Kinetic Theory for Complex Neuronal Networks

Dedicated to the 70th Birthday of Professor Vladimir Evgenyevich Zakharov

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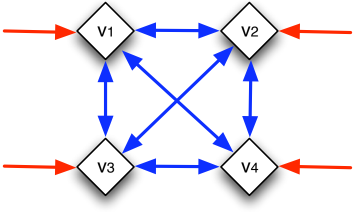
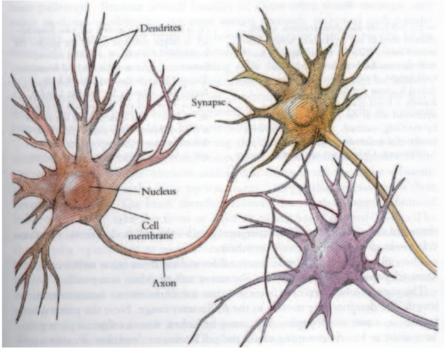
Outline

- Kinetic Theory for Integrate & Fire Systems
- Maximum Entropy Closure
- Mean-Field and Fokker-Planck Limits
- Neuronal Network Oscillations
- Complex Networks

Neurons

- axons, soma, dendrites
- pre-synaptic, post-synaptic (junctions: synapses)
- excitatory, inhibitory





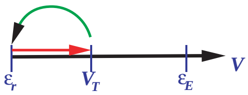
Excitatory Linear Integrate-And-Fire Neuronal Network

$$\tau \frac{dV^i(t)}{dt} = -(V^i(t) - \varepsilon_r) - G_E^i(t)(V^i(t) - \varepsilon_E), \quad i = 1, \ldots, N$$

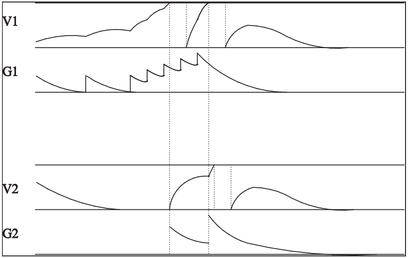
$$\sigma \frac{dG_E^i(t)}{dt} = -G_E^i(t) + f \sum_k \delta(t - t_{ik}) + \frac{S}{N} \sum_{j \neq i} \sum_k \delta(t - \tilde{t}_{jk})$$

- $V^i(t)$ – membrane potential $\quad G_E^i(t)$ – conductance
- Poisson trains: t_{ik}-external, rate $\nu(t)$, $\tilde{t}_{jk}$-network, rate $Nm(t)$
- $m(t)$-firing rate per neuron

Mechanism:



Voltage and Conductance:

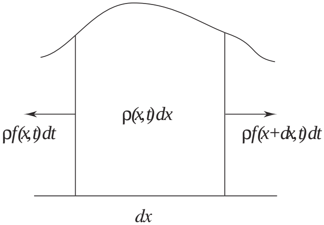


Boltzmann Equation

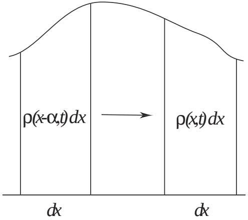
$$\frac{dx}{dt} = f(x) + \alpha \sum_k \delta(t - t_k)$$

- t_k – Poisson train, rate ν at $t = t_k$, x jumps by α.
- Probability density $\rho(x,t)$.

$t \neq t_k$:



$t = t_k$:



$$\frac{\partial \rho}{\partial t} = \frac{\partial (f\rho)}{\partial x} + \nu[\rho(x-\alpha) - \rho(x)]$$

Diffusion Approximation

$$\frac{\partial \rho}{\partial t} = \frac{\partial (f\rho)}{\partial x} + \nu[\rho(x-\alpha) - \rho(x)]$$

If $\alpha \ll 1$, $\nu \gg 1$, $\alpha\nu = \mathcal{O}(1)$, Taylor expand the difference term:

$$\begin{aligned}
\frac{\partial \rho}{\partial t} &= \frac{\partial (f\rho)}{\partial x} - \alpha\nu\frac{\partial \rho}{\partial x} + \frac{\alpha^2\nu}{2}\frac{\partial^2 \rho}{\partial x^2} \\
&= \frac{\partial}{\partial x}\left[f\rho - \alpha\nu\rho + \alpha\frac{\alpha\nu}{2}\frac{\partial \rho}{\partial x}\right] \\
&= -\frac{\partial J}{\partial x}
\end{aligned}$$

Boltzmann-Diffusion Equation for the I&F System

$$\frac{\partial \rho}{\partial t} = \frac{\partial}{\partial v}\left\{\left[\left(\frac{v-\varepsilon_r}{\tau}\right) + g\left(\frac{v-\varepsilon_E}{\tau}\right)\right]\rho\right\} + \frac{1}{\sigma}\frac{\partial}{\partial g}\left\{[g-\bar{g}(t)]\,\rho + \sigma_g^2(t)\frac{\partial \rho}{\partial g}\right\} = -\frac{\partial J_v}{\partial v} - \frac{\partial J_g}{\partial g}$$

$$\bar{g}(t) = \nu(t) f + m(t) S \qquad \sigma_g^2(t) = \frac{f^2 \nu(t)}{2\sigma} + \frac{S^2 m(t)}{2\sigma N}$$

BC: $J_v(\varepsilon_r, \rho, t) = J_v(V_T, \rho, t) = m(t) \quad \Rightarrow \quad$ *Nonlinear Problem*

Maximum Entropy Closure: Eliminate Conductance (David Cai, Adi Rangan)

Hierarchy: $\varrho(v,t) = \int_{-\infty}^{\infty} \rho(v,g,t)\,dg \qquad \mu_n(v,t) = \int_{-\infty}^{\infty} g^n \frac{\rho(v,g,t)}{\varrho(v,t)}\,dg$

Entropy: $S[\rho] = -\int_{-\infty}^{\infty} \rho(v,g,t)\log\frac{\rho(v,g,t)}{\rho_0(g)}\,dg, \quad \rho_0(g) = \frac{1}{\sqrt{2\pi}\sigma_g}\exp\left[-\frac{(g-\bar{g})^2}{2\sigma_g^2}\right]$

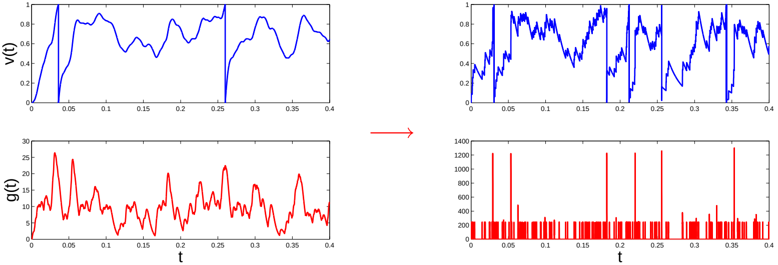
$\rho_0(g)$ – equilibrium distribution of conductance

$$\max S[\rho], \quad \text{constraints: } \varrho(v) \;\; \mu_1(v) \Rightarrow \mu_2(v) = \mu_1^2(v) + \sigma_g^2$$

$\Rightarrow$ **2 Kinetic Equations** for $\varrho(v)$ and $\mu_1(v)$
plus nonlinear boundary conditions involving $m(t)$
$\Rightarrow$ Traded 1 PDE in 3 variables for 2 PDE's in 2 variables

(Cai & al. [2004], Cai & al. [2006], Rangan & Cai [2006])

Fokker-Planck Equation for instantaneous conductance scale:



$$\tau \frac{\partial \rho}{\partial t} = \frac{\partial}{\partial v}\left\{\left[\left(1+\bar{g}(t)+\sigma_g^2(t)\right)v-\left(\bar{g}(t)+\sigma_g^2(t)\right)\varepsilon_E-\varepsilon_r\right]\rho(v,t)+\sigma_g^2(t)\,(\varepsilon_E-v)^2\,\frac{\partial \rho(v,t)}{\partial v}\right\} = -\frac{\partial J(v,t)}{\partial t}$$

$$\bar{g}(t) = \nu(t)f + m(t)S \qquad \sigma_g^2(t) = \frac{1}{2}\left[f^2\nu(t) + \frac{S^2 m(t)}{N}\right] \qquad \text{BC: } J(\varepsilon_r,t) = J(V_T,t) = m(t)$$

$$\frac{\partial \rho}{\partial t} = 0 \quad \Rightarrow \quad \rho = \rho(v) \qquad \text{Gain Curves: } \int_{\varepsilon_r}^{V_T} \rho(v)dv = 1 \quad \Rightarrow \quad m = m(f\nu)$$

(Cai & al. [2004], Cai & al. [2006], Kovačič & al. [2009])

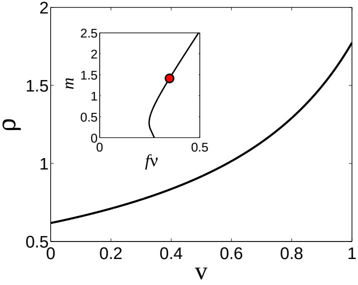
Mean-Driven Limit: $\sigma_g^2/\bar{g} \to 0$

Voltage PDF: $\rho(v) = \dfrac{\tau m}{(\bar{g}+1)(V_S - v)}$ $\qquad V_S = \dfrac{\varepsilon_r + \bar{g}\varepsilon_E}{\bar{g}+1} > V_T$

Gain Curve: Exact Parametrization in $g > B = \dfrac{V_T - \varepsilon_r}{\varepsilon_E - V_T}$:

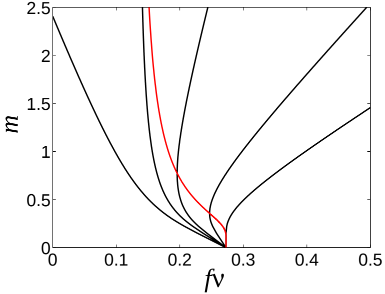
$$m = \frac{(1+g)}{\tau \ln \dfrac{(1+B)g}{g-B}} \qquad f\nu = g - \frac{S(1+g)}{\tau \ln \dfrac{(1+B)g}{g-B}}$$

Voltage PDF:



$S = 0.1,\ \tau = 1$

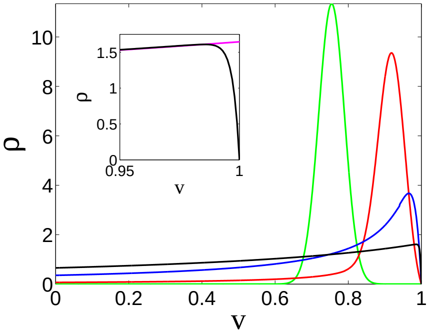
Gain curves:



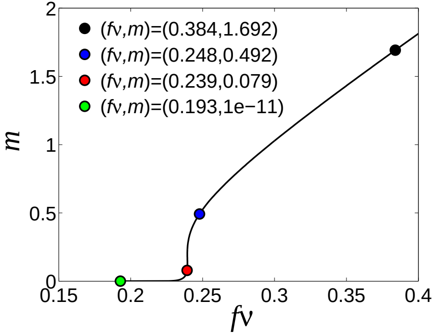
$S = 0.3,\ S = \tau \ln B,\ 0.2,\ 0.1,\ 0$

Probability Density Functions along a Gain Curve: $\sigma_g^2/\bar{g} \ll 1$

Voltage PDF:

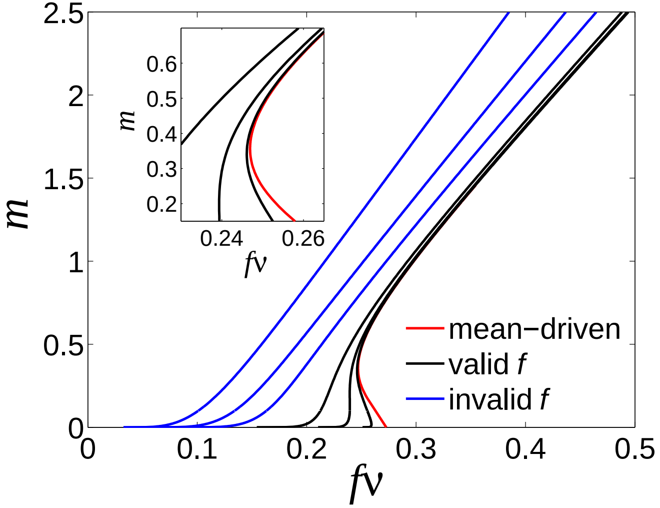


Gain Curve:



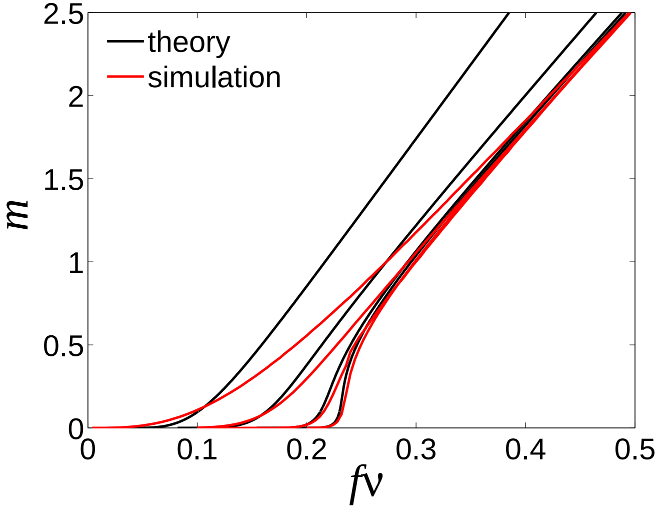
$\tau = 1,\ f = 0.001,\ S = 0.1,\ N = 1000$

Gain Curves and Hysteresis: $\sigma_g^2/\bar{g} \ll 1$



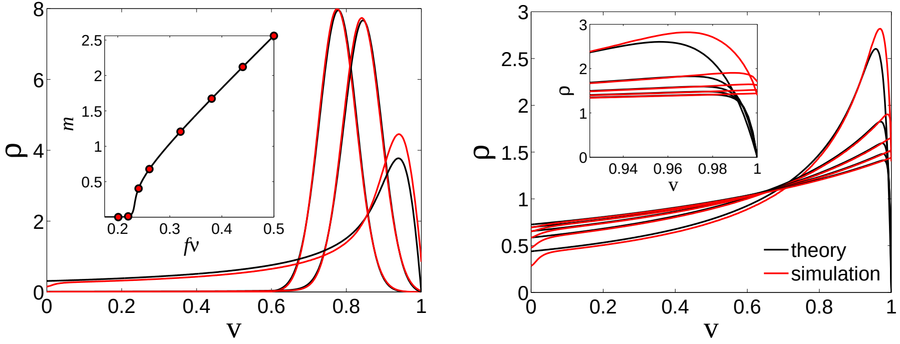
Left to right: $f = 0.1,\ 0.05,\ 0.025,\ 0.005,\ 0.001,\ 0.0001,\ 0$

Comparison with Simulations: Gain Curves



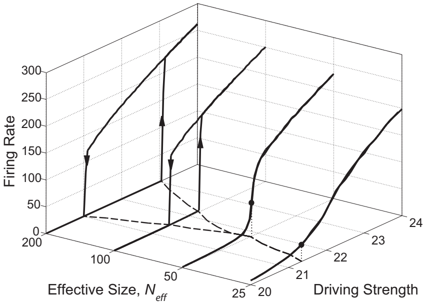
$f = 0.1,\ 0.025,\ 0.005,\ 0.002$

Comparison with Simulations: PDF's

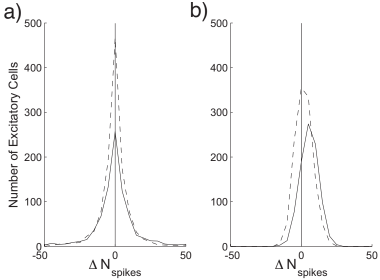


$f = 0.002, \ \tau = 1, \ S = 0.1, \ N = 500$

Hysteresis in More Realistic Models



Conductance-based, excitatory I&F, 50% simple 50% complex cells, sparse, finite conductance time

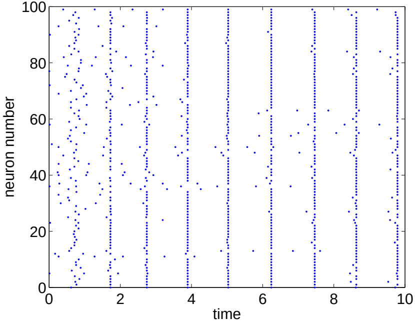


Realistic model of orientation tuning in primary visual cortex, excitatory neurons: (a) simple cells, (b) complex cells

(Tao & al. [2006])

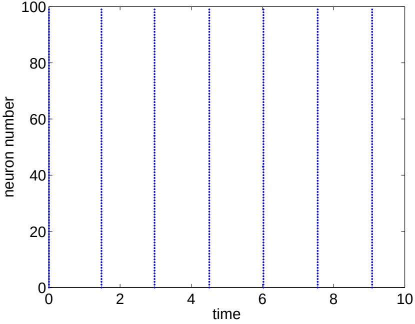
Synchronous Oscillations (Katie Newhall)

Partial synchrony



$$f = 0.01, \; f\nu = 1.2,$$
$$S = 0.4, \; N = 100$$

Total synchrony



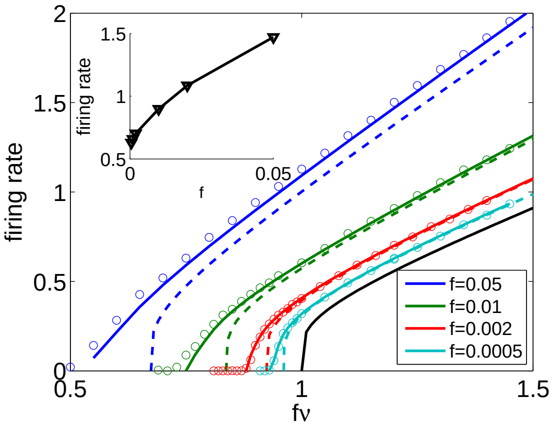
$$f = 0.001, \; f\nu = 1.2$$
$$S = 2.0, \; N = 100$$

(Newhall & al. [2009], Newhall & al. [2010])

Gain Curves: period^{-1} v/s $f\nu$

dashed - Gaussian approx.
solid - first passage time
circles - simulations
black - deterministic rate

- Good agreement where diffusion approximation valid
- For fixed (superthreshold) $f\nu$, dependence on f is linear (larger fluctuations, fires faster)

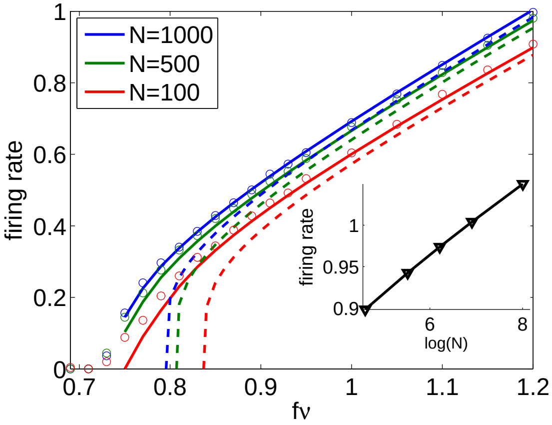


N=100, S=5.0

Gain Curves: period^{-1} v/s $f\nu$

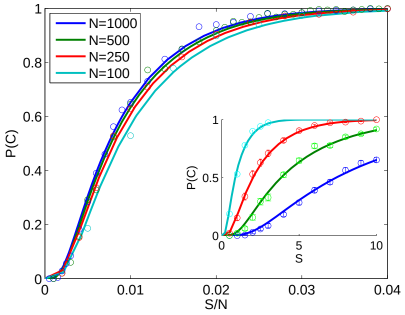
dashed - Gaussian approx.
solid - first passage time
circles - simulations

- For fixed (superthreshold) $f\nu$, dependence on N is logarithmic (more neurons, fires faster)



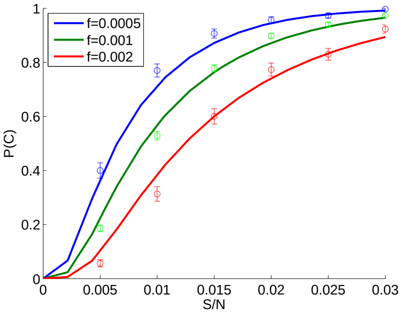
$f = 0.01, S = 20.0$

Probability for Network to Synchronize



$f\nu = 1.2, f = 0.001$

Larger network needs larger coupling to maintain synchrony



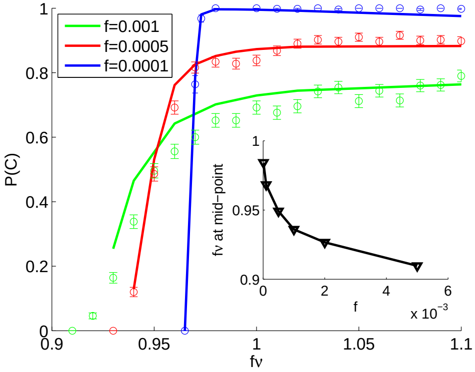
$f\nu = 1.2, N = 100$

Larger fluctuations need larger coupling to maintain synchrony

Phase Transition in Synchrony

As fluctuations $\to 0$, probability for synchrony approaches deterministic limit:

- No firing for subthreshold drive
- 100% firing for superthreshold drive.

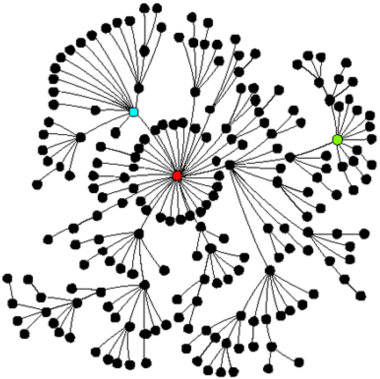


$N = 100, \quad S = 1.5$

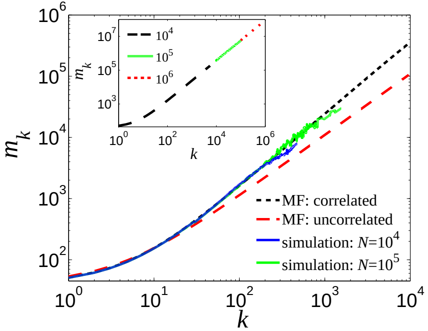
Architectural v/s Functional Connectivity in Complex Networks (Maxim Shkarayev)

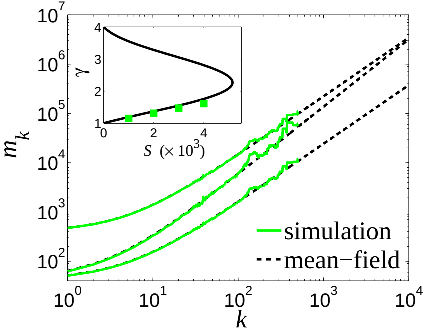
Complex networks:

- incoming (outgoing) degree of a neuron = number of connections from (to) other neurons
- Scale Free: degree distribution $P(k) \sim k^{-\gamma}$, $2 < \gamma < 3$
- Statistical quantities depend on neuron's degree: $\rho_k(v,t)$, $m_k(t)$
- Functional connectivity: firing rate distribution or membrane-potential correlations



Scale-Free Tree

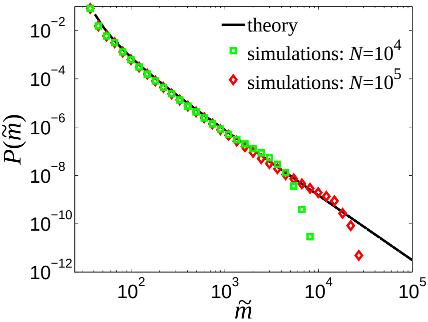




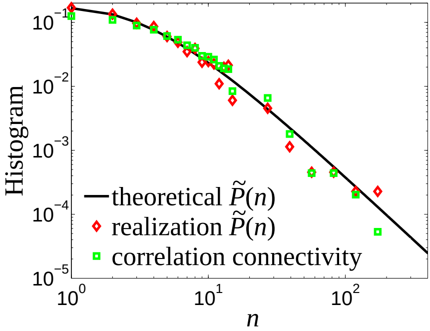
Mean-field description suffices

$m_k = k^{-\gamma}$

Functional from Architectural Connectivity



Firing rate distribution is scale free



Membrane potential correlations distribution is scale free

Conclusions

- Statistical description of the neuronal voltages, conductances, and network firing rate
- Reduction to time and voltage alone via a closure using maximum entropy principle
- Fokker-Planck description yields bifurcation structure in asynchronous regime
- Fokker-Planck description yields period and probability of oscillations
- Mean-field description infers functional from architectural connectivity
- Thanks to NSF