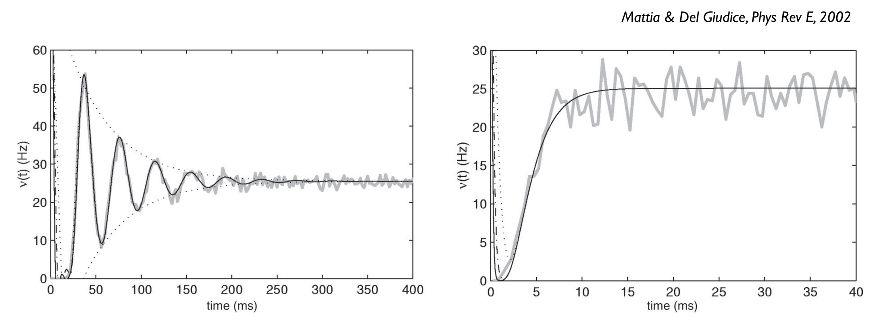
Sharp changes in input cause transient synchrony. while a simple rate model always exponentially relaxes toward steady-state.

Previous efforts: Solving for the firing rate requires tracking the voltage distribution with a Fokker-Planck equation. The boundary conditions make this difficult to solve.

Mattia & Del Giudice, Phys Rev E, 2002

Mattia and Del Giudice derive an expression for the eigenfunctions and (approximate) eigenvalues of the Fokker-Planck operator for the constant-leak IAF neuron. Their solution is of the form:

$$\nu(t) = \Phi(\mu,\sigma^2) + \tfrac{\sigma^2}{2\theta}e^{\xi}\sum_{n\neq 0} c_{\lambda_n}\zeta(\lambda_n)^2 e^{\lambda_n t}$$



Brunel & Hakim, Neural Computation, 1999

Brunel and Hakim use an expansion around the steady-state solution to obtain a linear approximation for the response to oscillating inputs of small amplitude. Approximating the firing rate dynamics ν(t) as:

$$\nu(t) = \nu_0\left[1 + \epsilon\hat{n}_0(\omega)e^{i\omega t} + \mathcal{O}(\epsilon^2)\right]$$

they find that the linear response function is:

$$\hat{n}_0(\omega) = \frac{\mu}{\sigma(1+i\omega\tau_m)}\,\frac{\frac{\delta U}{\delta y}(y_\theta,\omega) - \frac{\delta U}{\delta y}(y_r,\omega)}{U(y_\theta,\omega) - U(y_r,\omega)}$$

where $U(y,\omega)$ is a combinations of hypergeometric functions. Although this solution is quite general, the equations are extremely unfriendly. This is only barely tractable for large network simulations, let alone any anayltic work.

Why this problem is hard: Boundary conditions make this difficult to solve.

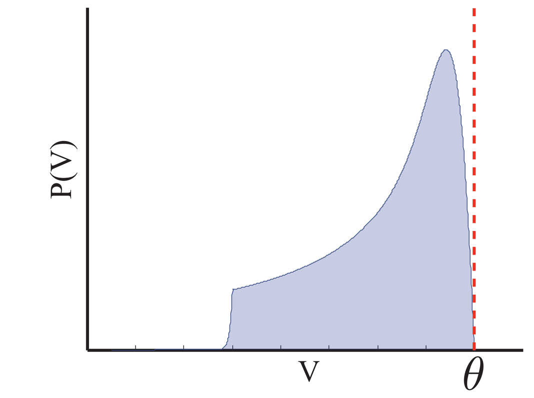
The Fokker-Planck equation for the standard Integrate-and-Fire neuron is:

$$\frac{\partial P}{\partial t} = -\frac{\partial}{\partial v}[(I-v)P] + D\frac{\partial^2 P}{\partial v^2}$$

with the boundary condition that:

$$P(\theta) = 0$$

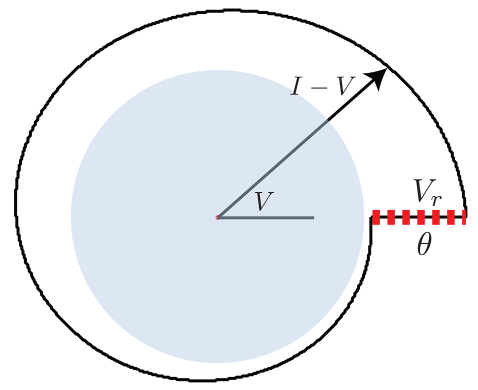
Intuitively, it is not surprising that this boundary condition makes the FP equation difficult to solve.



An approximation that simplifies the boundary conditions:

If we think of voltage as a periodic variable and allow flow in either direction across threshold, the dynamics are effectively unchanged, provided that:

$$I - V_r \gg D$$

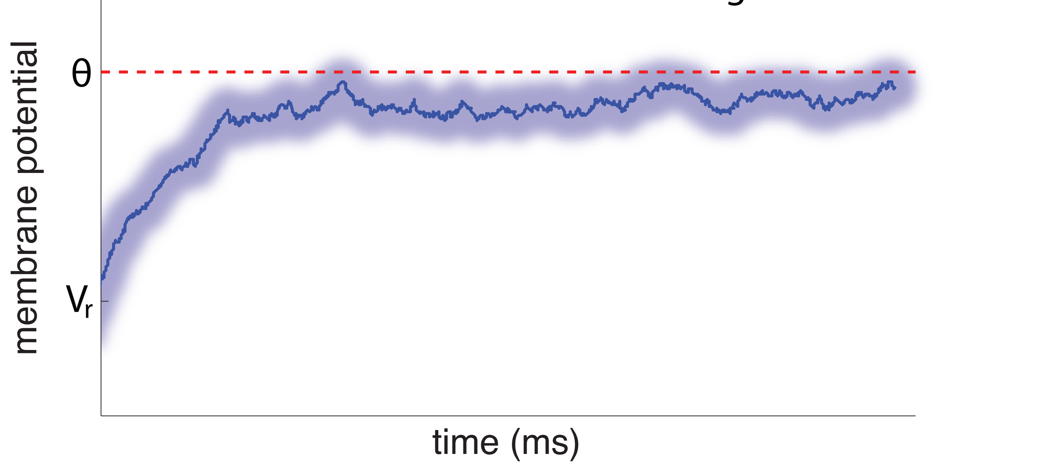


Approach: *assuming a simple form for P(v)*

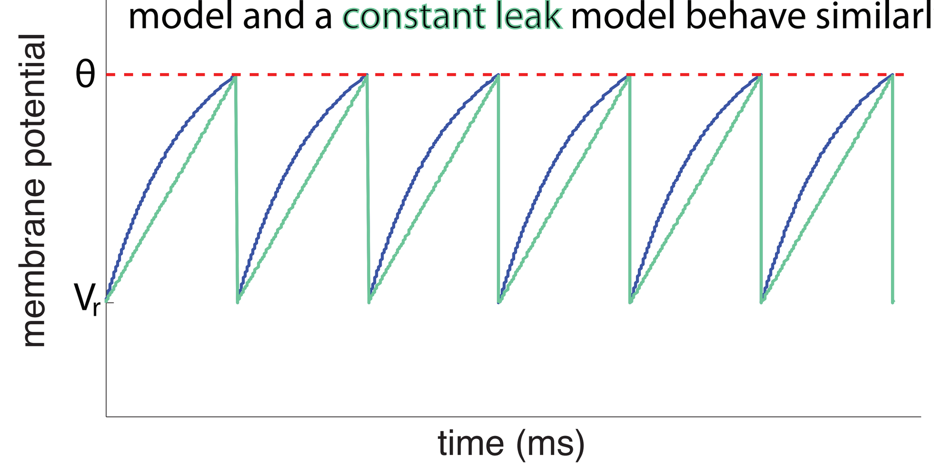
Formulating the model: If we assume P(v) to be a Gaussian on a ring (von Mises distribution), we can attempt to formulate a model by describing the dynamics of the voltage moments:

Approximations that simplify boundary conditions:

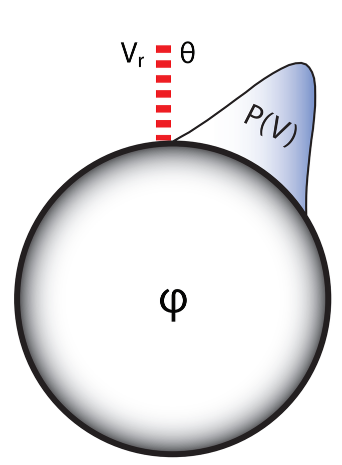
If the input is significantly below threshold, then threshold has a minimal effect on the voltage distribution



If the input is significantly above threshold, a leaky model and a constant leak model behave similarly



$$\text{bounded leaky IAF} \Rightarrow \begin{cases} \text{unbounded constant-leak IAF} & \text{for } I \gg \theta \\ \text{unbounded leaky IAF} & \text{for } I \ll \theta \end{cases}$$



Temporal dynamics of the moments:

$$\frac{d\mu}{dt} = \int_{-\infty}^{\infty} V\frac{\partial P}{\partial t}dV$$

$$\frac{d\sigma^2}{dt} = \int_{-\infty}^{\infty} V^2\frac{\partial P}{\partial t}dV$$

Given a mean input I and input variance $2D$, the evolution of the voltage probability density is described by a Fokker-Planck equation:

$$\frac{\partial P}{\partial t} = -\frac{\partial}{\partial v}[f(I,v)P] + D\frac{\partial^2 P}{\partial v^2}$$

where in the leaky IAF $f(I,v) = I - v$
and in constant leak IAF $f(I,v) = I - k$

Plugging in the Fokker-Planck equation into the right-hand side of the moment equations and computing the integrals, we have:

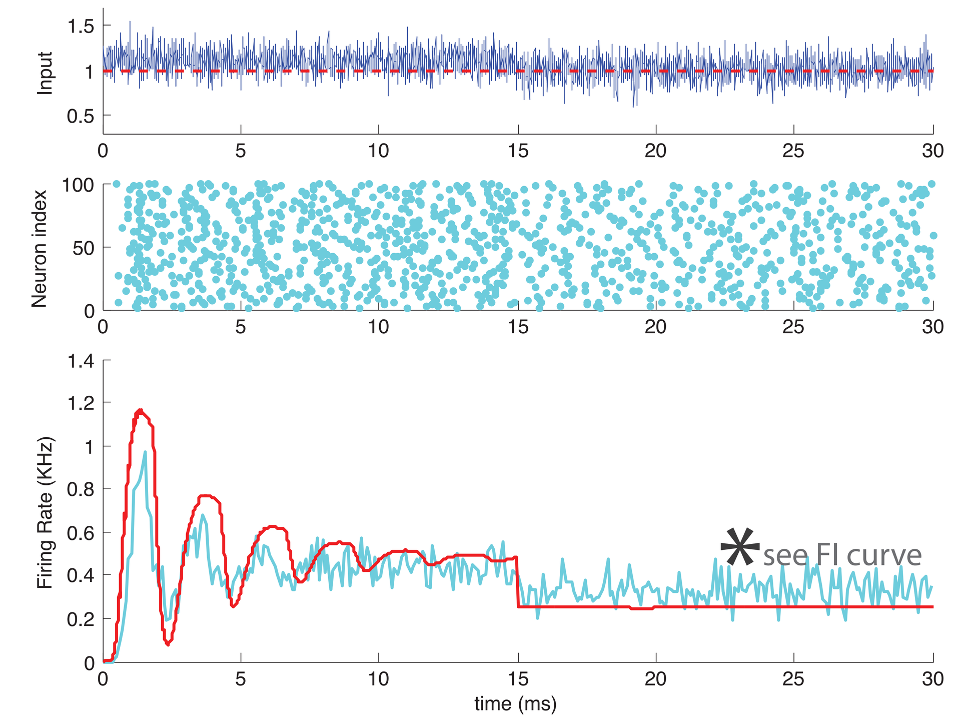
$$\frac{d\mu}{dt} = I(t) - \mu$$

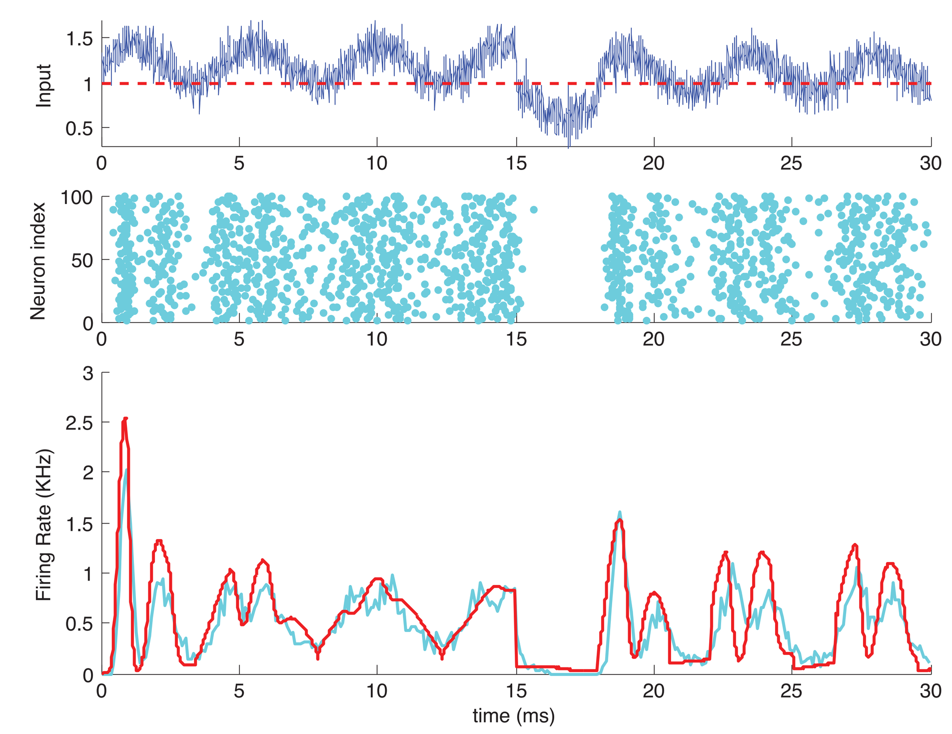
$$\frac{d\sigma^2}{dt} = 2D - \Theta[-I(t)]\sigma^2$$

where for the mean dynamics, we have used the leaky model for super- and supra-threshold input. We do this to avoid a discontinuity in the dynamics, but it comes at a cost -- in order to achieve a steady-state firing rate, we have to modify the rate equation. The firing rate is given by the unidirectional flux at threshold, where we replace the drift term by its steady-state:

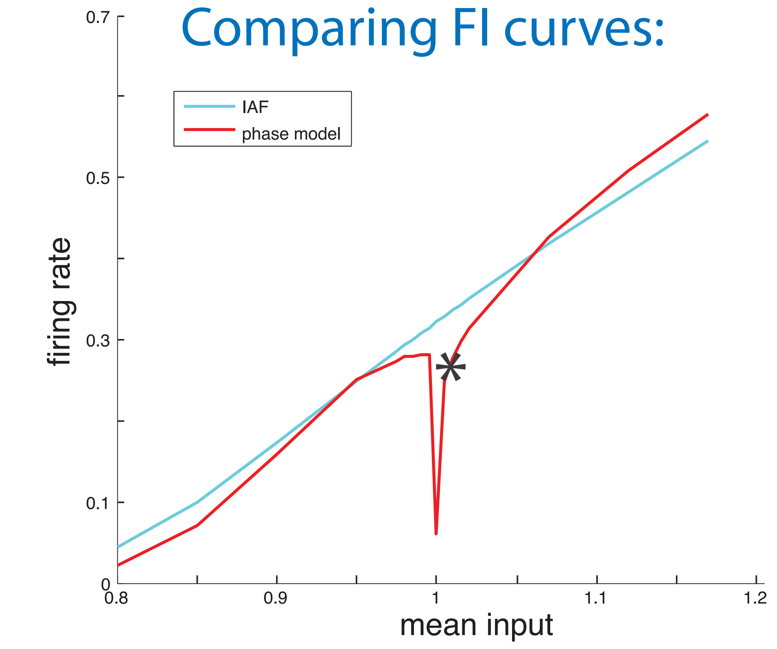
$$\nu(t) \equiv S_1(\theta) = \left[\Phi(I) + \sqrt{\frac{D}{2}}\right]P(\theta)$$

Sample Results





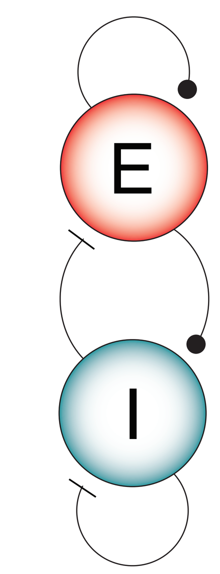
Comparing FI curves:



Extensions: *A Simple Circuit Model*

Starting with a classic linear rate network, the Wilson-Cowan model:

$$\begin{pmatrix}\dot{r}_e\\ \dot{r}_i\end{pmatrix} = \begin{pmatrix} w_{ee}-1 & -w_{ei} \\ w_{ie} & -w_{ii}-1\end{pmatrix}\begin{pmatrix}r_e\\ r_i\end{pmatrix} + \begin{pmatrix}I_e^{ext}\\ I_i^{ext}\end{pmatrix}$$



where each rate equation is now a function of the underlying voltage distribution:

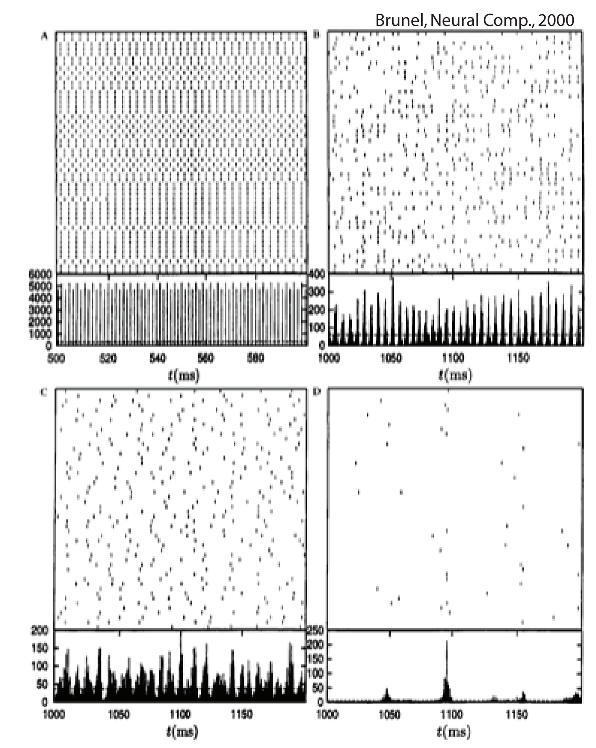
$$I_e = \frac{I_e^{ext} + (w_{ee}-1)\sqrt{\frac{D}{2}}P_e(\theta) - w_{ei}\left(I_iP_i(\theta) + \sqrt{\frac{D}{2}}P_i(\theta)\right)}{1-(w_{ee}-1)P_e(\theta)}$$

$$I_i = \frac{I_i^{ext} + w_{ie}\left(I_eP_e(\theta) + \sqrt{\frac{D}{2}}P_e(\theta)\right) - (w_{ii}+1)DP_i(\theta)}{1+(w_{ii}+1)P_i(\theta)}$$

$$\frac{d\mu_x}{dt} = I_x(t) - \mu_x$$

$$\frac{d\sigma_x^2}{dt} = 2D - \Theta[-I_x(t)]\sigma_x^2$$

We want to ask what firing regimes are possible. In principle this should make possible firing regimes of synchrony/asynchrony and regular/irregular firing. It would be nice if this qualitatively matches the parameter space outlined by Brunel (2000) for a network of leaky IAF neurons



References:
Fusi S, Mattia M. Collecctive Behavior of Networks with Linear (VLSI) Integrate-and-Fire Neurons. Neural Computation, 1999.
Brunel, N. Dynamics of networks of randomly connected excitatory and inhibitory spiking neurons. J. Physiol. (Paris), 2000.
Brunel N, Hakim V. Fast global oscillations in networks of integrate-and-fire neurons with low firing rates. Neural Computation, 1999.
Ermentrout and Kopell. Parabolic Bursting in an Excitable System Coupled With a Slow Oscilation. SIAM J Appl. Math 1986.
Mattia M, Del Giudice P. Population dynamics of interacting spiking neurons. Phys. Rev. E., 2002.
Wilson, H.R. & Cowan, J.D. Excitatory and inhibitory interactions in localized populations of model neurons. Biophys. J., 1972.