Part II

Mechanistic Models of cortical circuits

From spiking neurons to firing rate equations (2 lectures, Laureline Logiaco)

Inhibition stabilized networks and supralinear stabilized networks (Mario Dipoppa)

Neural variability in rate models ; The choice of spiking vs. rate modeling (Mario Dipoppa)

Hopfield's memory network model and its equilibrium theory (Alessandro Ingrosso)

Chaotic rate networks studied with dynamic mean field theory (Alessandro Ingrosso)

Empirical vs. mechanistic modeling

Empirical models → Mechanistic models

Use a very flexible model that is empirically adjusted to observed data.

Use (bio)physically defined components.
Constrain the interactions between components (using data or making assumptions).
The behavior of the system mainly emerges due to the specific model constraints.

Part I of the class: empirical modeling

data $\longrightarrow$ $\boxed{\text{Fitting procedure}}$ $\longrightarrow$ fitted model

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- **tear appart the processing of one area from the one of upstream areas**

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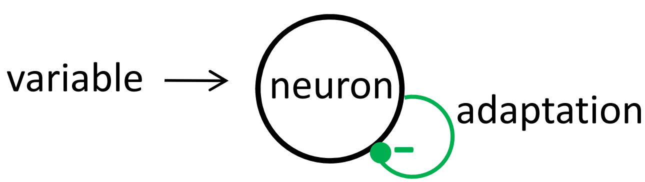
- **effective modeling rather than explicit link to specific neuronal embodied objects; predictions?**

real circuit



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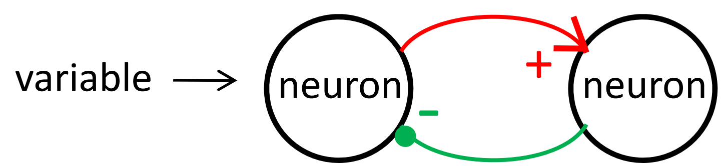

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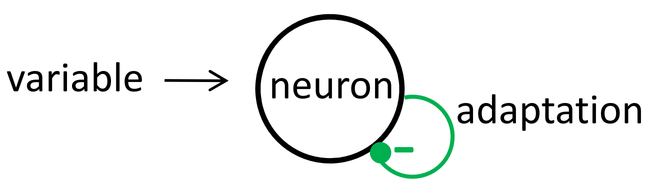

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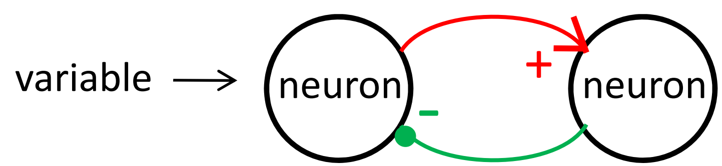
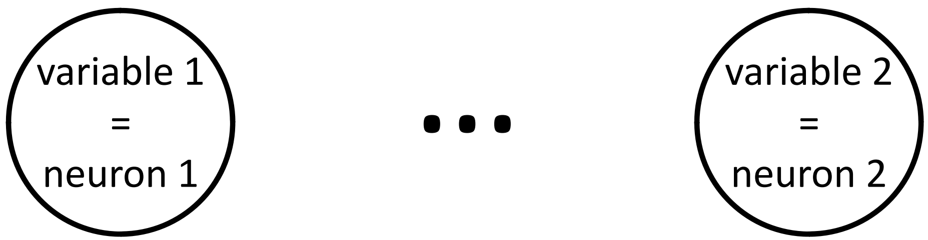


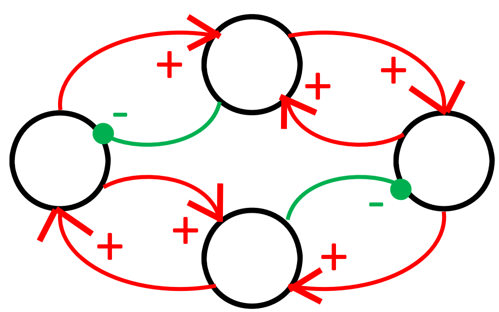
- **complex fitted model can be hard to understand**

Alternative to empirical modeling: mechanistic modeling

1) Define model variables as biophysically defined components, e.g. neurons:



2) Define the interactions between components (using insights from data if possible)



3) Analyze, or predict, or observe through simulations, the connected system's behavior; compare to reality

Why mechanistic models?

- Pros:

Mapping between the world and model components made explicit at some level of description (often, individual neurons or populations of neurons)

Attempts to explain the function of the whole system through interactions between model components

When successful, brings both an understanding of the function and predictions

- Cons:

Model often built with missing information (e.g. need to make assumptions about the connectivity)

No automatic « recipe » to make the model resemble the data at the system level

No automatic « recipe » to build intuition about emerging function in a complex system

Difficulty choosing the right level of description (brain area, neuronal population, single neuron, ion channel)

Difficulty choosing what to model and what to leave out

A mechanistic approach: from single neurons to population activity

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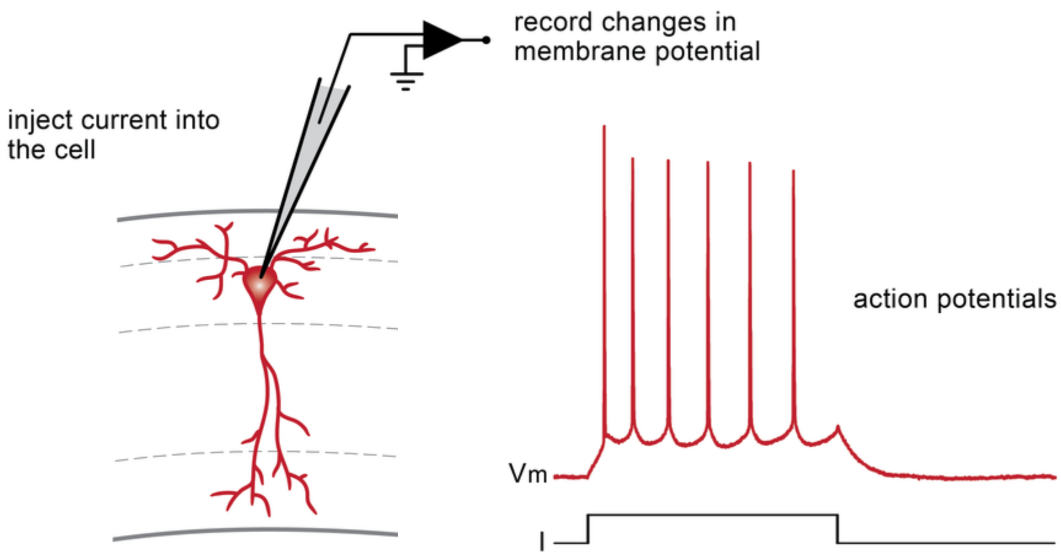
How to choose a good single neuron model?

Map the input-output (spike times)

In a (silent) slice:



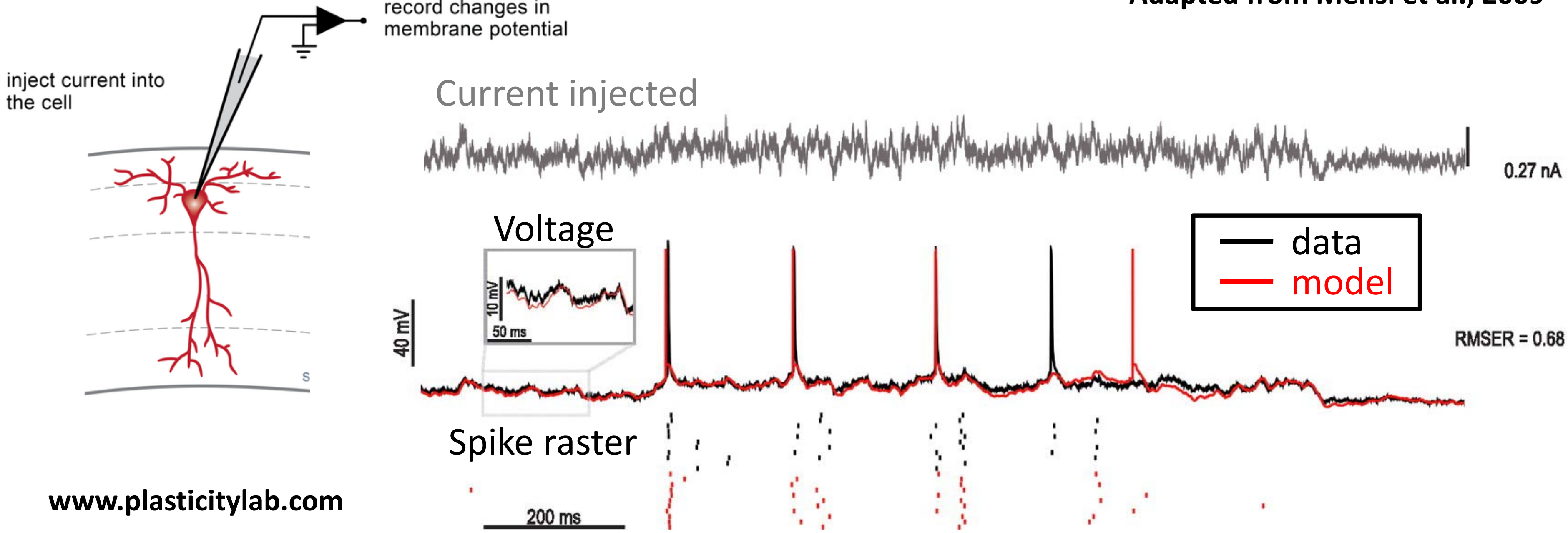
www.plasticitylab.com

A mechanistic approach: from single neurons to population activity

How to choose a good single neuron model?
Map the input-output (spike times)

Single neurons show reliable spiking patterns in response to in-vivo like fluctuating currents

Adapted from Mensi et al., 2009



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~80% of spikes predicted with 4 ms precision

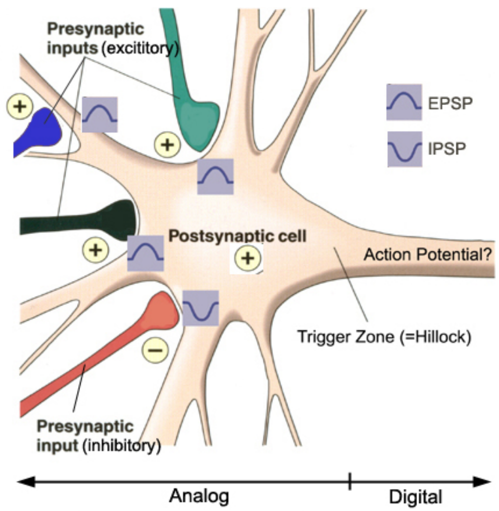
A mechanistic approach: from single neurons to population activity

Modeling the input-output function of neuron i:

$$\frac{p(spike)}{dt} \leftarrow \lambda_i(t) = \lambda_o \exp\left(X_{syn,\,i}(t) + \eta * S_i(t)\right)$$

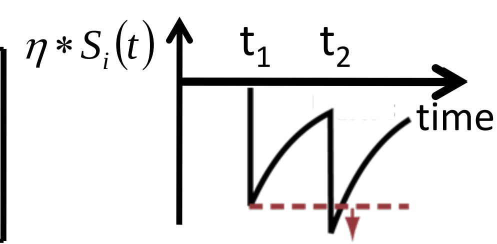
Where: **1.** $X_{syn,\,i}(t)$ is the synaptic input filtered by the neuron's membrane

$$X_{syn,\,i}(t) = \sum_{exc.\,inputs} EPSP + \sum_{inh.\,inputs} IPSP$$



2. η is a spike-history filter with long timescales

$S_i = \sum_{t_{spike,\,i}} \delta\left(t - t_{spike,\,i}\right)$ is the spike train



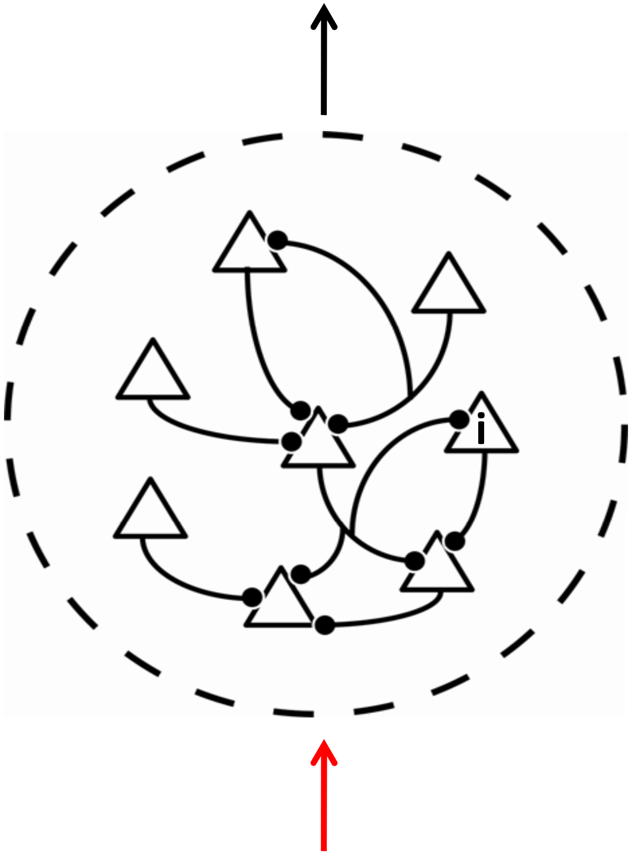
A mechanistic approach: from single neurons to population activity

Model for single neuron i:

$$\lambda_i(t) = \lambda_o \exp\left(X_{syn,\,i}(t) + \eta * S_i(t)\right)$$

A mechanistic approach: from single neurons to population activity

Population rate R(t)



External input (t)

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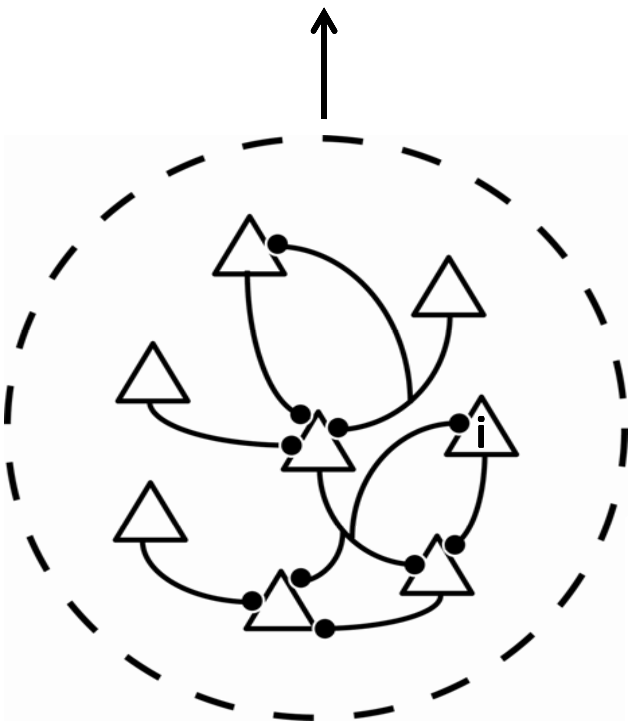

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Description of correlations between different $X_{syn,i}(t)$

A mechanistic approach: from single neurons to population activity

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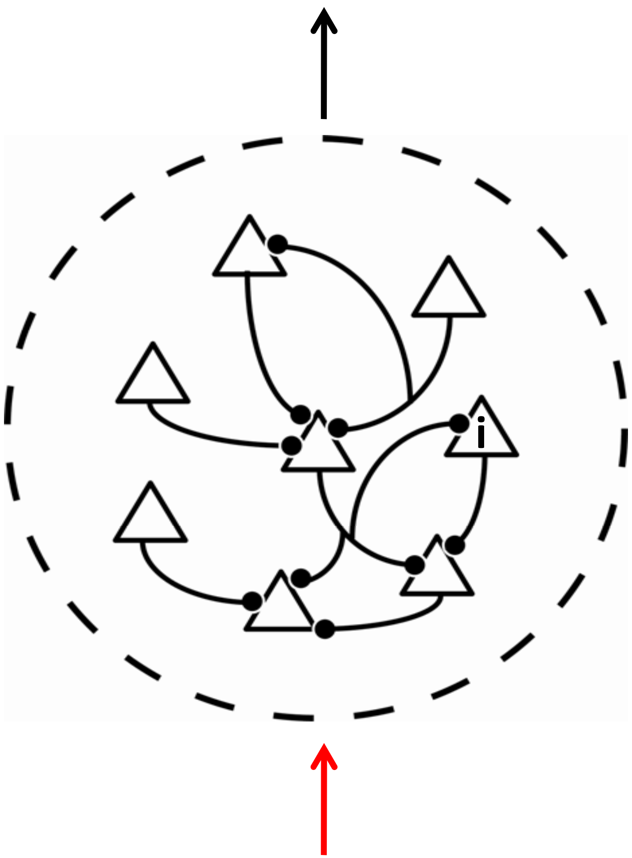

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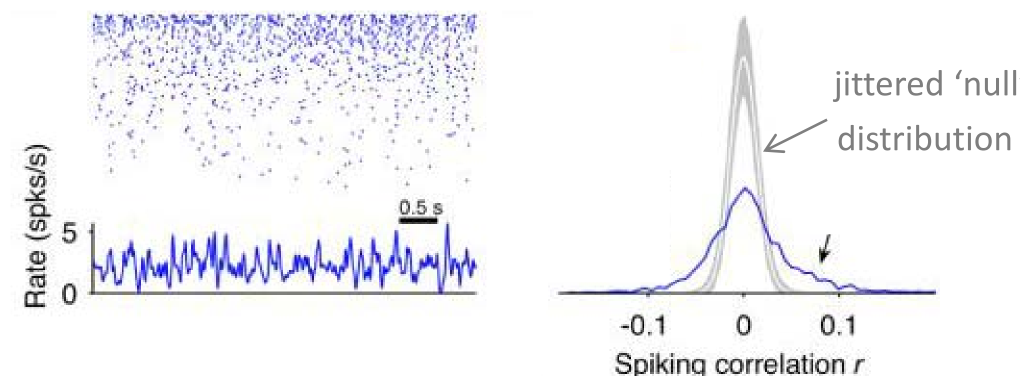
Raster of different neurons in rat's cortex in vivo



=> approximatively independent spike trains within a network.
Plausible causes: sparse connections and/or strong E-I balance

Renart et al, 2010

A mechanistic approach: from single neurons to population activity

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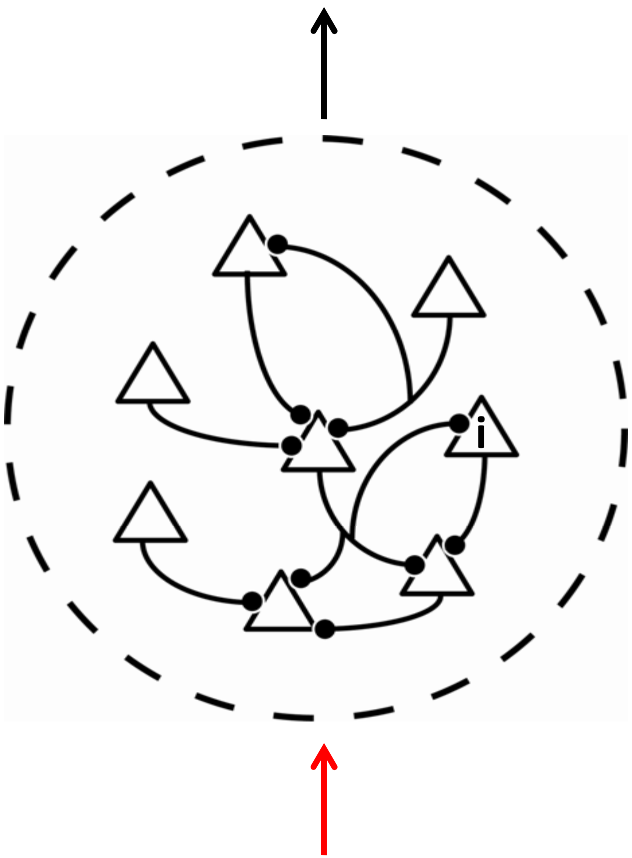

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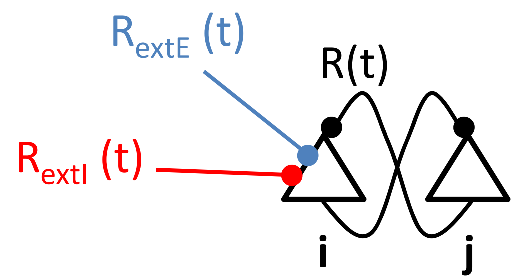
We want to compute: $E_{neurons}\left[\lambda_i(t)\right] = R(t)$

assuming uncorrelatedness between synaptic inputs.

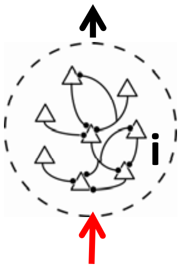


$$X_{syn,i}(t) = \sum_g \sum_{j \to i \in g} \sum_{spikes\ neuron\ j:\, s_j} \kappa_g * \delta\left(t - t_j\right)$$

WHITE BOARD TIME!

From single neurons to population rate

Population rate R(t)



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Steps:

-computing the input's mean and variance across the population

-separating the contribution of the input variability and of the intrinsic variability given a fixed input

-approximating the history dependence of the intrinsic variability through past escape rates (~Poisson)

-expressing the adaptation effect as a linear and a non-linear contribution in response to different inputs

-neglecting the variance of the nonlinear adaptation effect when averaging the rate over different inputs

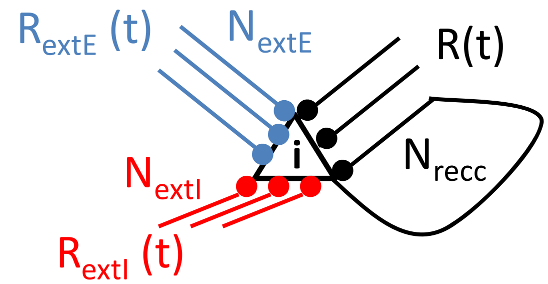
From single neurons to population rate

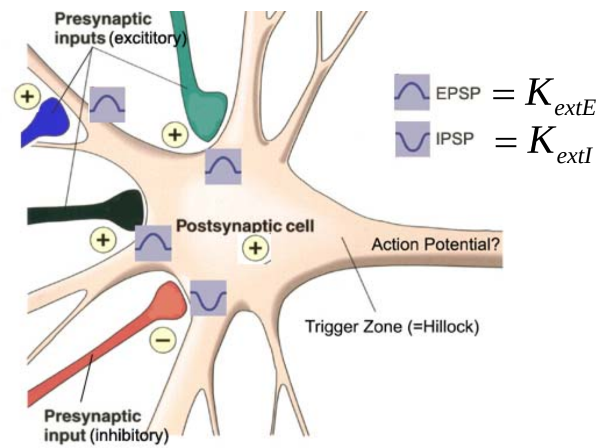
GLM: $\rho_i(t) = \lambda_o \exp\left(X_{syn,i}(t) + \eta * S_i(t)\right)$

Assume different neurons receive i.i.d. $X_{syn,i}(t)$

$$\boxed{R(t) = E_{neurons\ i}\left[\rho_i(t)\right] \approx \lambda_0 \exp\left(\mu_Z(t) + \left(\frac{\sigma_Z^2(t)}{2}\right)\right)}$$

Z: « effective drive», Gaussian variable related to X but approximately accounting for adaptation





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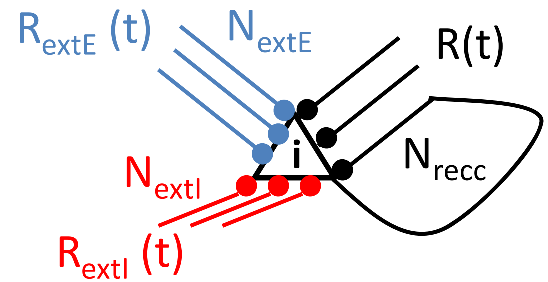

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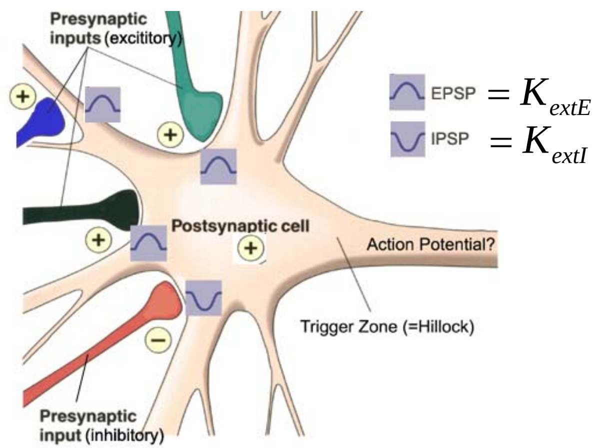

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MEAN DRIVE: $$\mu_Z \approx E_{neurons\ i}\left[X_{syn,i}(t) + \eta * S_i(t)\right]$$

$$= N_{extE}\ K_{extE} * R_{extE} + N_{extI}\ K_{extI} * R_{extI} + N_{recc}\ K_{recc} * R + \tilde{\eta} * R$$

VARIANCE DRIVE: $$\sigma_Z^2 = N_{recc}\ \Lambda_{recc}^2 * R + N_{extE}\ \Lambda_{extE}^2 * R_{extE} + N_{extI}\ \Lambda_{extI}^2 * R_{extI}$$

with $$\forall s,\quad \Lambda^2(s) = \left(\mathrm{K}(s) + \tilde{\eta} * \Gamma_{R_b} * \mathrm{K}(s)\right)^2$$

From single neurons to population rate

How successful is this approach, compared to ‘naive’ approximations?

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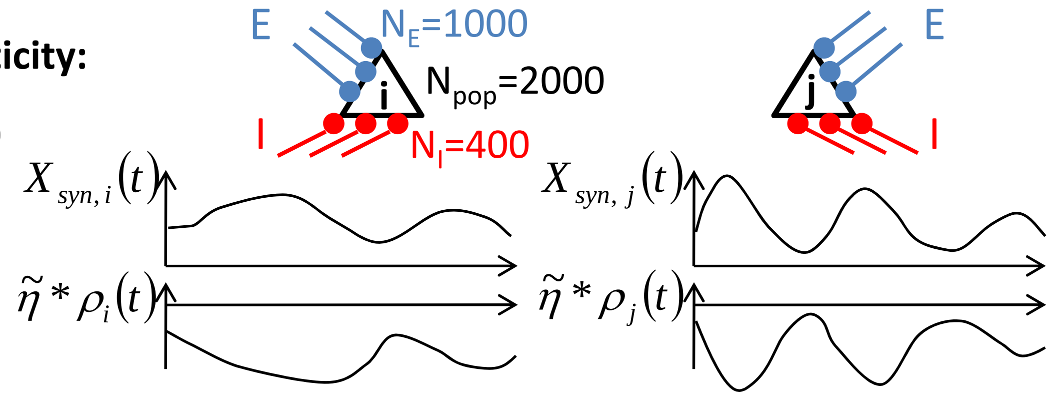

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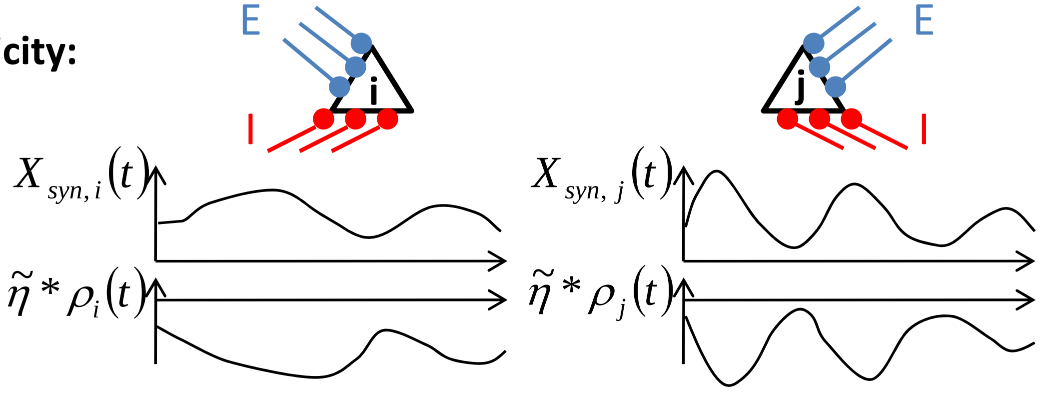

Steady state: fluctuations due to finite, i.i.d. input

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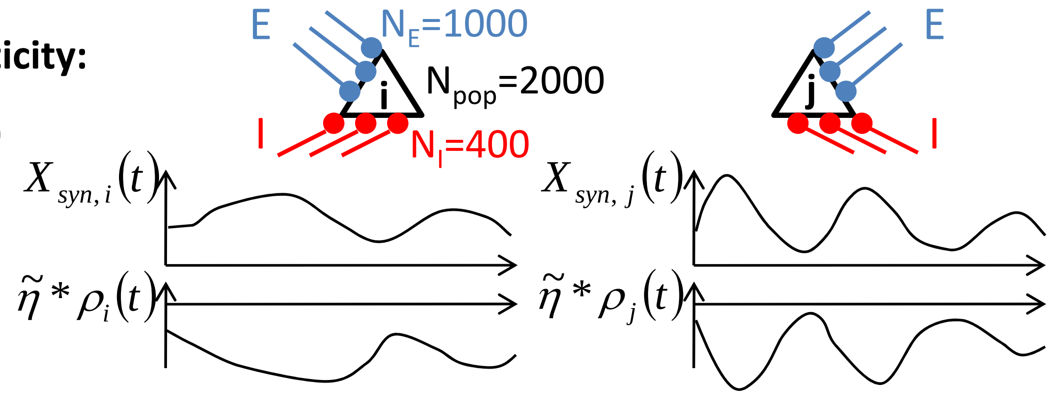

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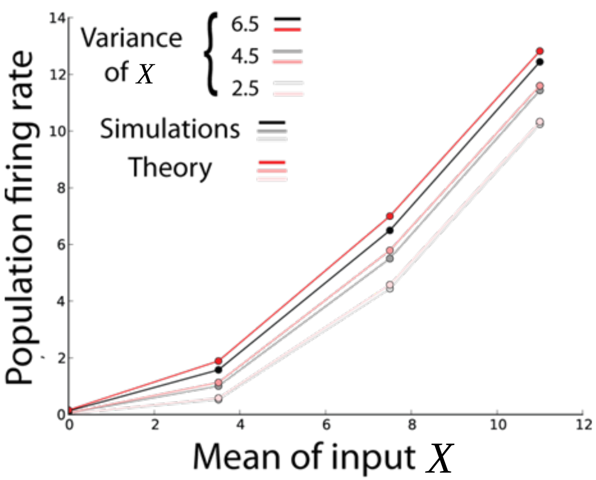
FULL THEORY

Lin. Approx. for var. of $\tilde{\eta} * \rho_i(t)$



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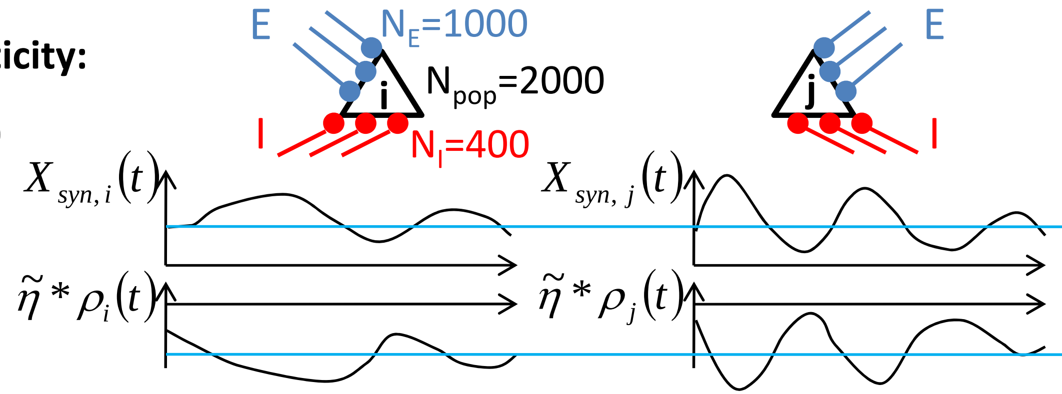

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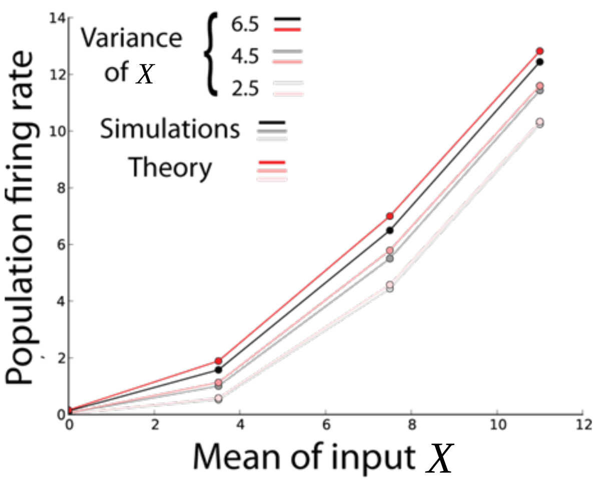

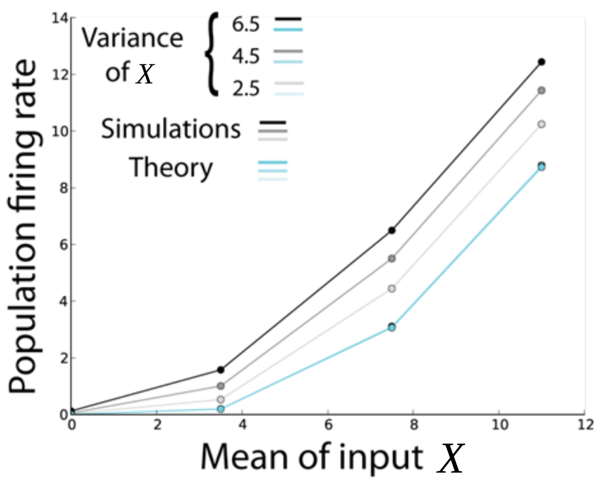

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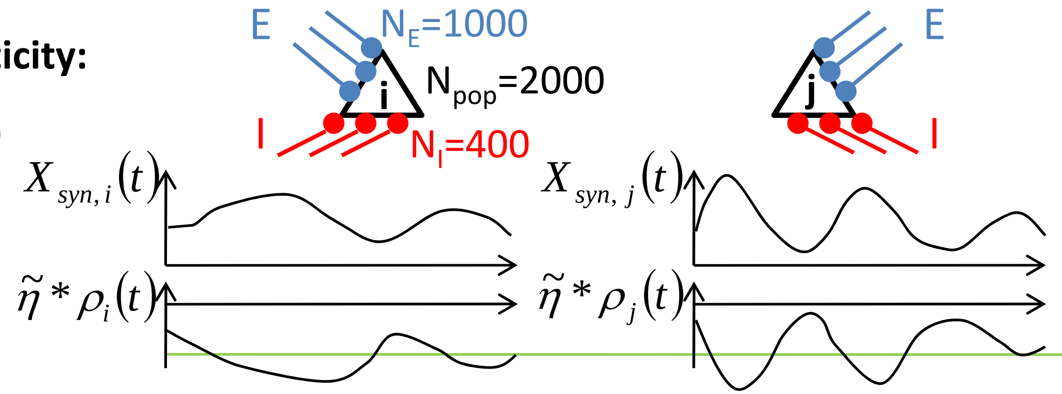

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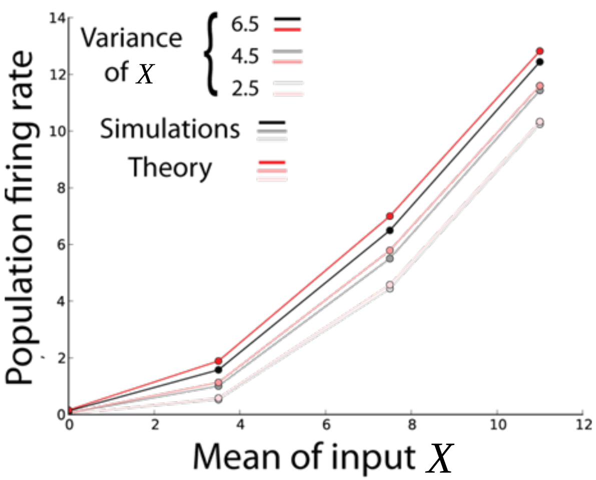

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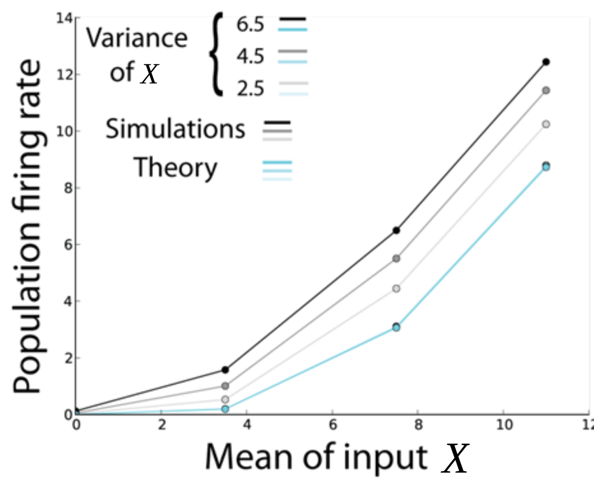
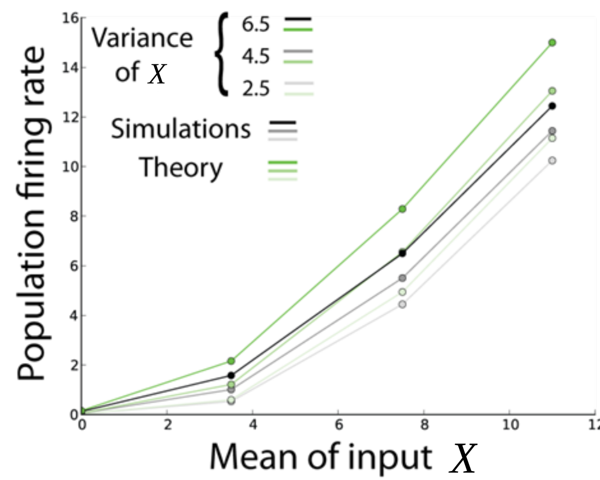


Neglect adaptation variability

$$R(t) = \lambda_o \exp\left(E[X_{syn}(t)] + \frac{\mathrm{var}[X_{syn}(t)]}{2} + \tilde{\eta} * R(t)\right)$$



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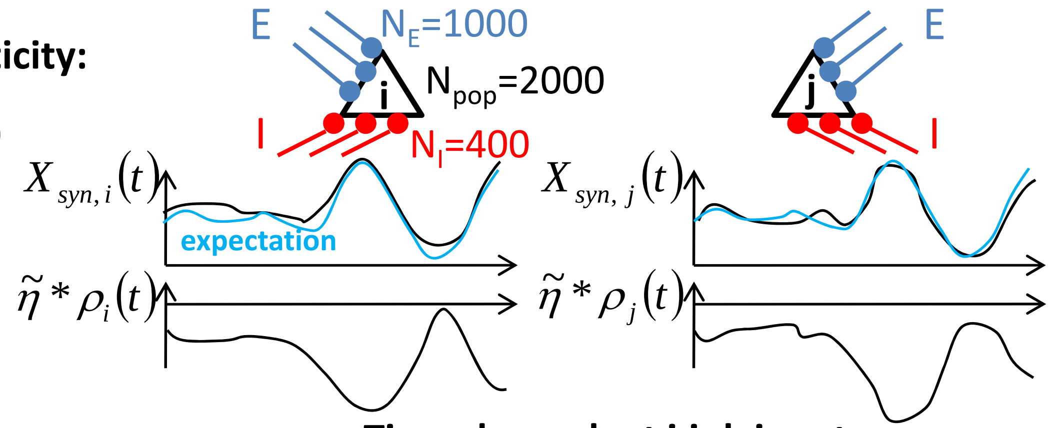

Time-dependent i.i.d. input

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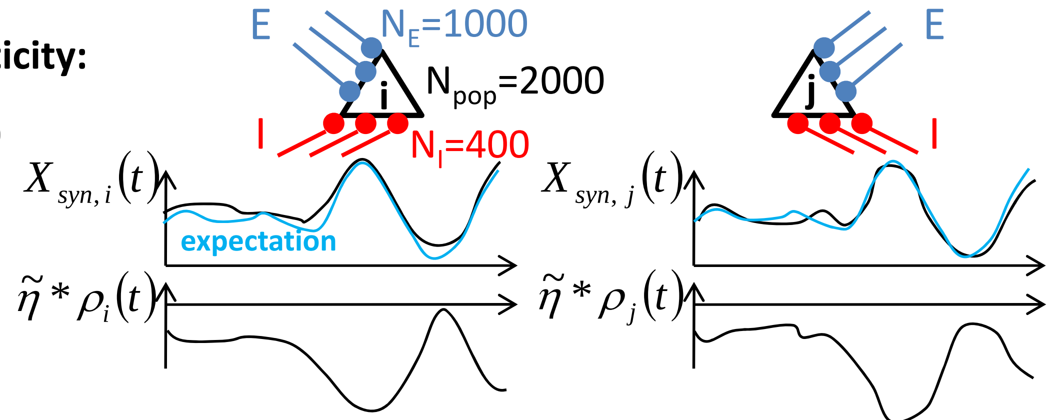

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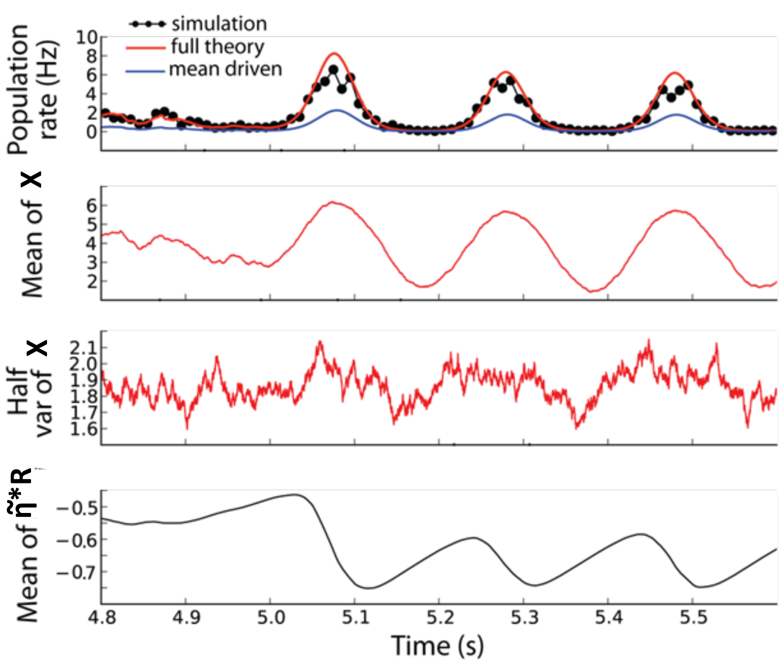

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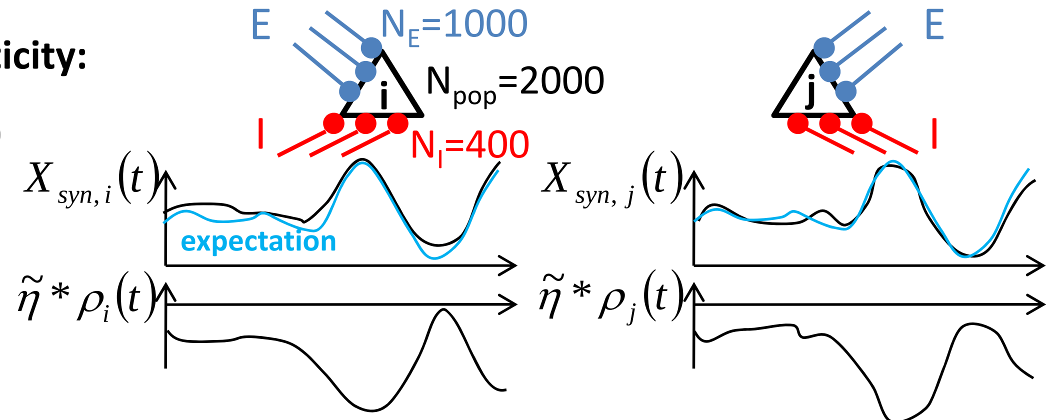
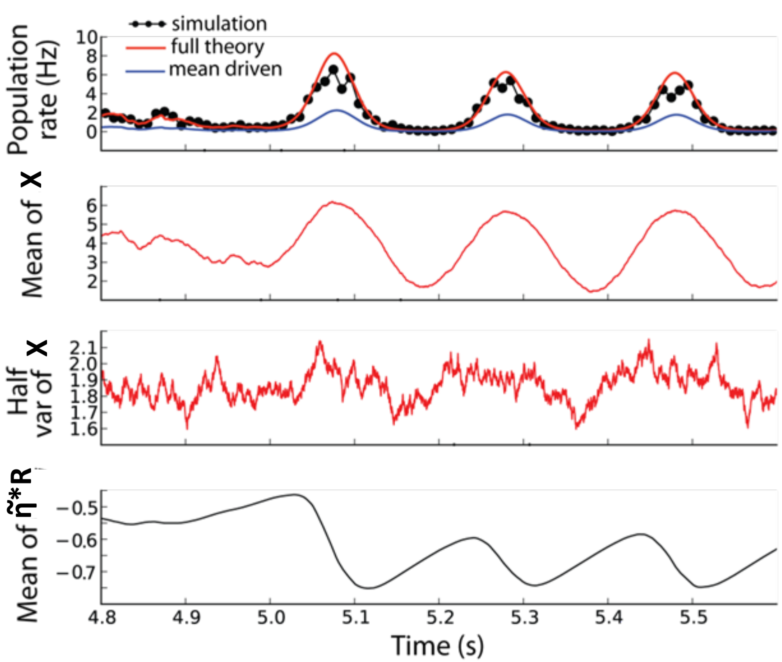
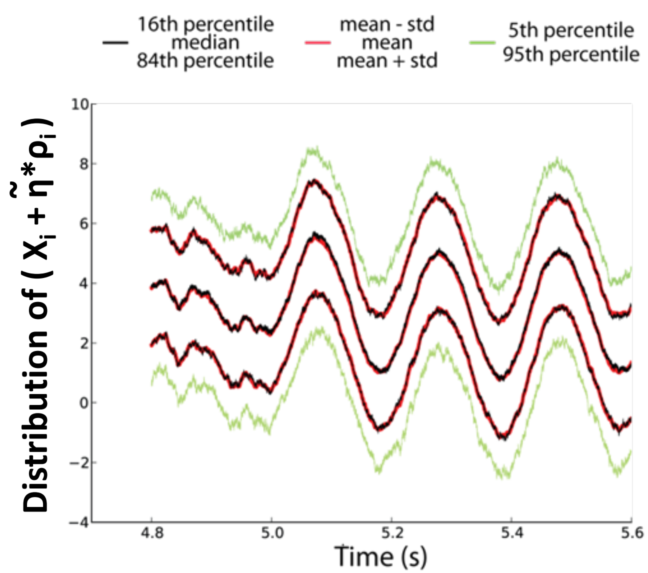


Time-dependent i.i.d. input



Gaussian distribution of instant drive in pop.



From single neurons to population rate

How successful is this approach, compared to 'naive' approximations?

Error from approx. of single-neuron stochasticity (S_i varies for fixed input):

Difference between:

$$\rho_i(t) = \lambda_o \exp\left(X_{syn}(t) + \eta * S_i(t)\right)$$

and the first order approximation:

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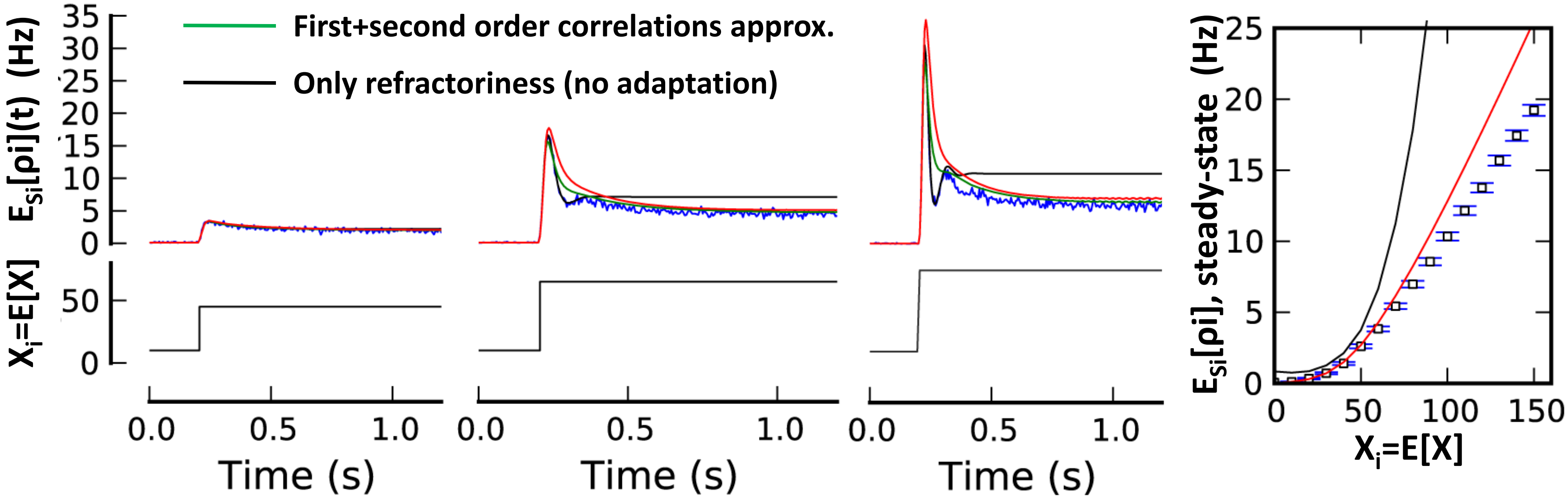

Naud and Gerstner, 2012

From single neurons to population rate

How successful is this approach? Effect of all approximations:

-Intrinsic stochasticity effects approximated through rate history
-variance of adaptation variable approximated through linear dependence on input variance
-Uncorrelated Poisson approximation for the recurrent input

Simulating a recurrent spiking inhibitory neurons network:

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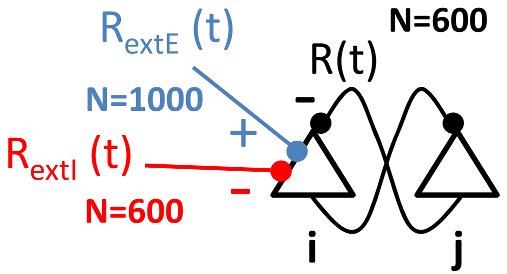

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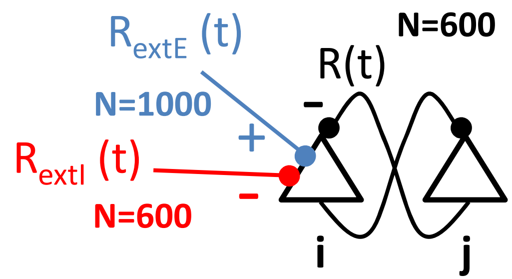

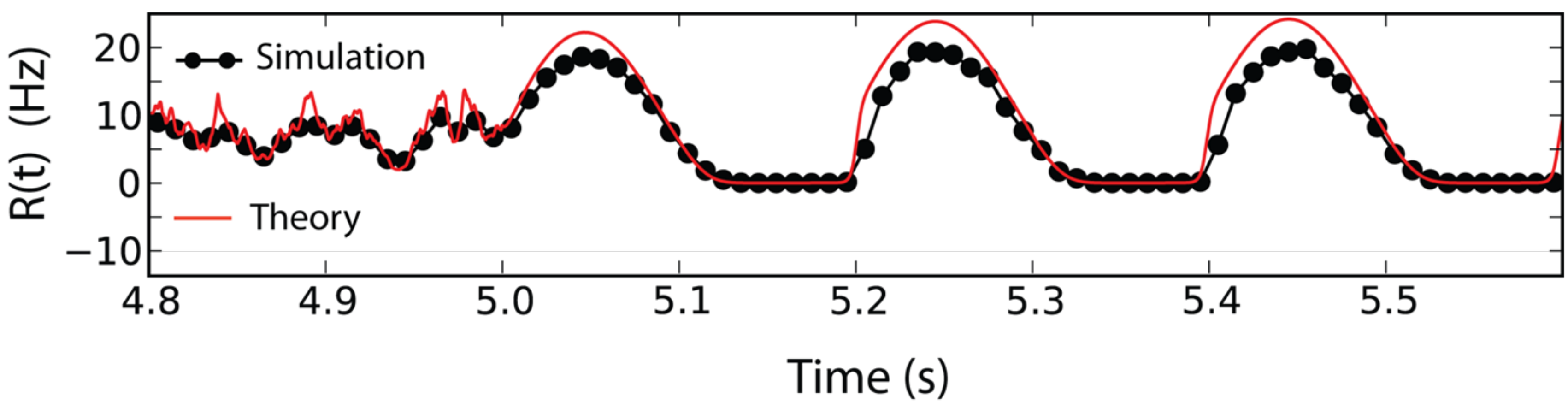

From single neurons to population rate

Reduction to non-linear differential equations:

$$\boxed{R\left(t\right)=E\left[\rho_i\left(t\right)\right]\approx\lambda_o\exp\left(\mu_Z(t)+\left(\frac{\sigma_Z^2(t)}{2}\right)\right)}$$

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$$\mu_Z(t) + \left(\frac{\sigma_Z^2(t)}{2}\right) \approx \sum_g \sum_{j=1}^{n_g} \left(\Lambda_{g,j} * R_g\right)(t) = \sum_g \sum_{j=1}^{n_g} V_{g,j}(t) \quad \text{where} \quad \Lambda_{g,j}(s) = A_{g,j} \exp\left(-\frac{s}{\tau_{g,j}}\right)\Theta(s)$$

Exact when: $\tilde{\eta}(s) = A_0 \exp\left(-\frac{s}{\tau_\eta}\right)\Theta(s)$, becomes more accurate with larger n_g

From single neurons to population rate

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$$\frac{dV_{g,j}}{dt} = -\frac{V_{g,j}}{\tau_{g,j}} + A_{g,j} R_g \Rightarrow \frac{dV_{recc,j}}{dt} = -\frac{V_{recc,j}}{\tau_{recc,j}} + A_{recc,j} \lambda_0 \exp\left(V_{recc,j} + \sum_{g \neq recc} \sum_{j=1}^{n_g} V_{g,j}\right)$$

For several recurrently coupled populations, set of coupled non-linear differential equations.

From single neurons to population rate

Extensions?

More heterogeneities (distribution of input rates/weights,…) or correlations as long as the effective drive stays ~ Gaussianly distributed among neurons

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$$\boxed{R\left(t\right)=E_{neurons\ i}\left[\rho_i\left(t\right)\right]\approx\lambda_0\exp\left(\mu_Z(t)+\left(\frac{\sigma_Z^2(t)}{2}\right)\right)}$$

Just need to compute:

$$\sigma_Z^2(t)=\mathrm{var}\left(\sum_g\sum_{j\in g}\left(\mathrm{K}_{g,j}\ +\tilde{\eta}*\Gamma_{R_b}*\mathrm{K}_{g,j}\ \right)*S_j\right)$$

1) Include spatiotemporal correlations
2) Use the law of total variance to account for the different sources of heterogeneities

Potential difficulties if/when needing self-consistency

Population-level predictions/validations:

$$R = E\left[r_i\right], \quad r_i \propto \exp(Z)$$

Z: Gaussian variable

$$R\,(t) \propto \exp\left(\mu_Z(t) + \left(\frac{\sigma_Z^2(t)}{2} \right) \right)$$

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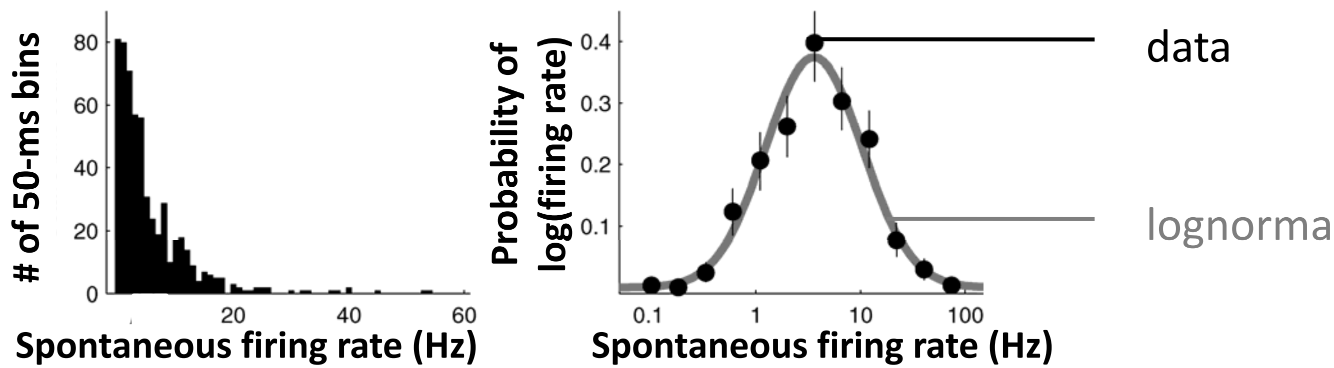
1) Log-normal distribution of <u>instantaneous</u> rates

Hromádka et al, 2008



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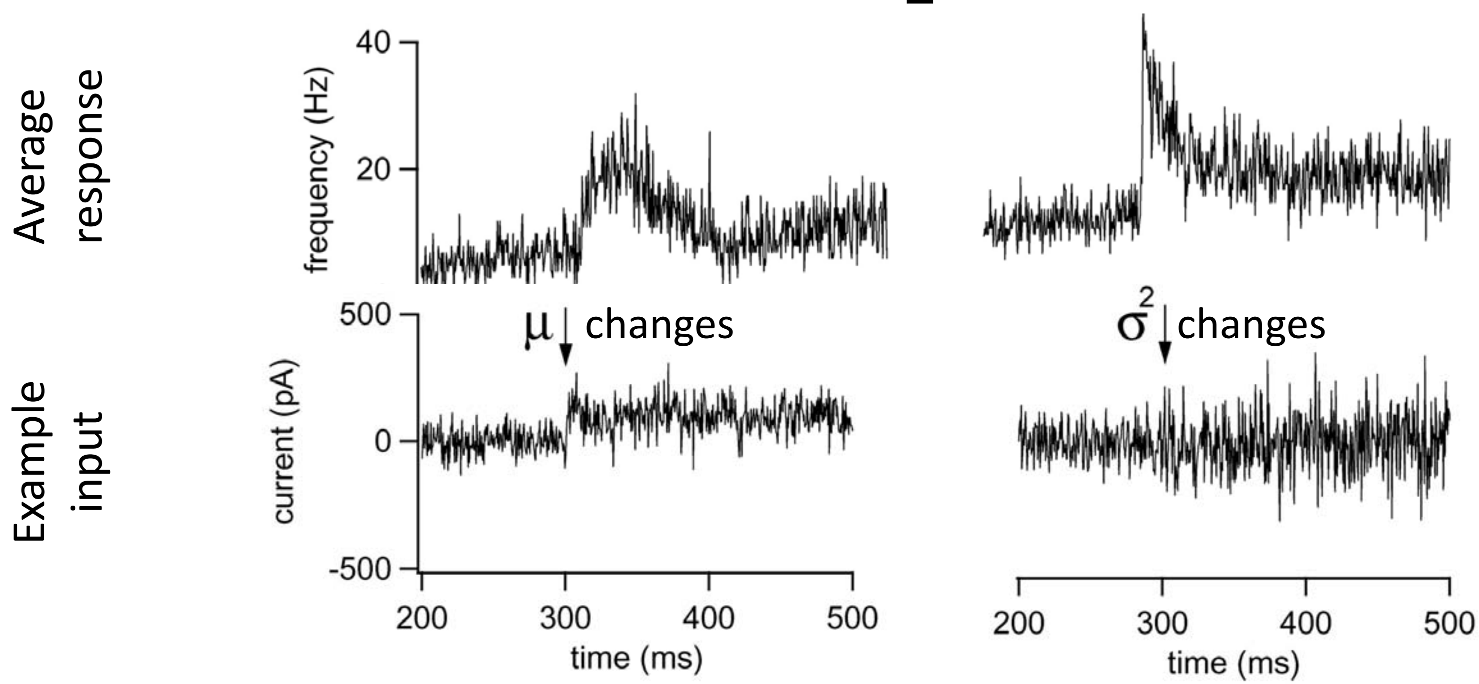
2) Response to change in variance *vs.* mean of population input

Silderberg et al, 2004

Response speed (both to input and adaptation):

$$\tau_{\sigma^2} \approx \frac{\tau_\mu}{2}$$



Other approaches to get firing rate equations: examples

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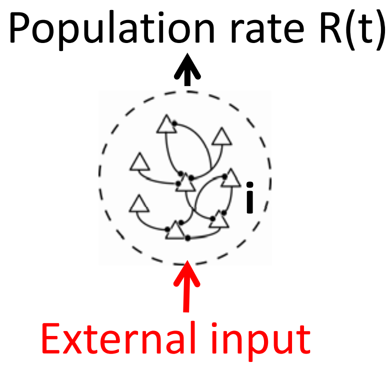
Population equations from different single neuron models: e.g. integrate-and-fire



Membrane potential u_i pulled towards resting by $f(u_i)$.
Input depolarizes neuron towards threshold Θ_{reset}.

$$\tau_m \frac{\mathrm{d}}{\mathrm{d}t} u_i = f(u_i) + R\, I_i(t) \quad \text{for} \quad u_i < \theta_{\text{reset}}$$

$$\lim_{N\to\infty} \left\{ \frac{\text{neurons with } u_0 < u_i(t) \le u_0 + \Delta u}{N} \right\} = \int_{u_0}^{u_0+\Delta u} p(u,t)\,\mathrm{d}u$$

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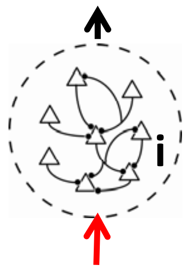
Population rate R(t)



External input

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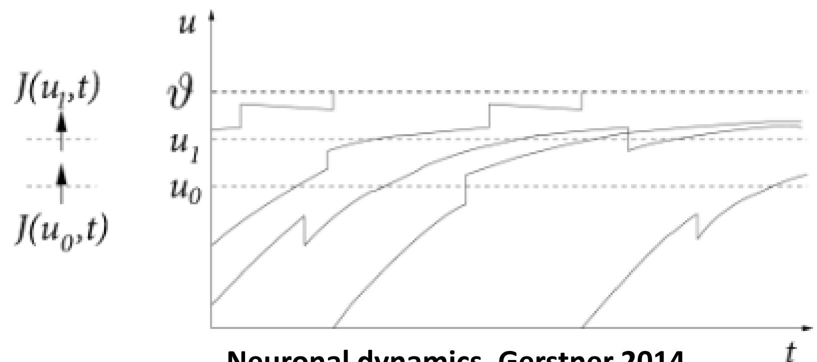
$$\frac{\partial}{\partial t} p(u,t) = -\frac{\partial}{\partial u} J(u,t) \quad \text{for} \quad u \ne u_r \quad \text{and} \quad u \ne \theta_{\text{reset}}$$

$$R(t) = J(\theta_{\text{reset}}, t)$$



Neuronal dynamics, Gerstner 2014
L. F. Abbott and C. van Vreeswijk, 1993
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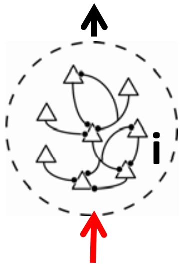

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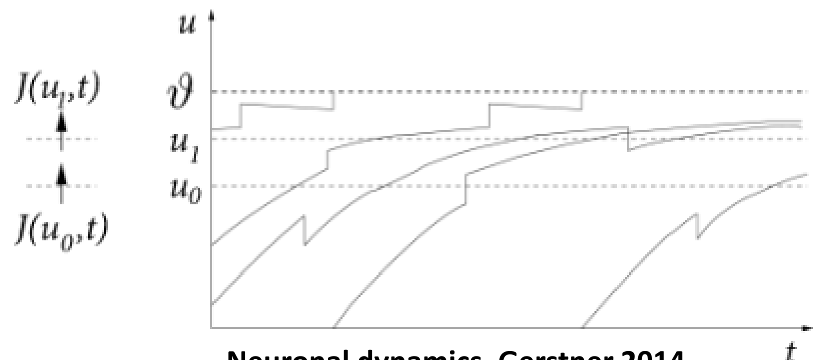

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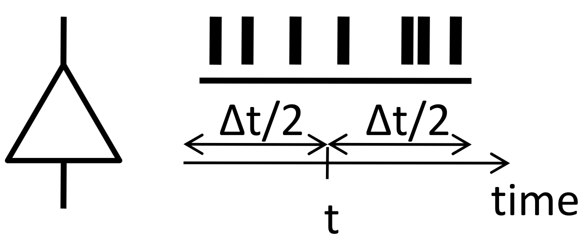
Rate as a time-average for each single neuron: if very slow dynamics or ergodic system



$R(t) = N_{spikes} / \Delta t$

Ostojic, 2014