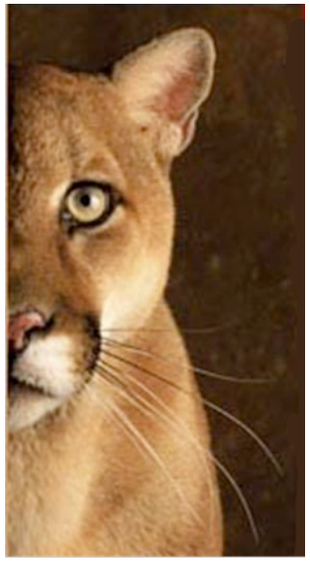
Linear Response and the Structure of Correlations in Networks

Krešimir Josić University of Houston



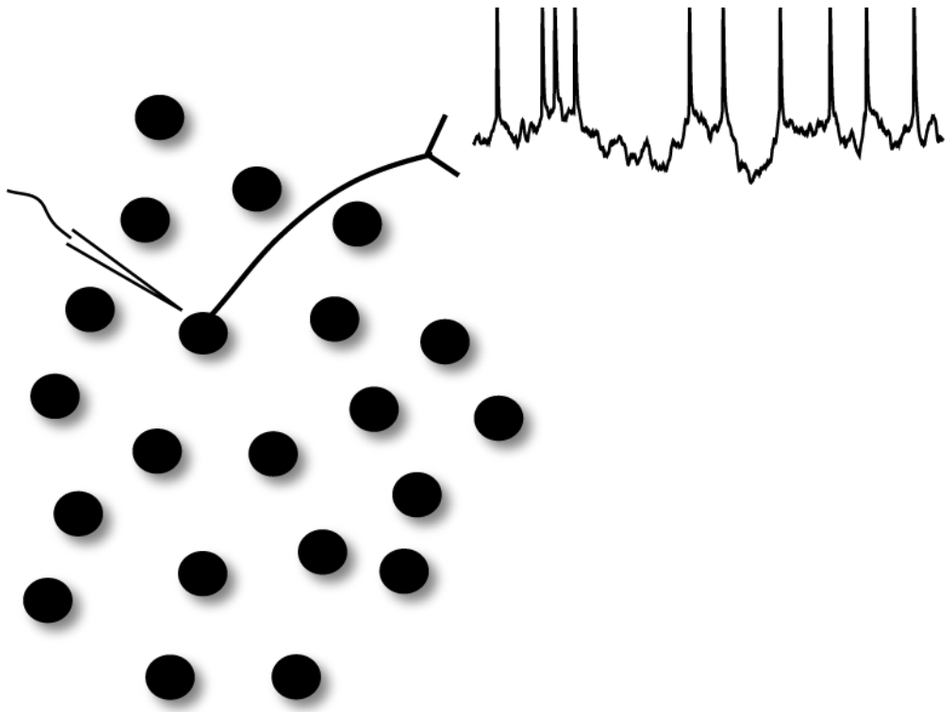
Outline

- Correlations in networks and linear response

- Distinct impact of inputs on membrane voltage and spiking correlations

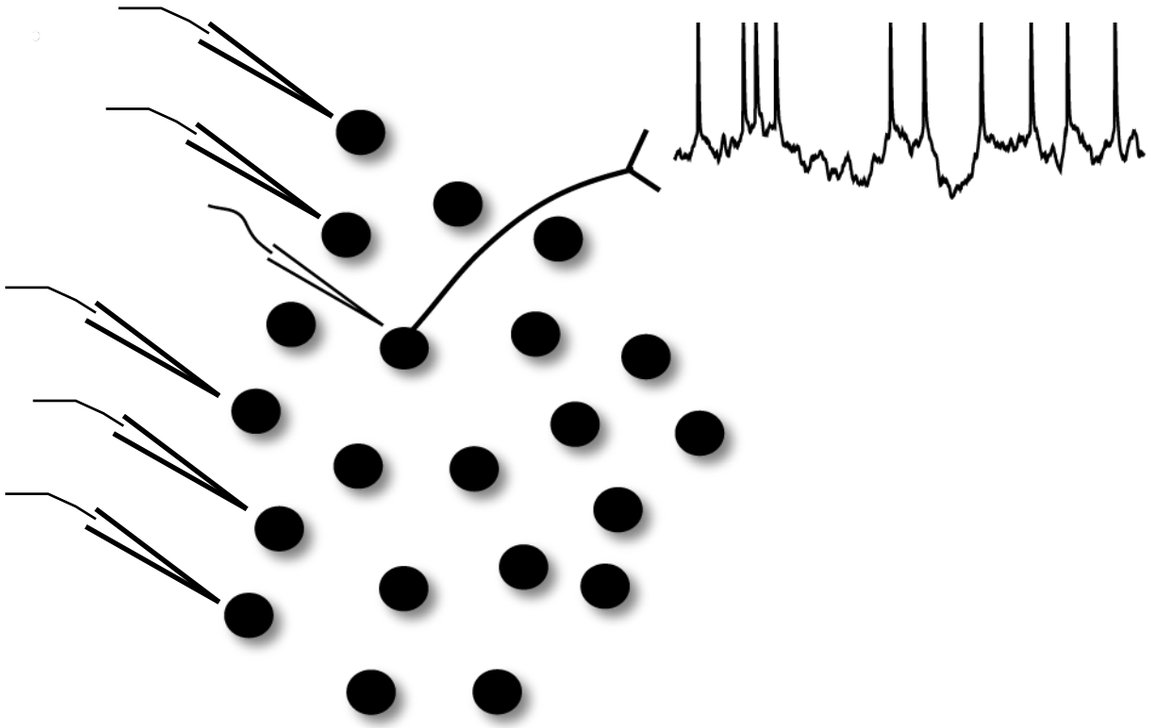
- The structure of correlations in neuronal networks

Recordings from neurons



Brunel and Hakim, 1999

Recordings from neurons



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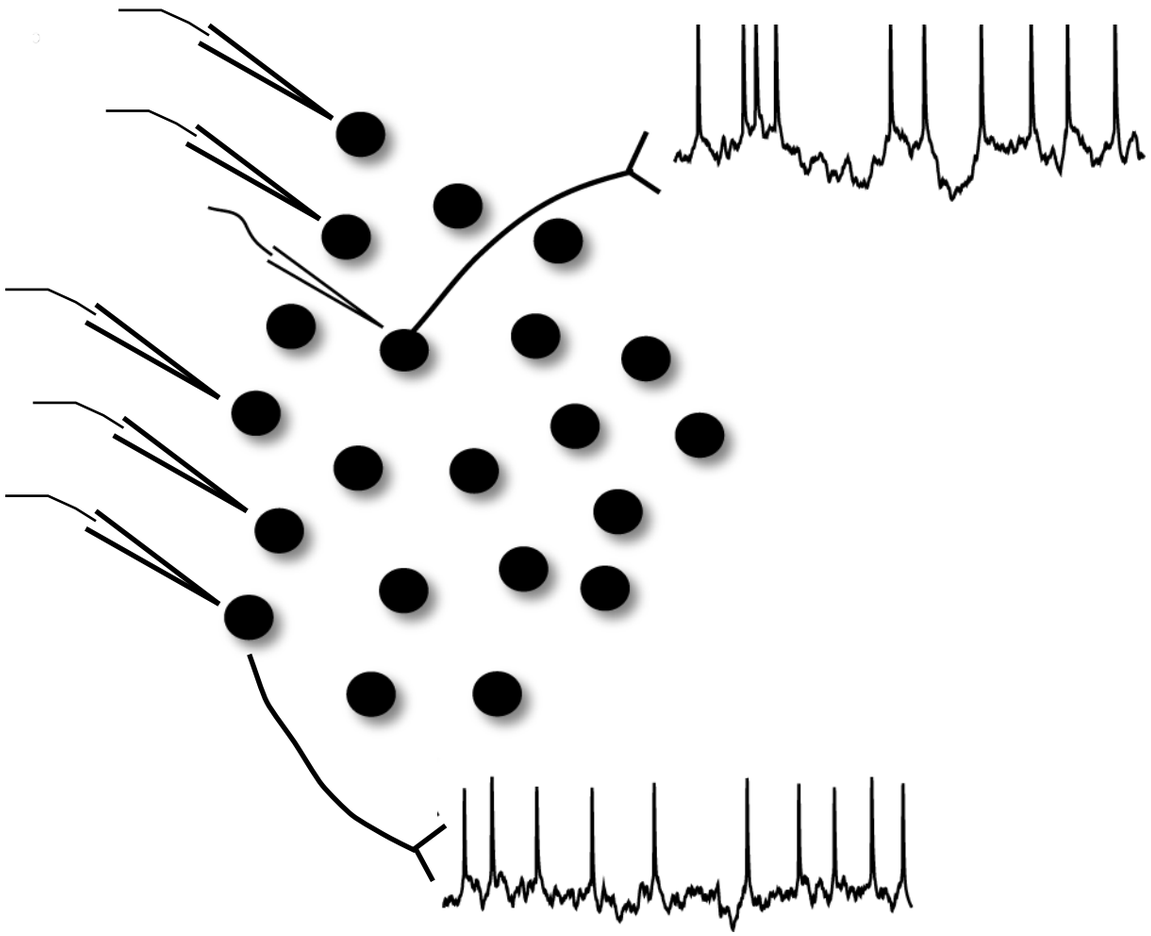

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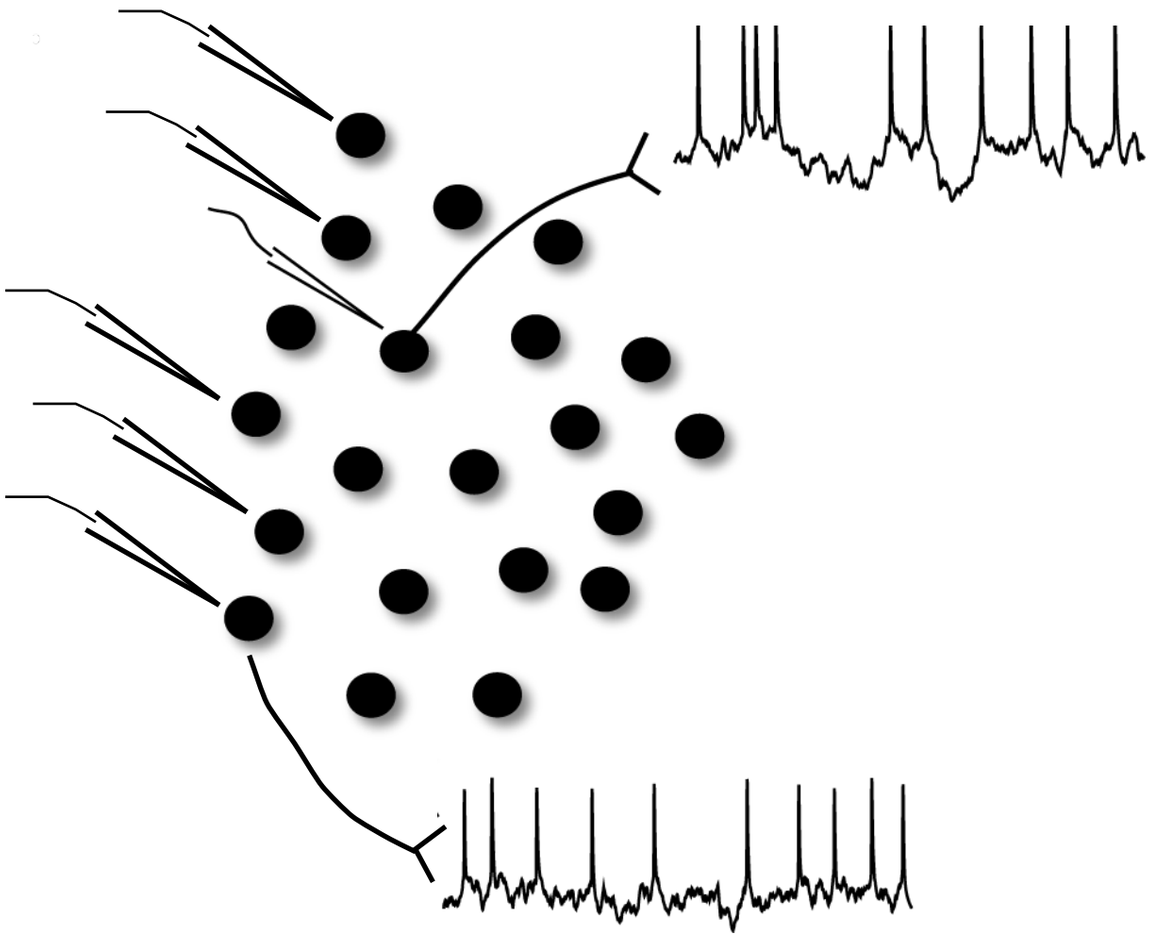
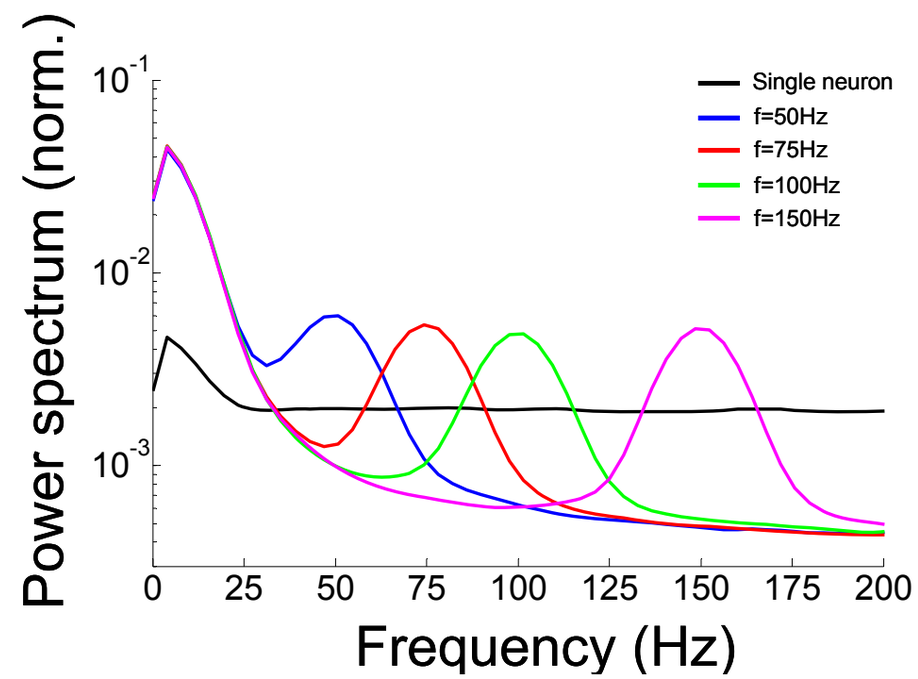
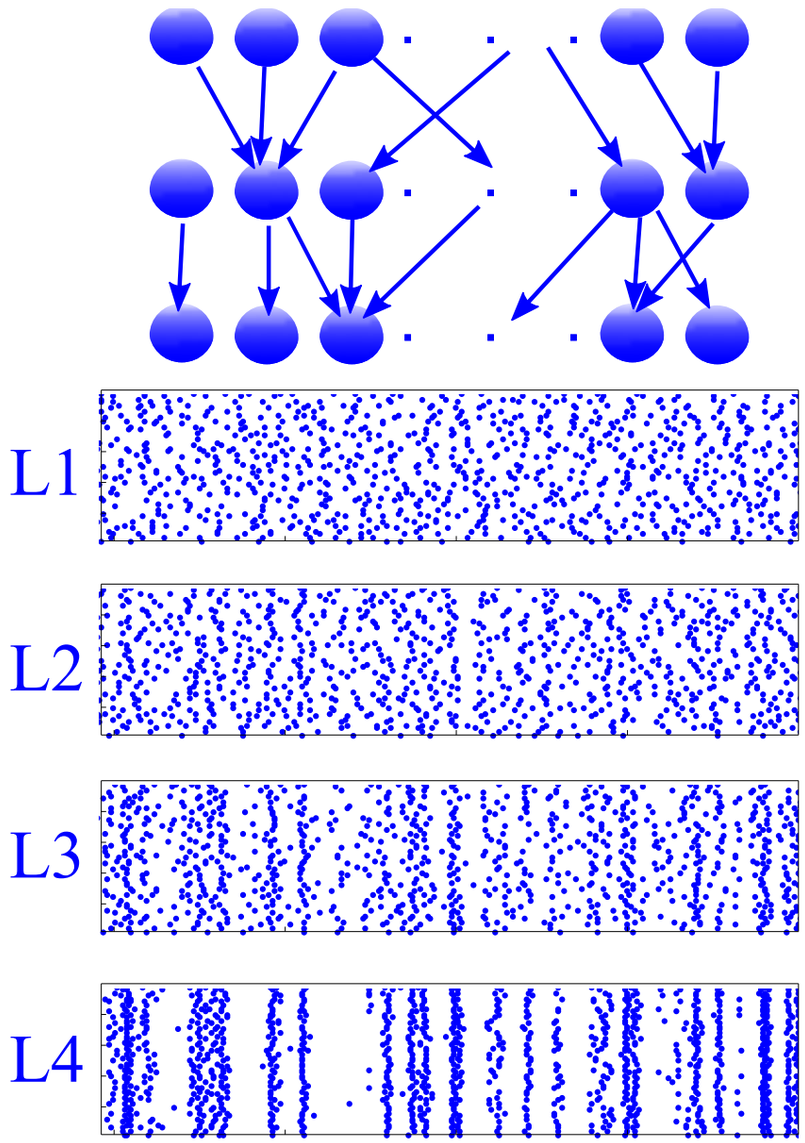


Oscillations can be observable on the population level



Brunel and Hakim, 1999
Gutnisky and Josić, 2010

Convergence can cause runaway synchronization



Reyes, '03,
Rosenbaum, Trousdale and Josić, '10, '11,
Renart, de la Rocha, et al. `10

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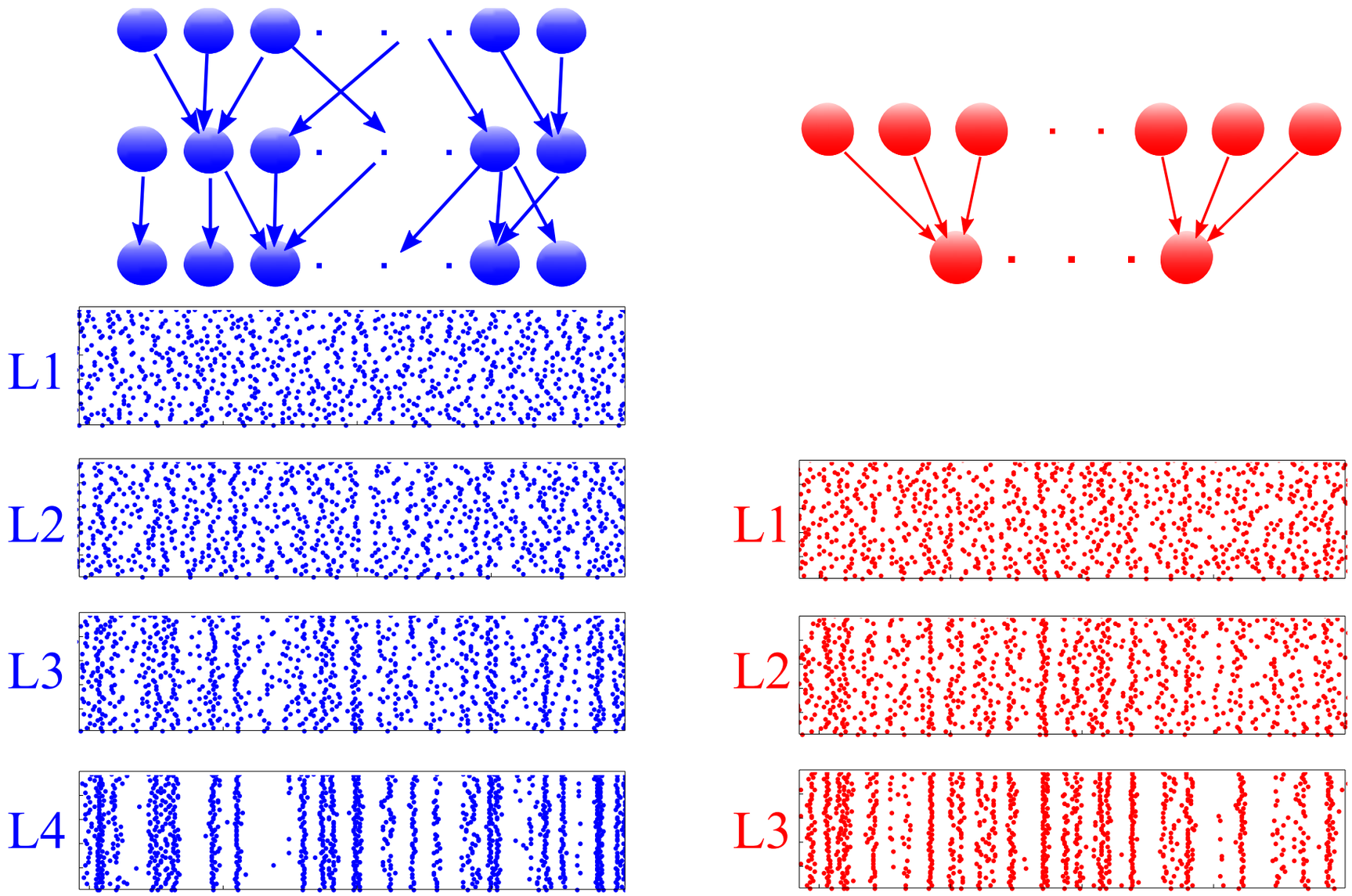

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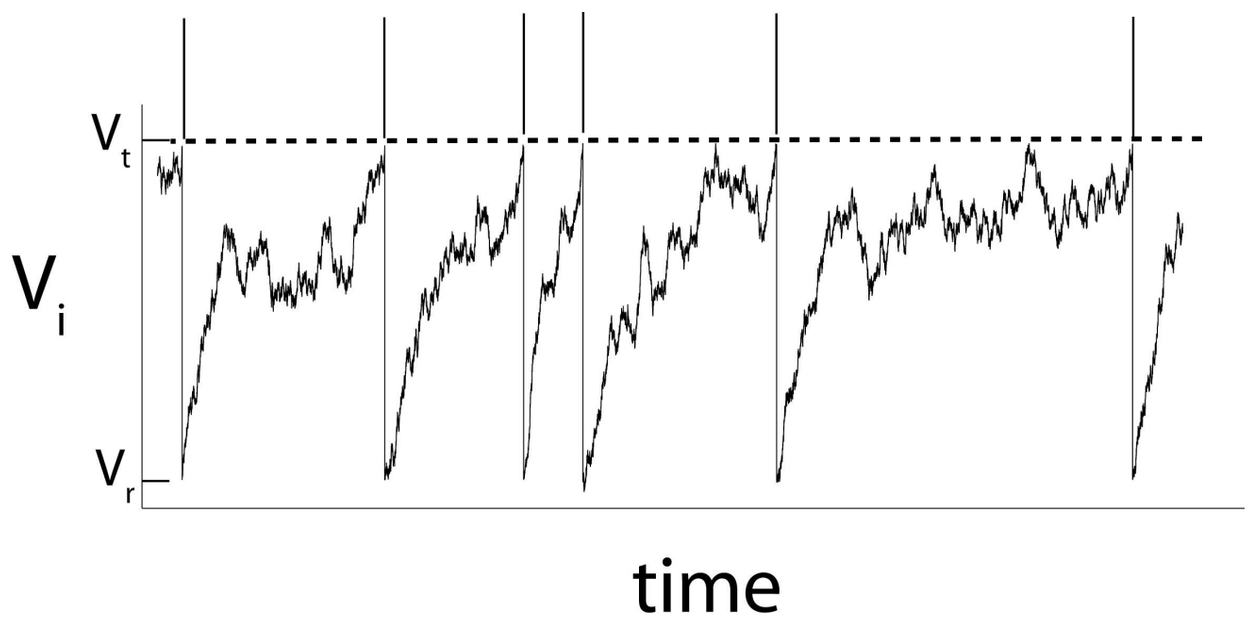
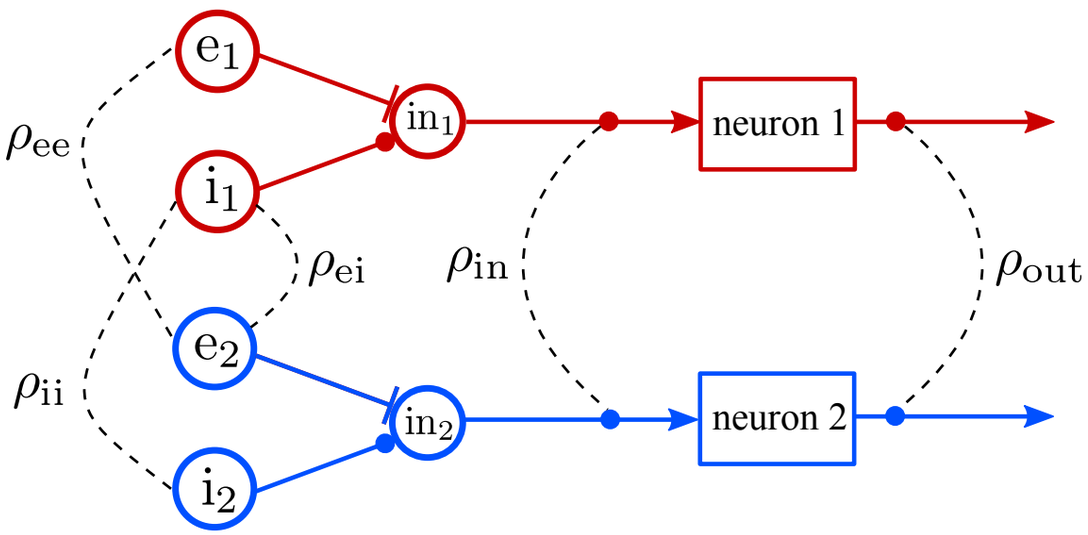
Integrate-and-Fire neurons

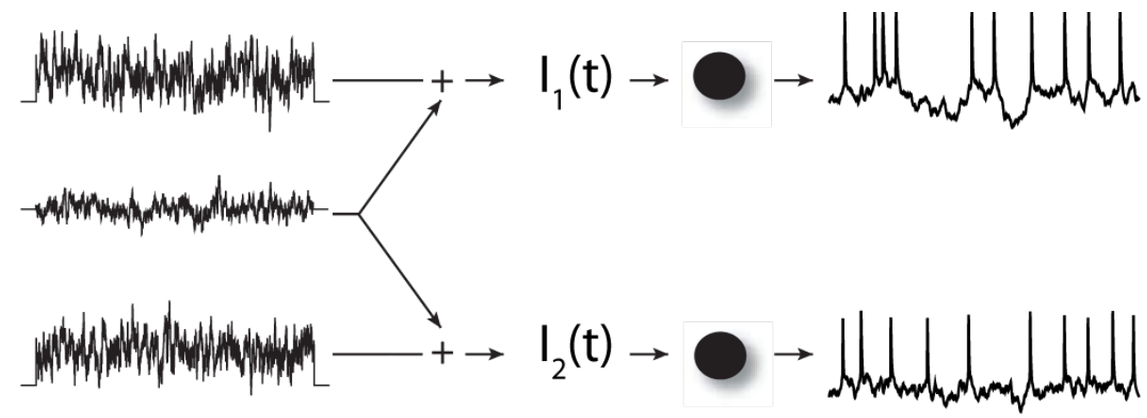
$$C\frac{dV}{dt} + gV = I(t)$$ Subthreshold integration of *I(t)*

$$V(t) = V_t \Rightarrow V(t^+) = V_r$$ Fire and Reset



The simplest question





$$\frac{dV_k}{dt} = -\frac{V_k}{\tau_m} + J_{\mathrm{e}}\,\mathrm{e}_k(t) - J_{\mathrm{i}}\,\mathrm{i}_k(t)$$

$$e_k(t) = \sum_j \delta(t - t^j_{e_k})$$

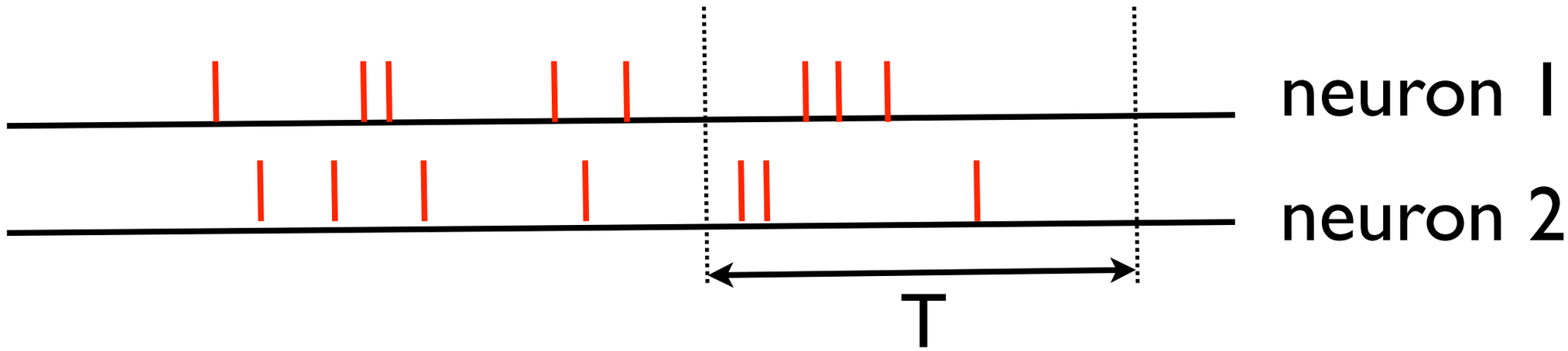
at rates r_{e} and r_{i}

$$\mu = \langle \mathrm{in}_k(t) \rangle = J_{\mathrm{e}} r_{\mathrm{e}} - J_{\mathrm{i}} r_{\mathrm{i}}.$$

$$C_{\mathrm{in}}(\tau) = J_{\mathrm{e}}^2 C_{\mathrm{e}}(\tau) + J_{\mathrm{i}}^2 C_{\mathrm{i}}(\tau) - 2 J_{\mathrm{e}} J_{\mathrm{i}} C_{\mathrm{ei}}(\tau)$$

de la Rocha, et al '07, Rosenbaum and Josić, '10

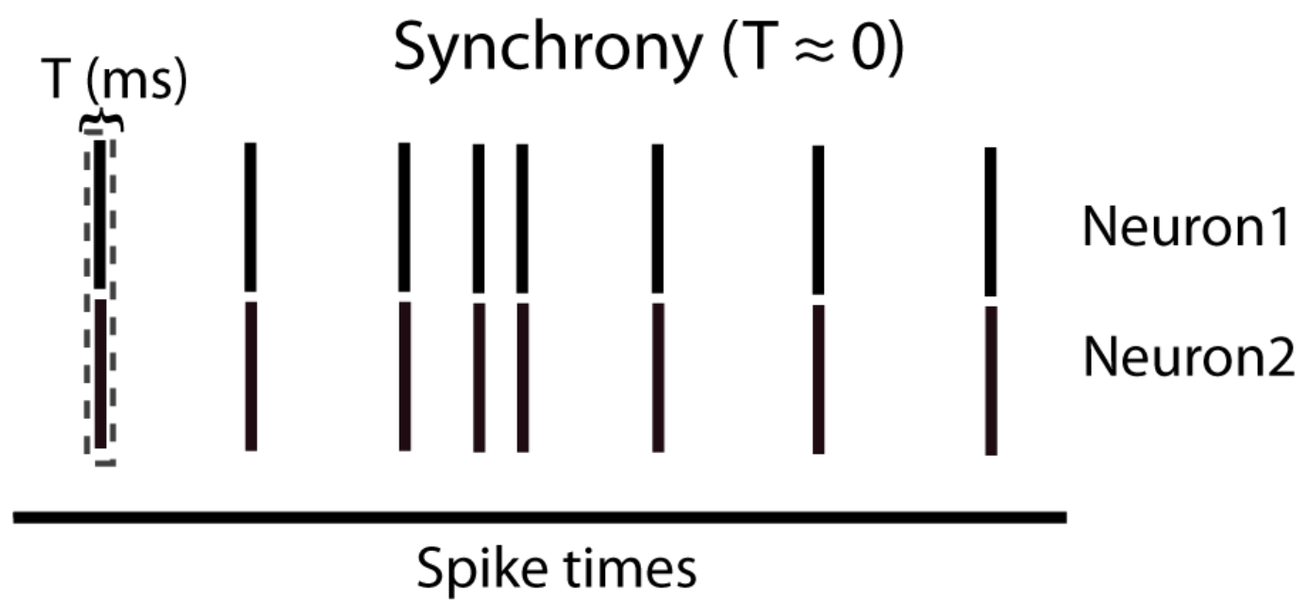
Correlations

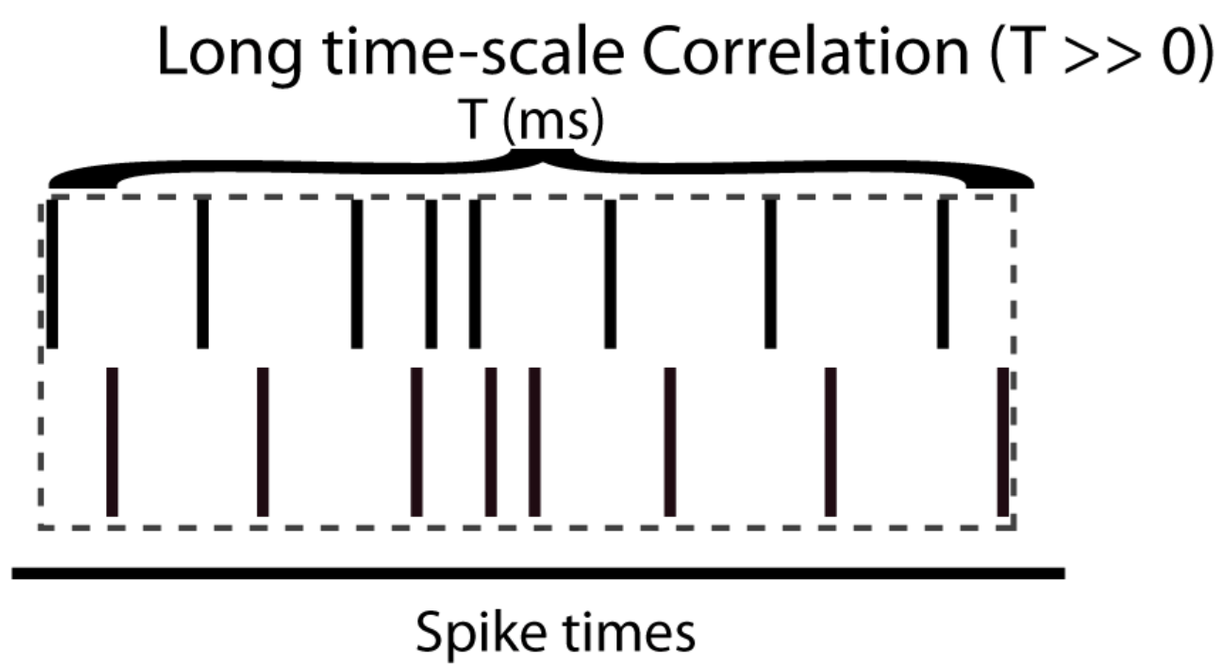


If n_i is the number of spikes of neuron i during a time T, the correlation coefficient of the output is

$$\rho_s(T) = \frac{\mathrm{Cov}(n_1, n_2)}{\sqrt{\mathrm{Var}(n_1)\mathrm{Var}(n_2)}} \qquad R_V(\tau) = \frac{\mathrm{Cov}(V_1(t), V_2(t+\tau))}{\sqrt{\mathrm{Var}(V_1(t))\mathrm{Var}(V_2(t+\tau))}}$$

Synchrony vs long timescale correlations





Weak excitation limit

Threshold is crossed rarely, and the membrane potential is a filtered version of the input

$$C_V(\tau) = (K * C_{\text{in}})(\tau), \quad \Longrightarrow \quad \frac{\int_{-\infty}^{\infty} C_V(\tau)d\tau}{\int_{-\infty}^{\infty} A_V(\tau)d\tau} = \frac{\int_{-\infty}^{\infty} C_{\text{in}}(\tau)d\tau}{\int_{-\infty}^{\infty} A_{\text{in}}(\tau)d\tau} = \lim_{T\to\infty} \rho_{\text{in}}(T)$$

Rosenbaum and Josić, '10, '11

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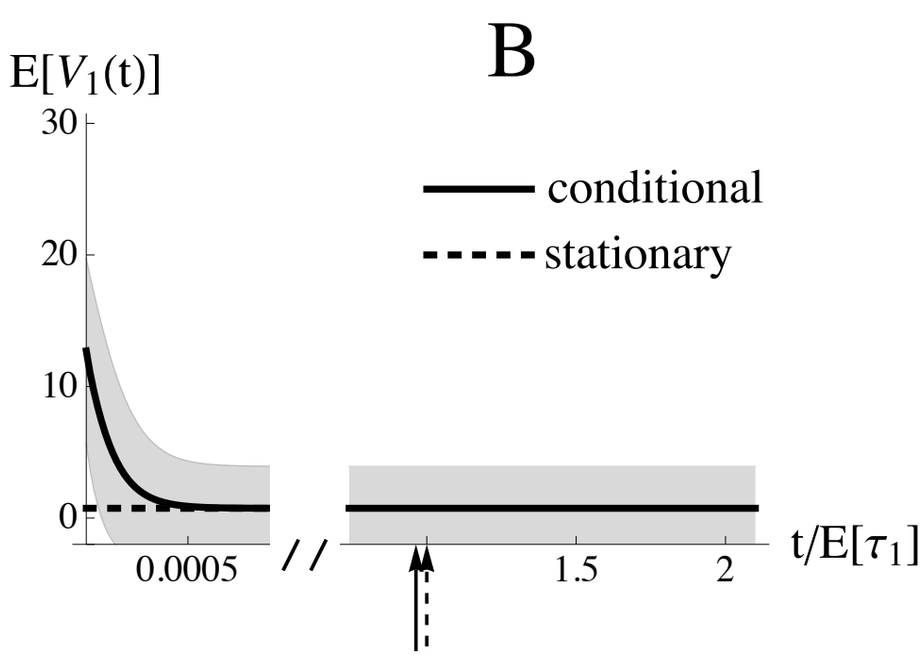
Spikes become statistically independent in this limit - *V* relaxes to the stationary distribution quickly compared to the timescale of spiking

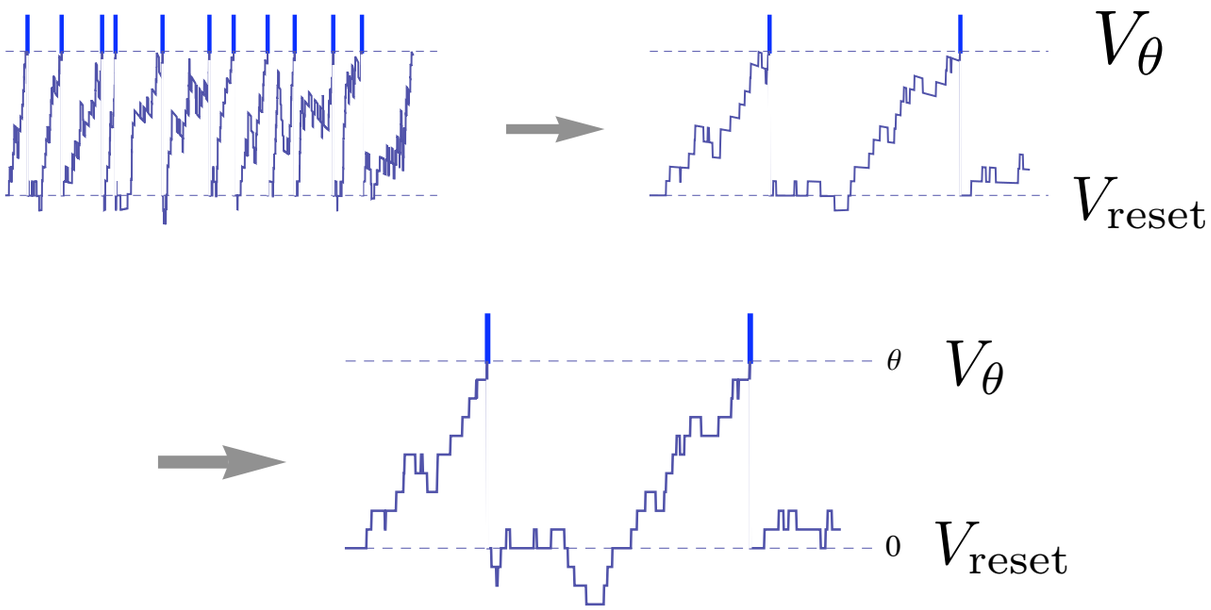


$$\Longrightarrow \quad \rho_s(T) \approx 0$$

Rosenbaum and Josić, '10, '11

Strong excitation limit

$J_{\mathrm{e}} r_{\mathrm{e}} \gg J_{\mathrm{i}} r_{\mathrm{i}} + V_{\mathrm{th}}/\tau_m$ we have perfect integrators $\dfrac{dV_k}{dt} = J_{\mathrm{e}}\, \mathrm{e}_k(t)$



If there are $N_E(T)$ input spikes,
there are $N_E(T)/V_\theta$ output spikes.

Perfect integrators preserve spiking correlations over long windows.

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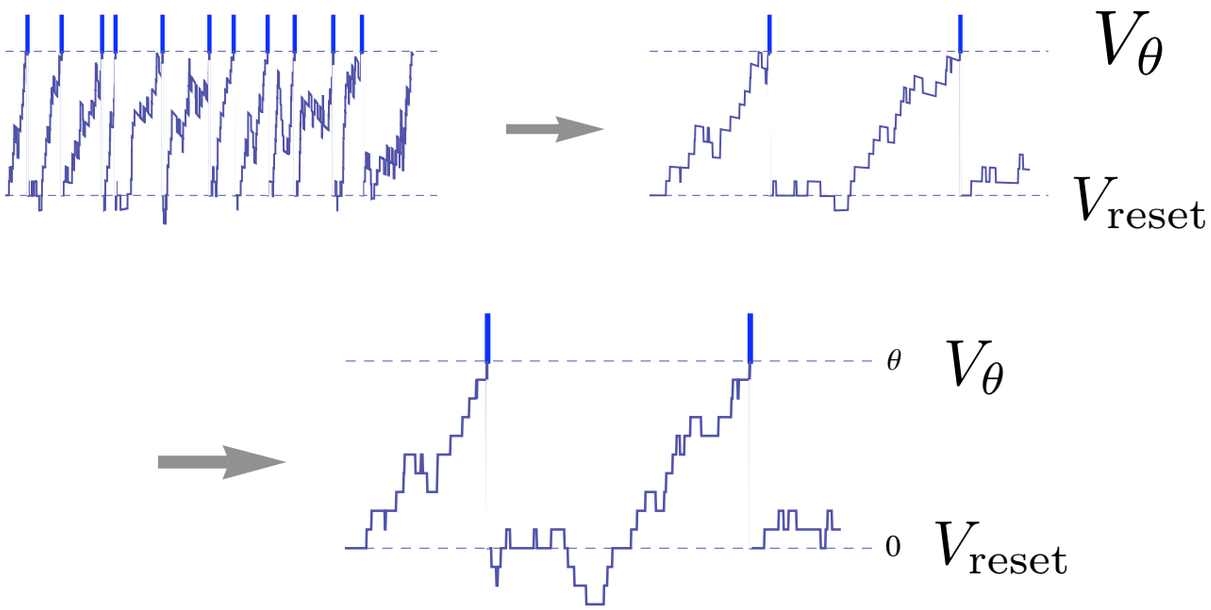

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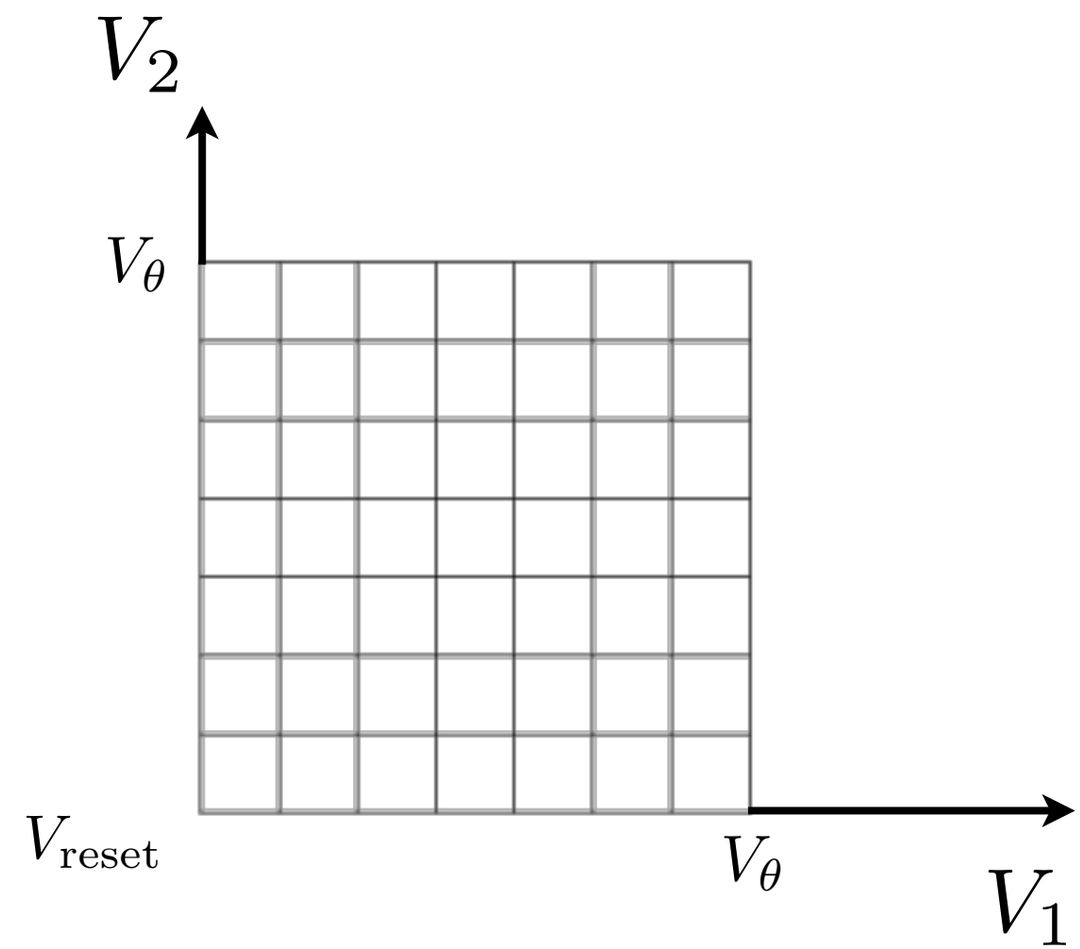
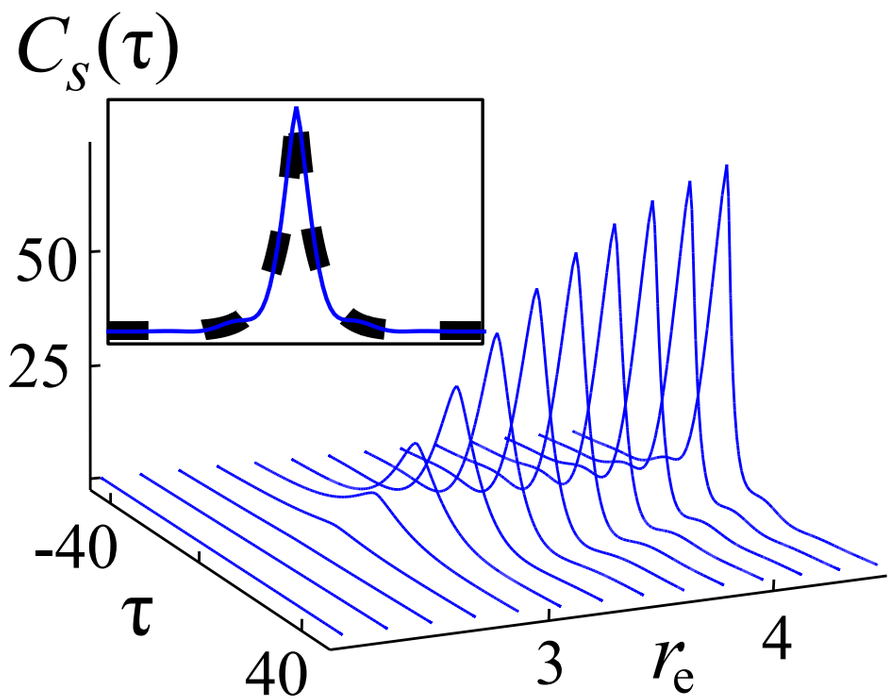
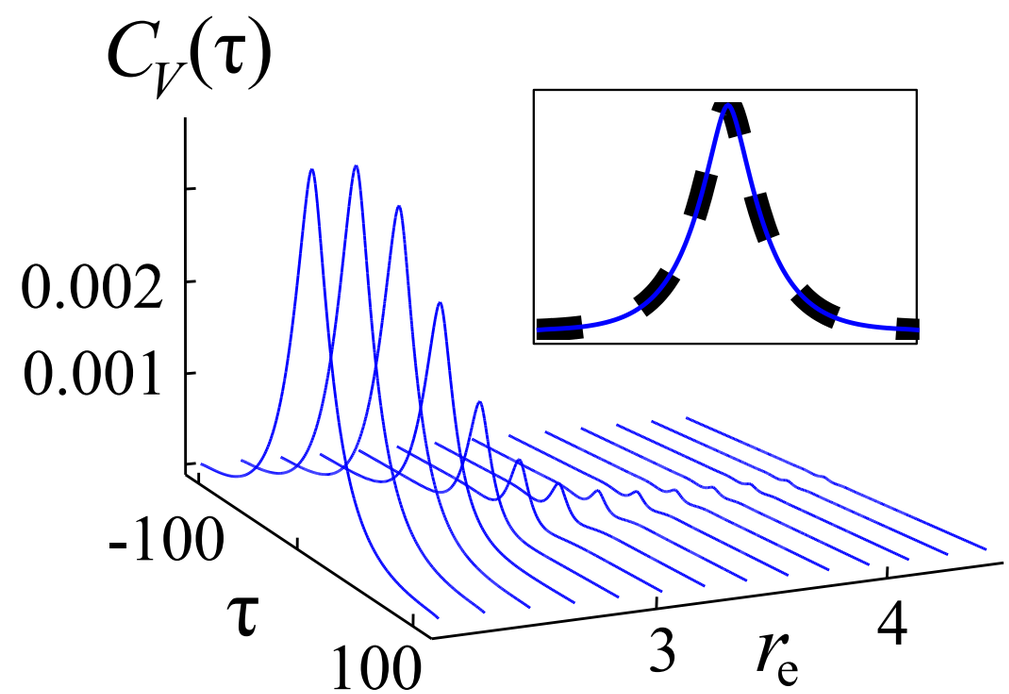


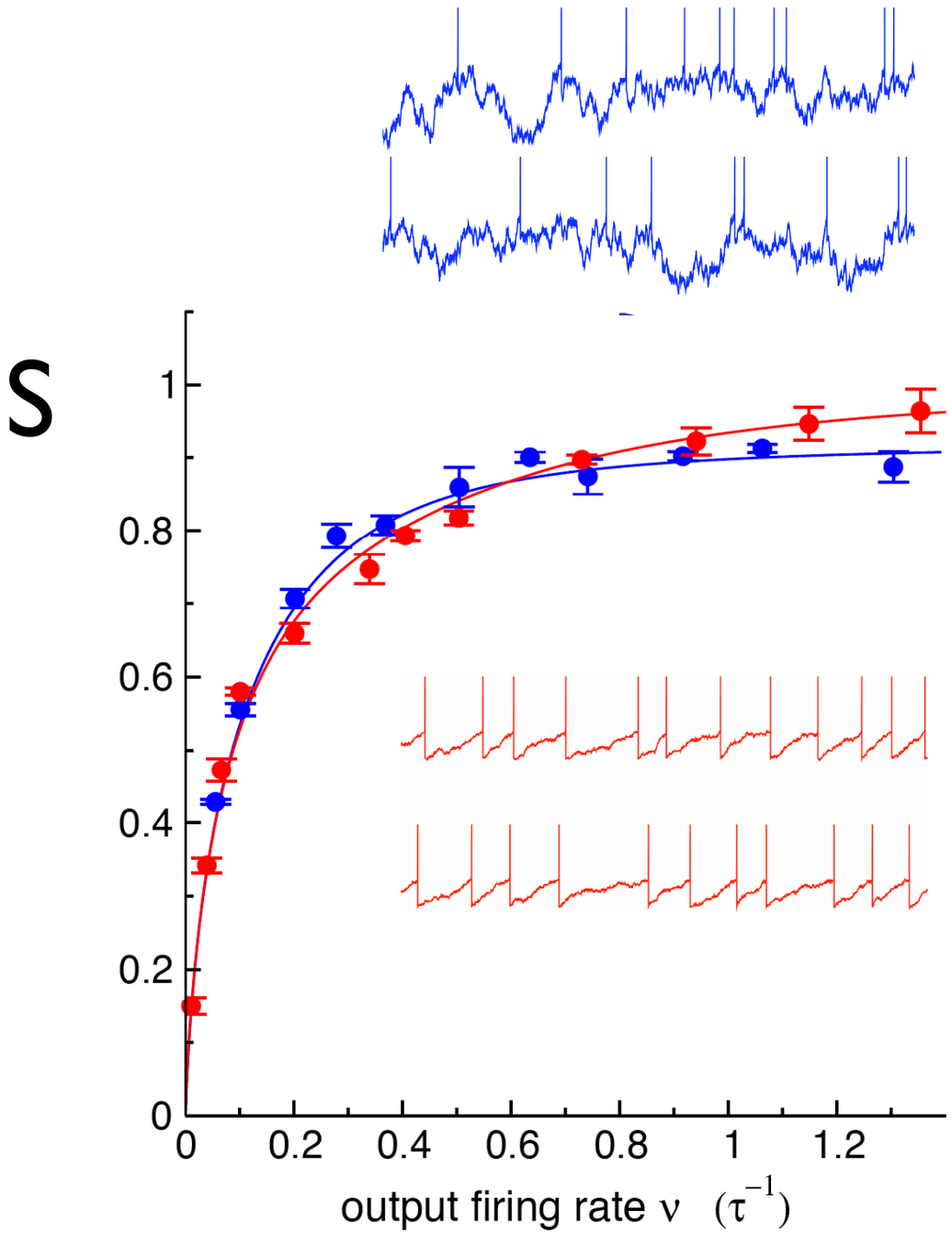
The distribution on the square is uniform, and hence the membrane voltages are independent.

This is reflected in the covariances





... and is consistent with previous observations



Theory

de la Rocha, Doiron, Shea-Brown, Josić, Reyes, '07

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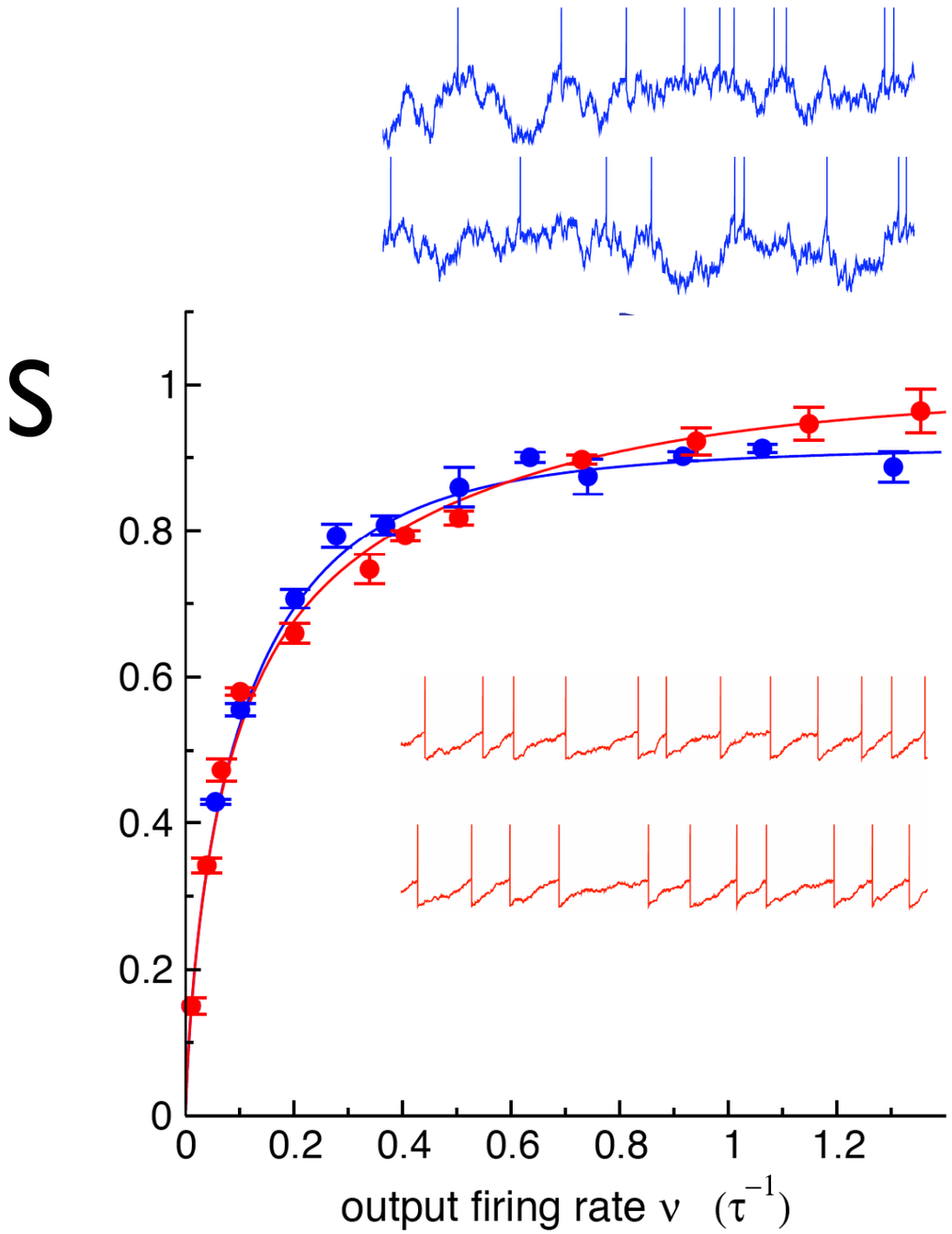

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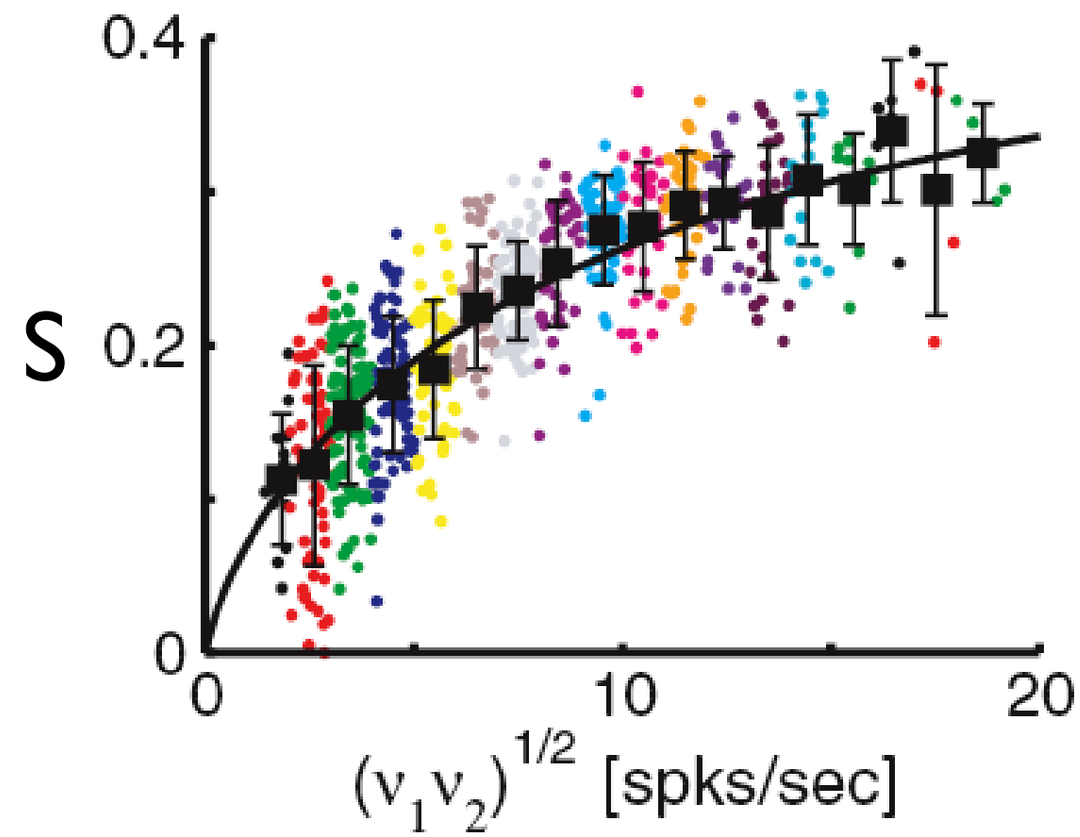


Experiment

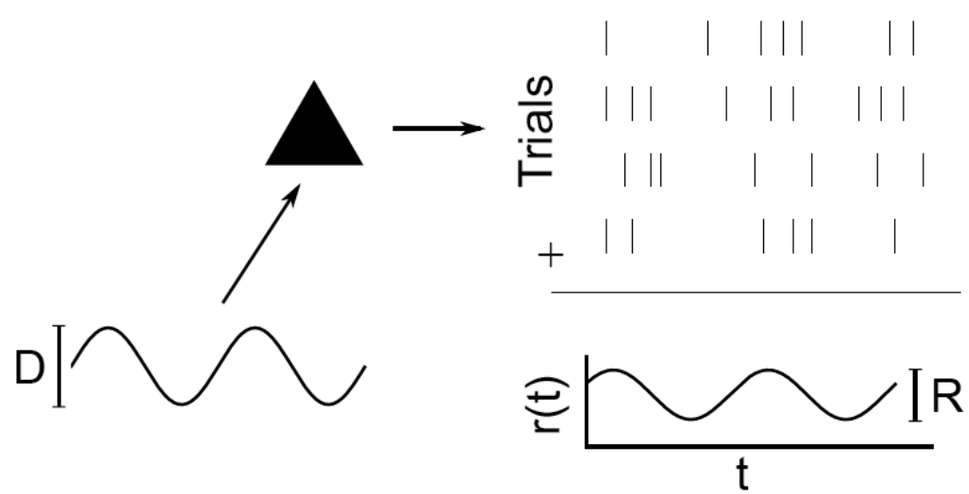
de la Rocha, Doiron, Shea-Brown, Josić, Reyes, '07

Linear response function

$$\langle V_k(t)\rangle = \langle V_0\rangle + \epsilon\,\chi_V(\omega)e^{i\omega t} + o(\epsilon)$$
$$r_s(t) \;=\; r_0 \;+ \epsilon\,\chi_s(\omega)e^{i\omega t} + o(\epsilon)$$

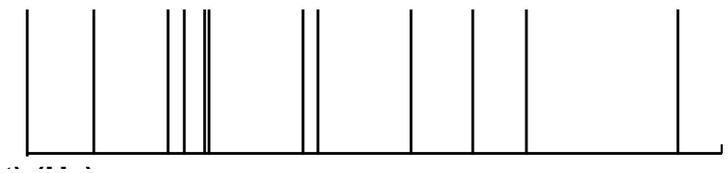
Output of a cell - spike train

Effect of a perturbation at frequency ω



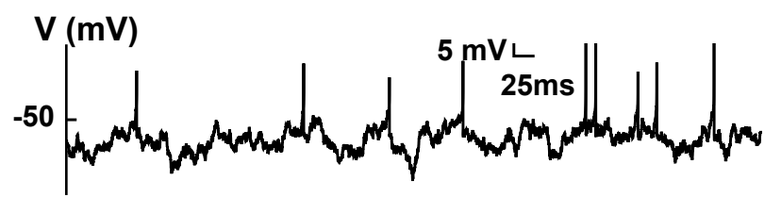
$$|\hat{A}(\omega)| = R/D$$

Linear response kernel, *A(t)*

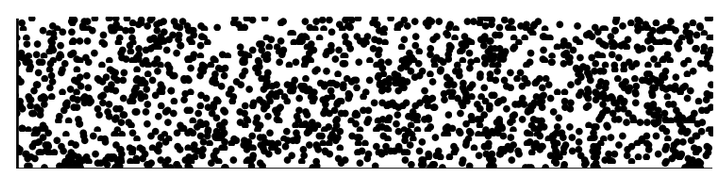


input to cell

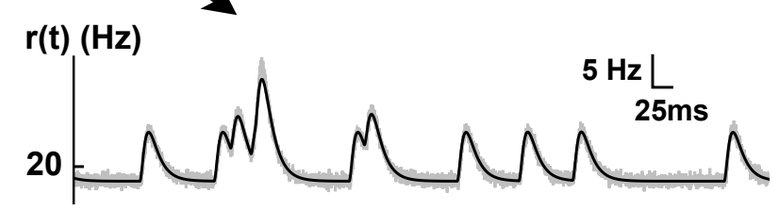
activity of cell



repeated trials



firing rate



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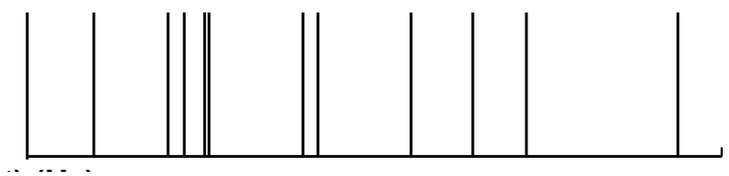

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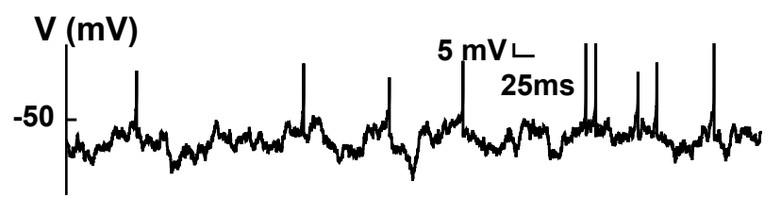

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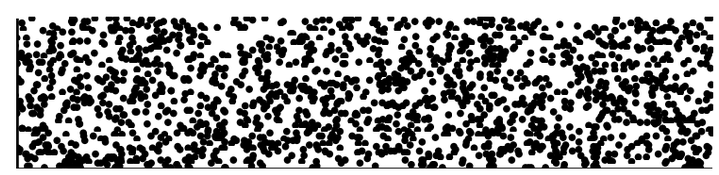

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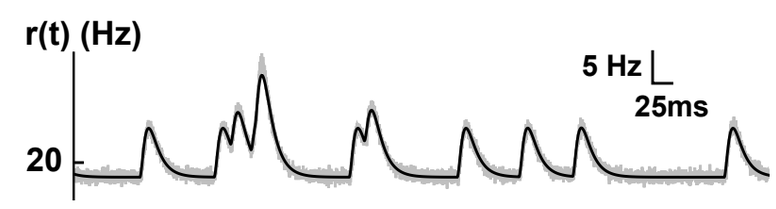

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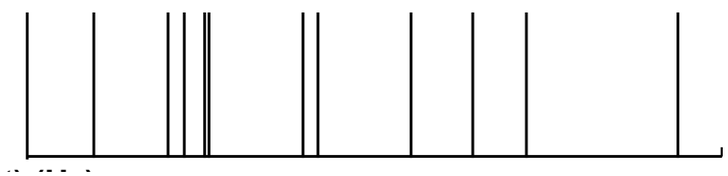
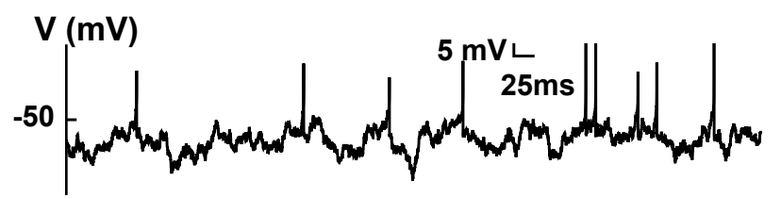


input to cell

$$r(t) = r_0 + (A * X)(t)$$

activity of cell



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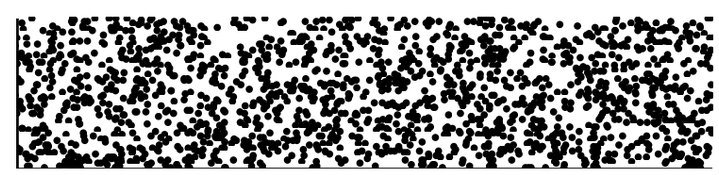

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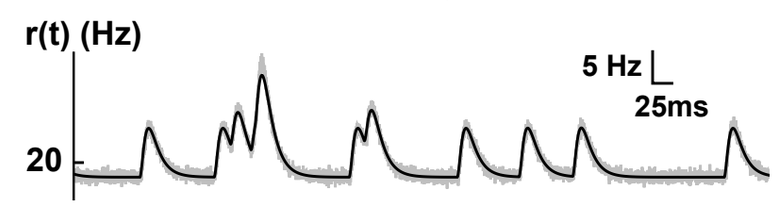
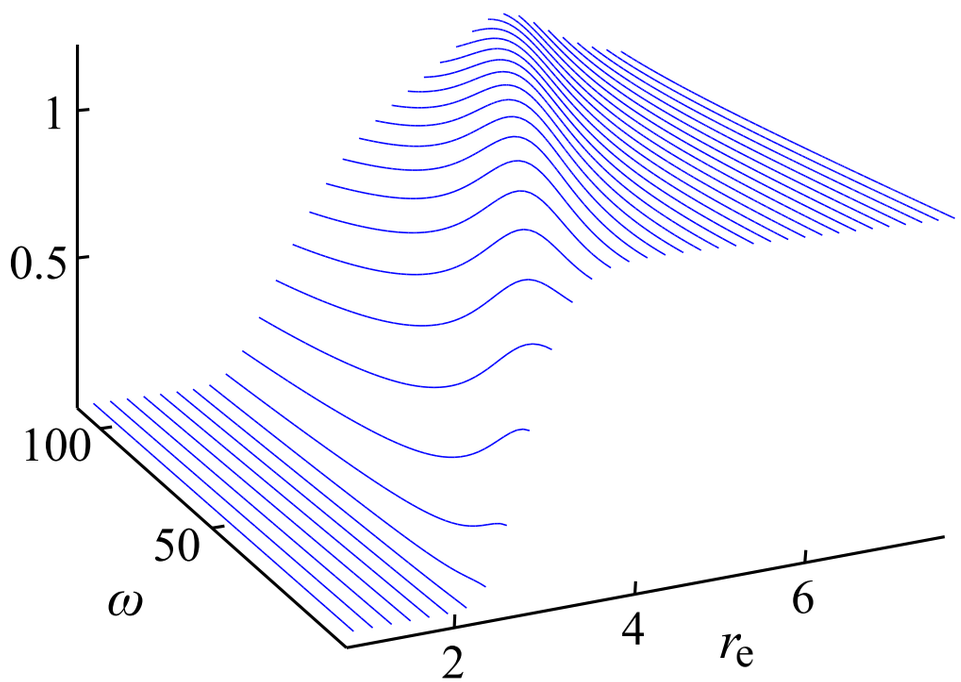


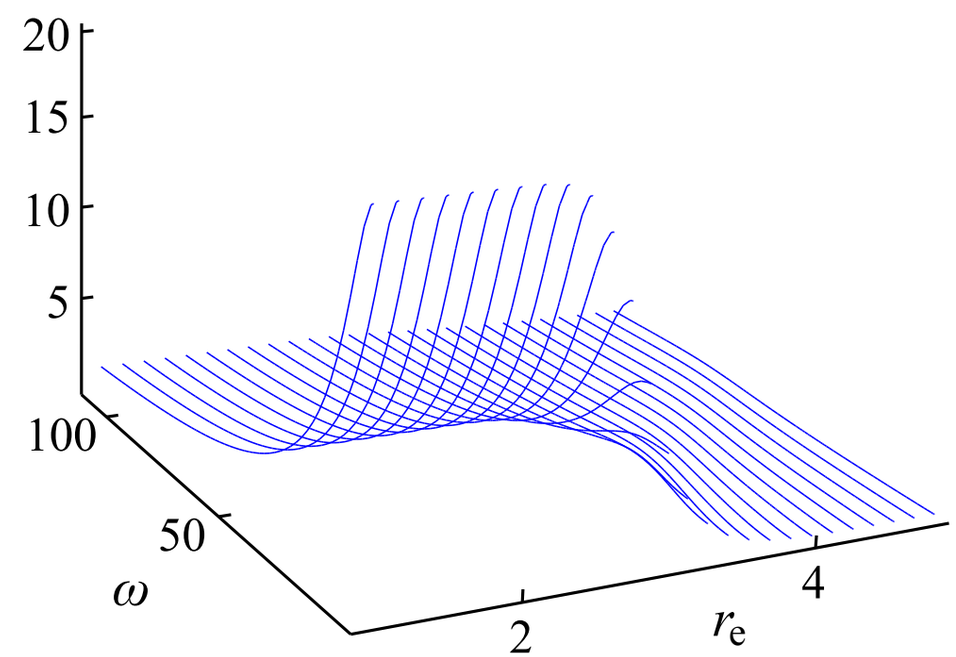
Linear response function

$$\chi_V(\omega) = \frac{\tau_m}{1 + i\omega\tau_m}\left(1 - (V_{\mathrm{th}} - V_{\mathrm{re}})\,\chi_s(\omega)\right)$$

$|\chi_s(\omega)|$



$|\chi_V(\omega)|$



Approximate cross-covariance functions

Weak excitation

$$|\chi_s(\omega)| \approx 0 \text{ and } |\chi_V(\omega)| \approx \tau_m/\sqrt{(1+\tau_m^2\omega^2)}$$

Strong excitation

$$|\chi_s(\omega)| \approx (V_{\text{th}} - V_{\text{re}})^{-1} \text{ and } |\chi_V(\omega)| \approx 0.$$

This gives us an analytically tractable expression for the covariances

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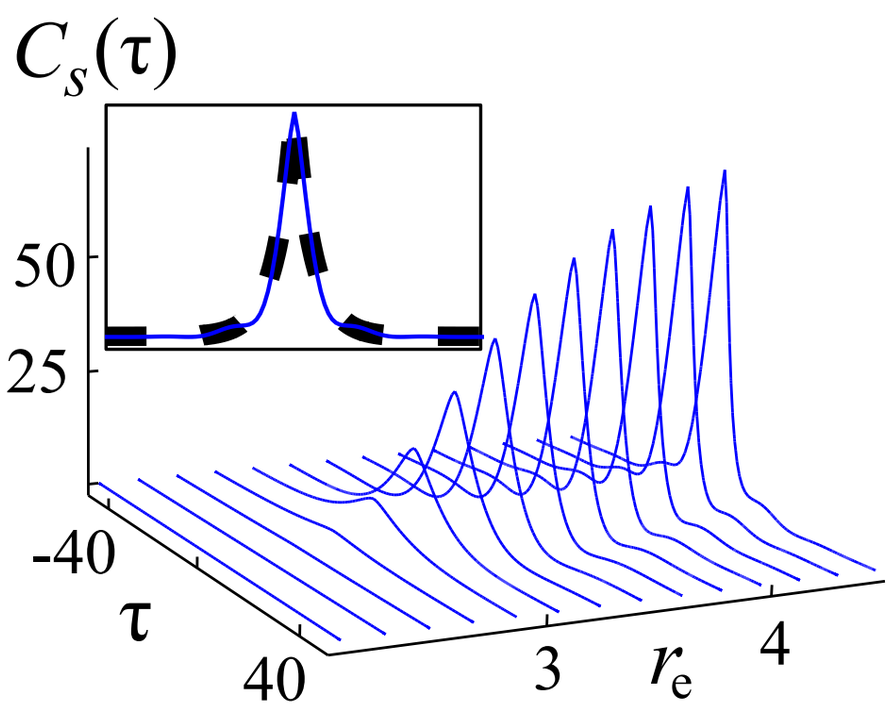
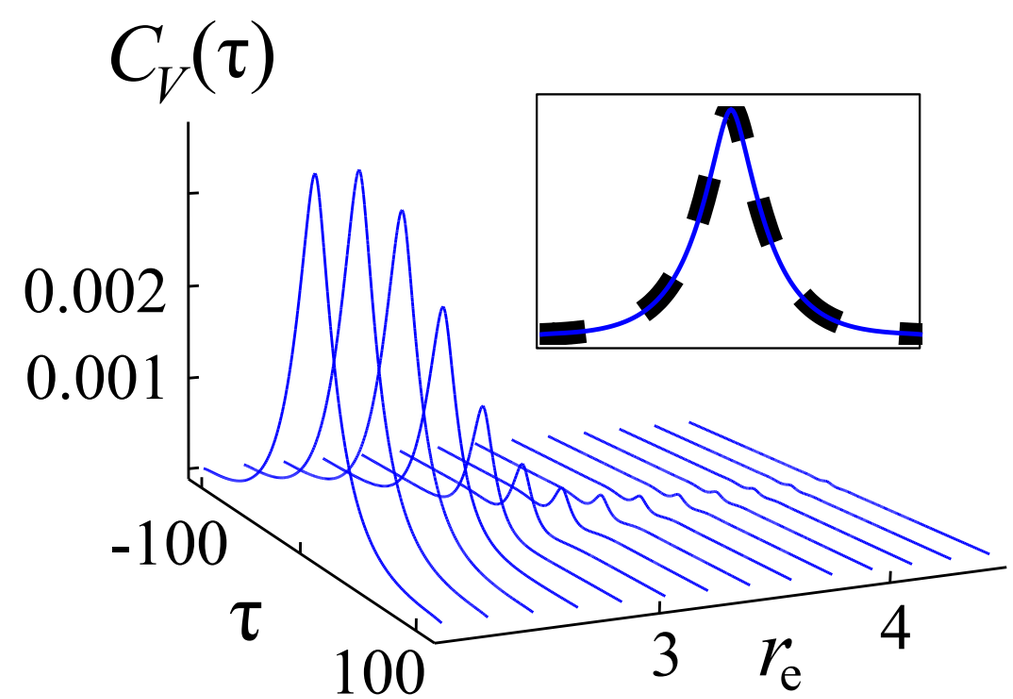
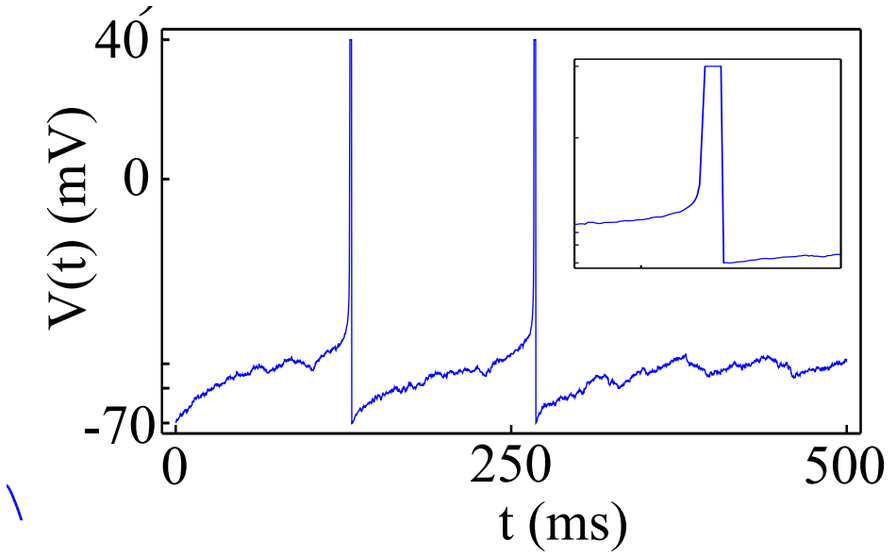


$$\widetilde{C}_s(\omega) \approx |\chi_s(\omega)|^2\, \widetilde{C}_{\rm in}(\omega)$$

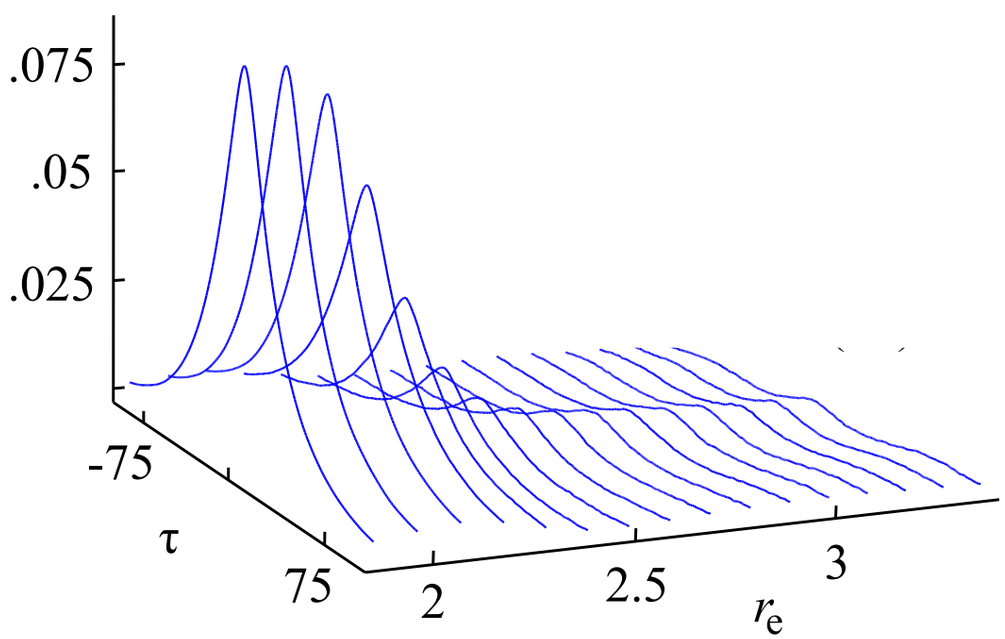


$$\widetilde{C}_V(\omega) \approx |\chi_V(\omega)|^2\, \widetilde{C}_{\rm in}(\omega)$$

Potential impacts on recordings

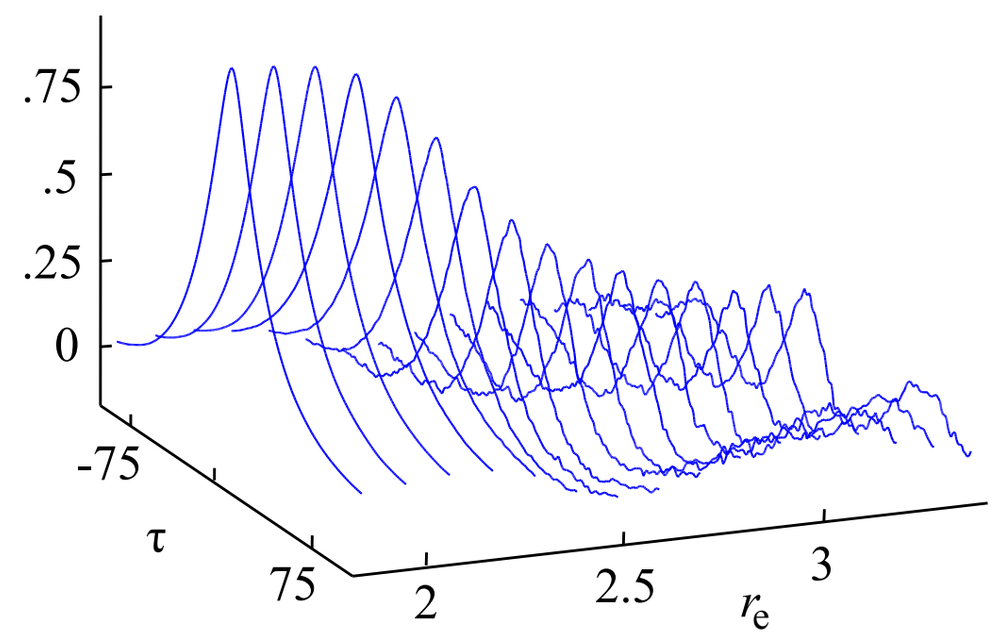


$R_V(\tau)$



Pair of cells

$R_{\text{signal}}(\tau)$



Two pools of 200 cells each

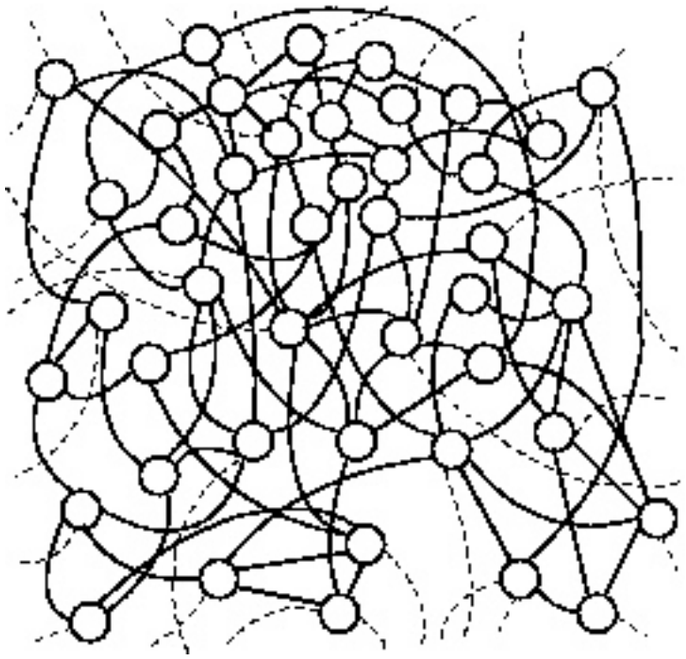
Structure or correlations in networks

$$\tau_i \dot{v}_i = -(v_i - E_{L,i}) + \psi(v_i) + E_i' + \sqrt{\sigma_i^2 \tau_i} \xi_i(t) + (f_i(t) - \langle f_i \rangle)$$

spike generating current synaptic connections

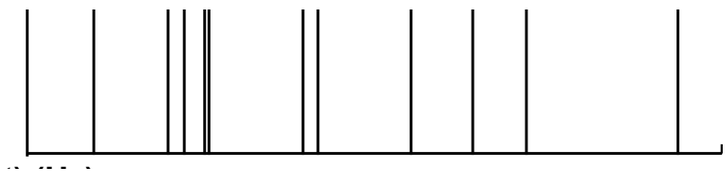
$$f_i(t) = \sum_j (\mathbf{J}_{ij} * y_j)(t)$$

$$\mathbf{J}_{ij}(t) = \begin{cases} \mathbf{W}_{ij} \left(\frac{t - \tau_{D,j}}{\tau_{S,j}^2} \right) \exp\left[-\frac{t - \tau_{D,j}}{\tau_{S,j}} \right] & t \geq \tau_{D,j} \\ 0 & t < \tau_{D,j} \end{cases}$$



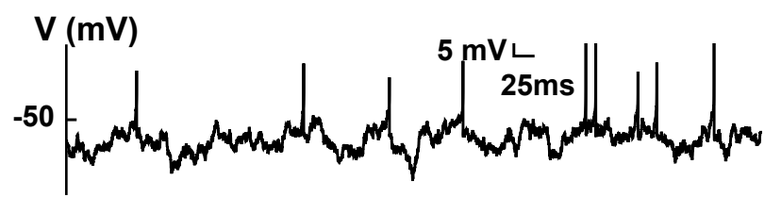
Nykamp

Linear response kernel, *A(t)*

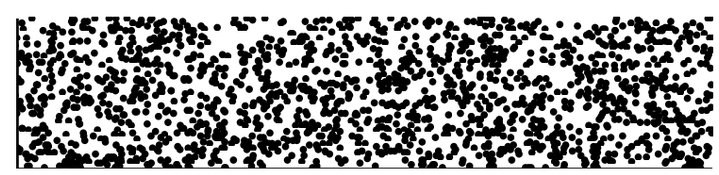


input to cell

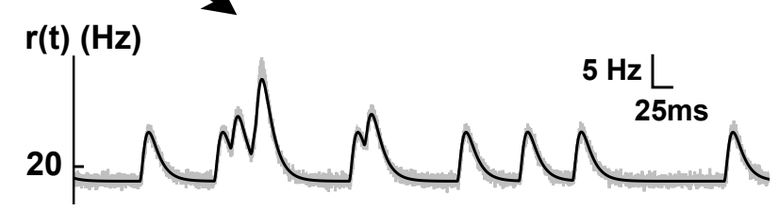
activity of cell



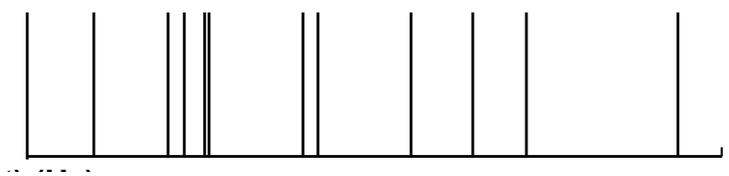
repeated trials



firing rate

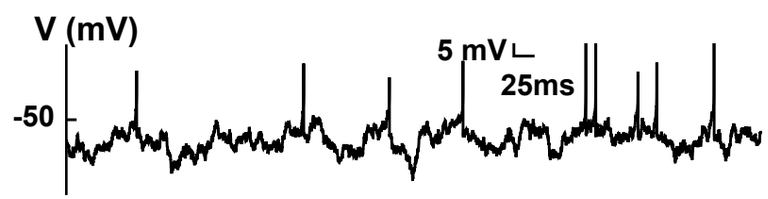


Linear response kernel, *A(t)*

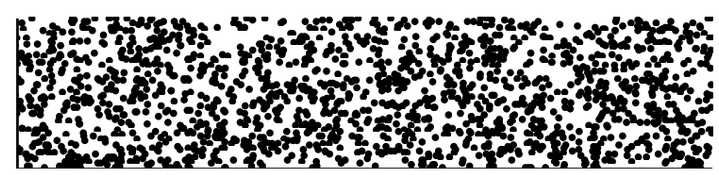


input to cell

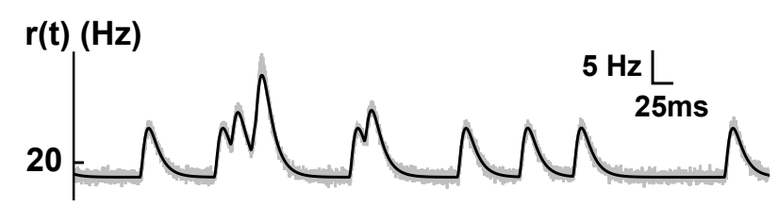
activity of cell



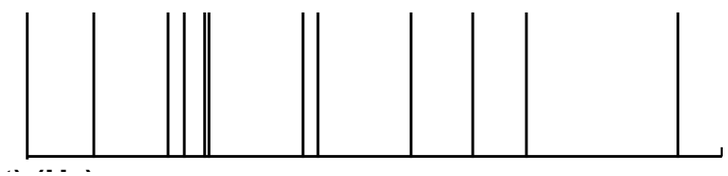
repeated trials



firing rate



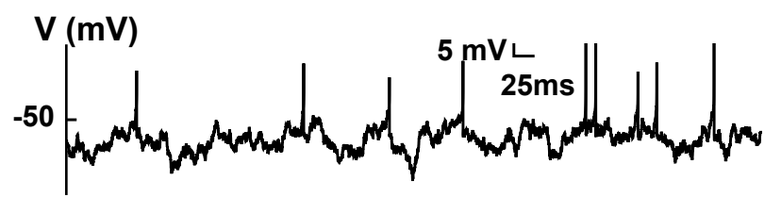
Linear response kernel, *A(t)*



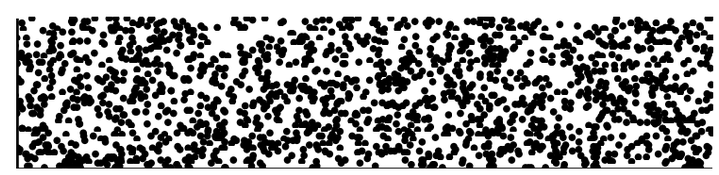
input to cell

$$r(t) = r_0 + (A * X)(t)$$

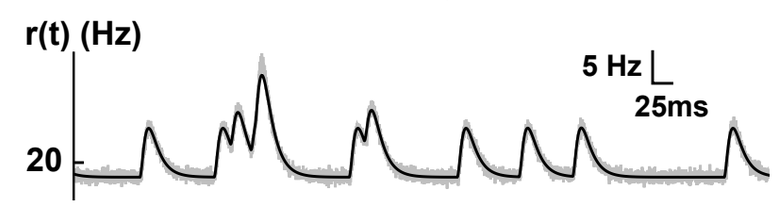
activity of cell



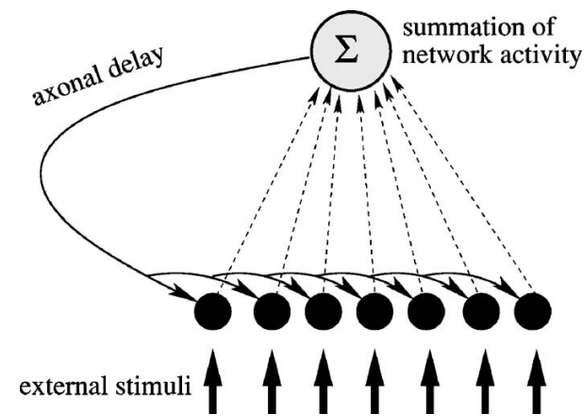
repeated trials



firing rate



Can we estimate the correlation structure?



Idea goes back to
Lindner, Doiron, Longtin, 2005

$$\tau \dot{v} = -(v - E_L) + \psi(v) + E + \sqrt{\sigma^2 \tau}\xi(t) + X(t)$$

$$y(t) = \sum_i \delta(t - t_i)$$

Linear response gives the output rate as

$$r(t) = r_0 + (A * X)(t)$$

But this is of no use in computing the cross correlation function

$$\mathbf{C}_{ij}(\tau) = \mathrm{cov}\left(y_i(t+\tau), y_j(t)\right)$$

Can we estimate the correlation structure?

$$\tau \dot{v} = -(v - E_L) + \psi(v) + E + \sqrt{\sigma^2 \tau}\xi(t) + X(t)$$

$$y(t) = \sum_i \delta(t - t_i)$$

Use linear response to obtain a mixed point/continuous process

$$y(t) \approx y^1(t) = y^0(t) + (A * X)(t)$$

Which averages out to the right thing

$$r(t) = r_0 + (A * X)(t)$$

Approximate network correlations

$$\tau_i \dot{v}_i = -(v_i - E_{L,i}) + \psi(v_i) + E_i' + \sqrt{\sigma_i^2 \tau_i}\xi_i(t) + (f_i(t) - \langle f_i \rangle)$$

$$X(t) = f_i(t) - \langle f_i(t) \rangle$$

The linear response approximation now takes the form

$$y_i^1(t) = y_i^0(t) + \sum_{\cdot} (\mathbf{K}_{ij} * [y_j^0 - r_j])(t)$$

$$\mathbf{K}_{ij}(t) \equiv (A_i * \mathbf{J}_{ij})(t)$$

We can use this to approximate the cross-correlation

$$\begin{aligned}\mathbf{C}_{ij}(\tau) \approx \mathbf{C}_{ij}^1(\tau) &= \mathbf{E}\big\{(y_i^1(t+\tau) - r_i)(y_j^1(t) - r_j)\big\} \\ &= \delta_{ij}\mathbf{C}_{ii}^0(\tau) + (\mathbf{K}_{ij} * \mathbf{C}_{jj}^0)(\tau) + (\mathbf{K}_{ji}^- * \mathbf{C}_{ii}^0)(\tau) + \sum_k (\mathbf{K}_{ik} * \mathbf{K}_{jk}^- * \mathbf{C}_{kk}^0)(\tau)\end{aligned}$$

Ostojic, Brunel, Hakim, 2009,
Trousdale, Yu, Shea-Brown, Josić, 2011

Impact of non-immediate neighbors

We use an iterative construction

$$y_i^{n+1}(t) = y_i^0(t) + \sum_j (\mathbf{K}_{ij} * [y_j^n - r_j])(t)$$

In matrix form

$$\begin{aligned}\mathbf{y}^{n+1}(t) &= \mathbf{y}^0(t) + (\mathbf{K} * [\mathbf{y}^n - \mathbf{r}])(t) \\ &= \mathbf{y}^0(t) + \sum_{k=1}^{n+1} (\mathbf{K}^{(k)} * [\mathbf{y}^0 - \mathbf{r}])(t)\end{aligned}$$

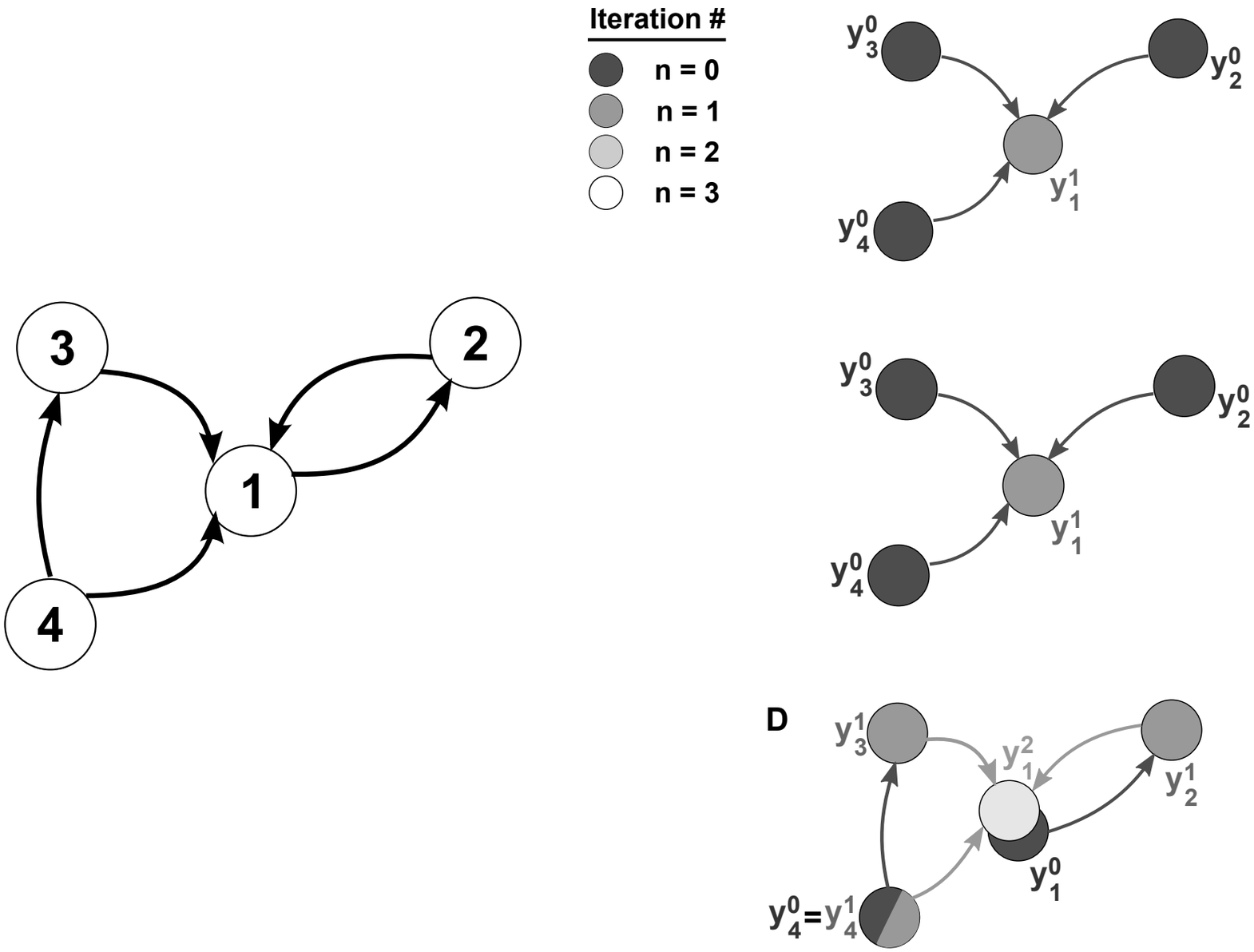
Which gives the n-th approximation to the cross-correlation

$$\begin{aligned}\mathbf{C}_{ij}(\tau) \approx \mathbf{C}^n(\tau) &= \mathbf{E}\{(\mathbf{y}^n(t+\tau) - \mathbf{r})(\mathbf{y}^n(t) - \mathbf{r})^T\} \\ &= \sum_{k,l=0}^{n} (\mathbf{K}^{(k)} * \mathbf{C}^0 * (\mathbf{K}^-)^{(lT)})(\tau), \quad n \geq 0,\end{aligned}$$

After taking the Fourier transform, and the limit $n \to \infty$

$$\tilde{\mathbf{C}}^\infty(\omega) = \lim_{n\to\infty} \tilde{\mathbf{C}}^n(\omega) = (\mathbf{I} - \tilde{\mathbf{K}}(\omega))^{-1} \tilde{\mathbf{C}}^0(\omega) (\mathbf{I} - \tilde{\mathbf{K}}^*(\omega))^{-1}$$

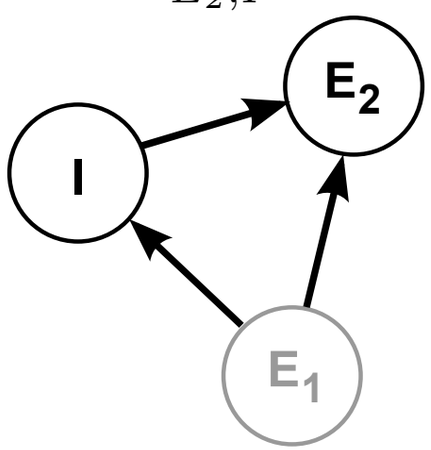
The iterative construction



Rangan 2009
Pernice et al, 2011
Trousdale, Yu, Shea-Brown, Josić, 2011

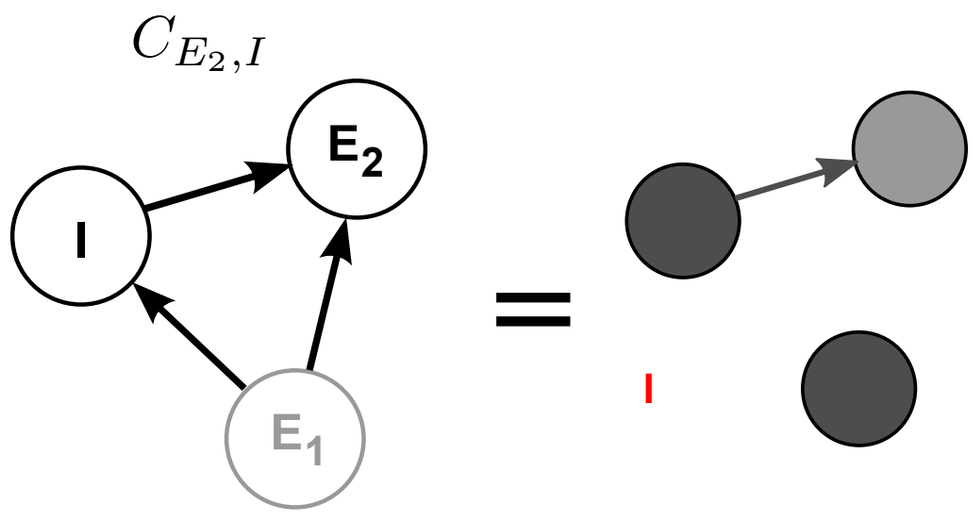
Example - microcircuits

$C_{E_2,I}$



$$
\begin{array}{c c}
 & \begin{array}{ccc} E_1 & E_2 & I \end{array} \\
\begin{array}{c} E_1 \\ E_2 \\ I \end{array} & \begin{pmatrix} 0 & 0 & 0 \\ \tilde{K}_{E_2E_1}(\omega) & 0 & \tilde{K}_{E_2I}(\omega) \\ \tilde{K}_{IE_1}(\omega) & 0 & 0 \end{pmatrix}
\end{array}
$$

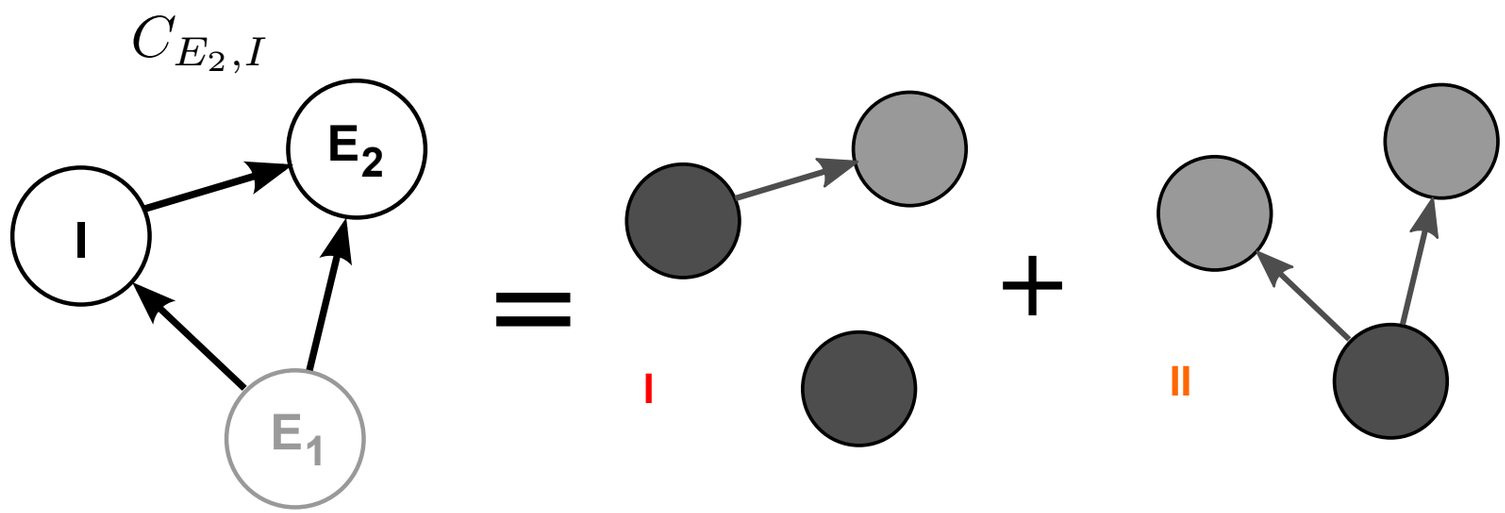
Example - microcircuits



$$
\begin{array}{c c}
 & \begin{array}{ccc} E_1 & E_2 & I \end{array} \\
\begin{array}{c} E_1 \\ E_2 \\ I \end{array} & \begin{pmatrix} 0 & 0 & 0 \\ \tilde{K}_{E_2E_1}(\omega) & 0 & \tilde{K}_{E_2I}(\omega) \\ \tilde{K}_{IE_1}(\omega) & 0 & 0 \end{pmatrix}
\end{array}
$$

$$
\tilde{C}^{\infty}_{E_2I} = \underbrace{(\tilde{A}_{E_2}\tilde{J}_{E_2I})\tilde{C}^0_I}_{\mathrm{I}}
$$

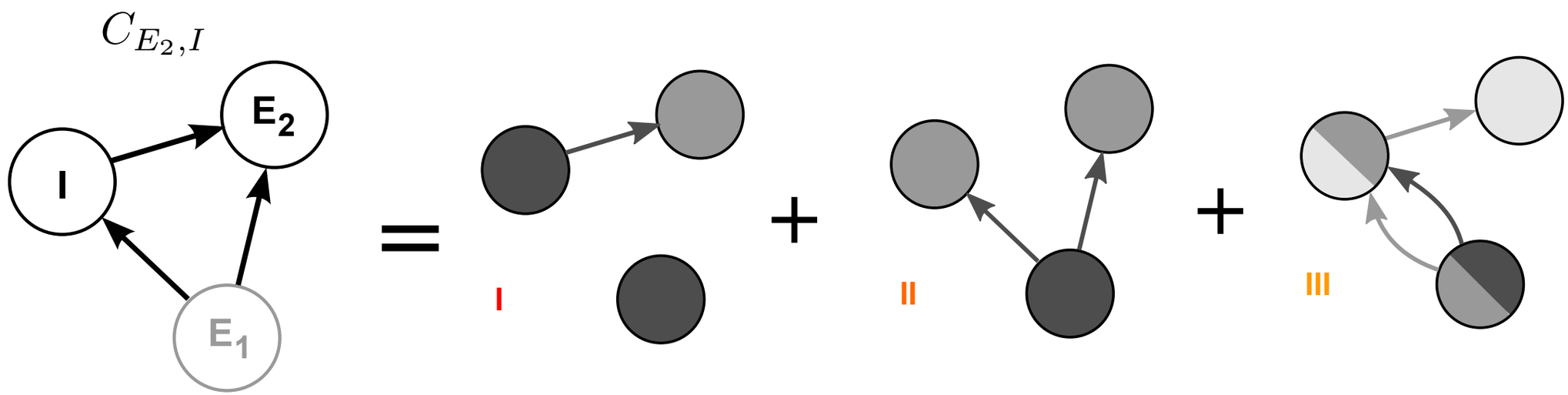
Example - microcircuits



$$
\begin{array}{c c}
 & \begin{array}{ccc} E_1 & E_2 & I \end{array} \\
\begin{array}{c} E_1 \\ E_2 \\ I \end{array} & \begin{pmatrix} 0 & 0 & 0 \\ \tilde{K}_{E_2E_1}(\omega) & 0 & \tilde{K}_{E_2I}(\omega) \\ \tilde{K}_{IE_1}(\omega) & 0 & 0 \end{pmatrix}
\end{array}
$$

$$
\tilde{C}^{\infty}_{E_2I} = \underbrace{(\tilde{A}_{E_2}\tilde{J}_{E_2I})\tilde{C}^0_I}_{\mathrm{I}} + \underbrace{(\tilde{A}_{E_2}\tilde{J}_{E_2E_1})(\tilde{A}_I\tilde{J}_{IE_1})^*\tilde{C}^0_{E_1}}_{\mathrm{II}}
$$

Example - microcircuits

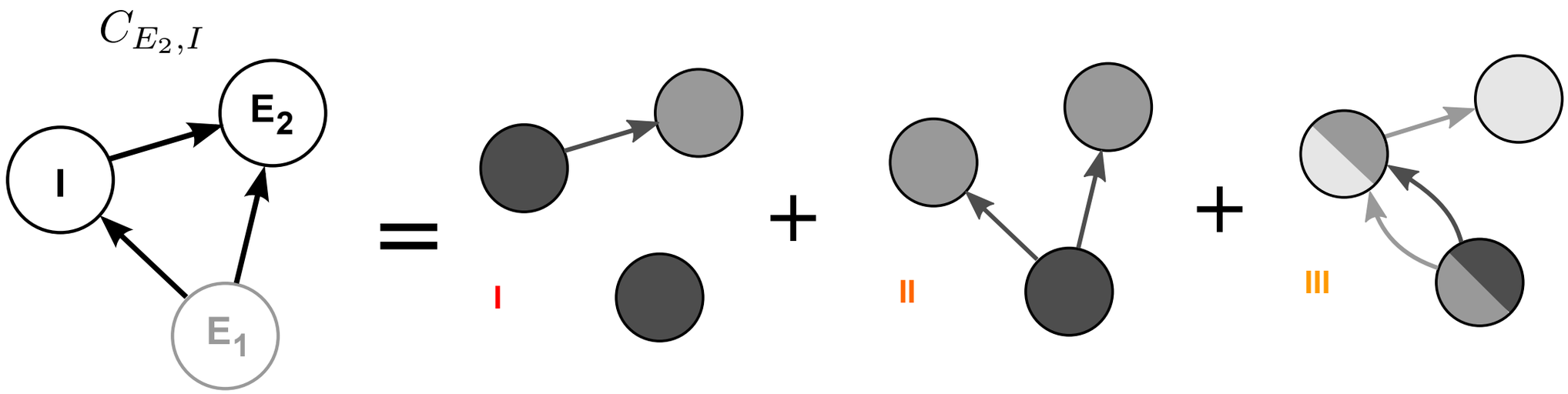


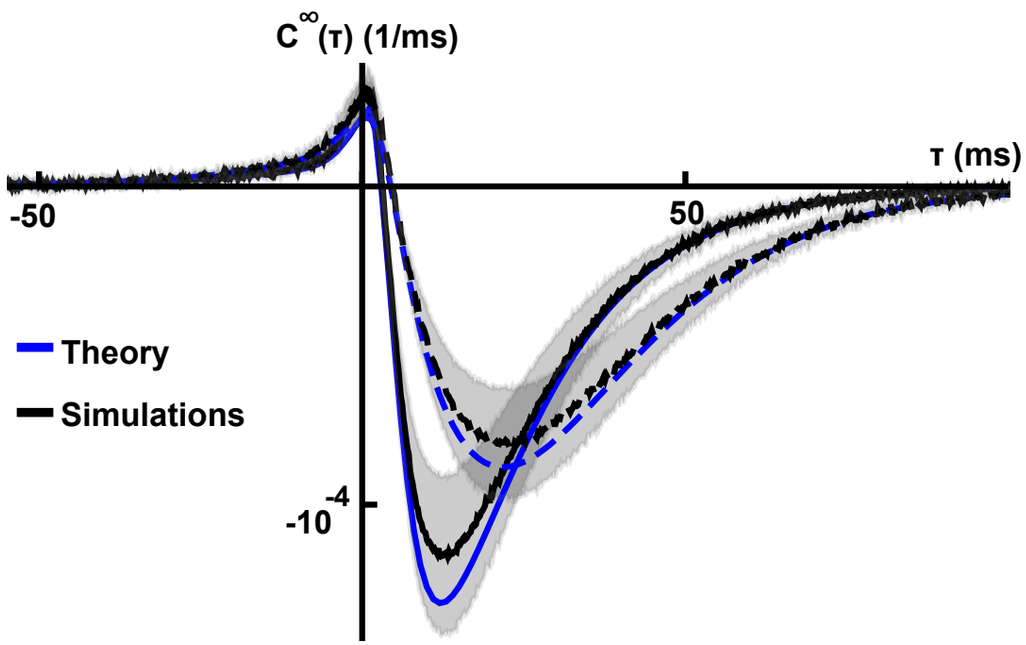
$$
\begin{array}{c c}
 & \begin{array}{ccc} E_1 & E_2 & I \end{array} \\
\begin{array}{c} E_1 \\ E_2 \\ I \end{array} & \begin{pmatrix} 0 & 0 & 0 \\ \tilde{K}_{E_2E_1}(\omega) & 0 & \tilde{K}_{E_2I}(\omega) \\ \tilde{K}_{IE_1}(\omega) & 0 & 0 \end{pmatrix}
\end{array}
$$

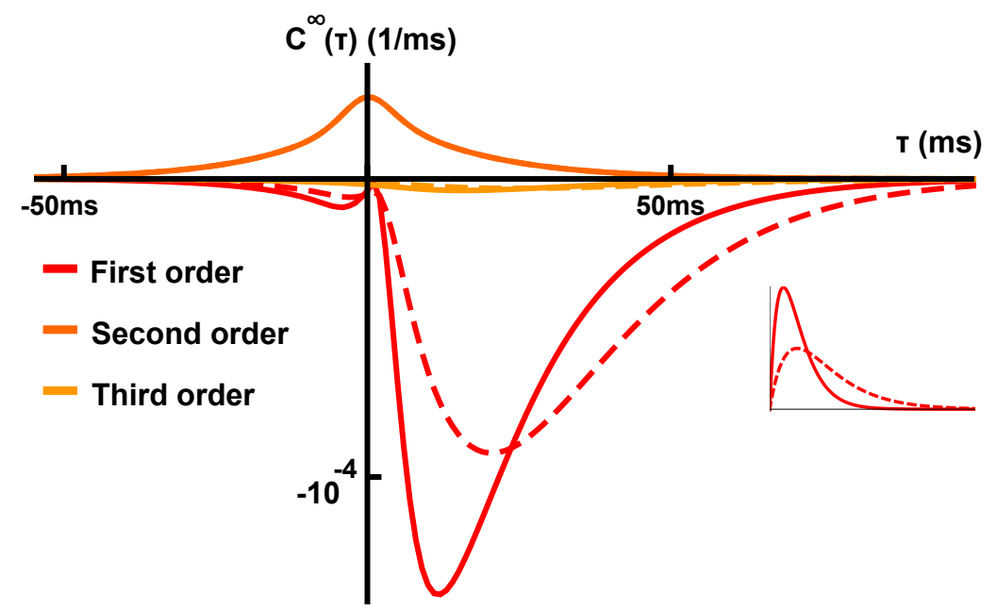
$$
\tilde{C}^{\infty}_{E_2I} = \underbrace{(\tilde{A}_{E_2}\tilde{J}_{E_2I})\tilde{C}^0_I}_{\mathrm{I}} + \underbrace{(\tilde{A}_{E_2}\tilde{J}_{E_2E_1})(\tilde{A}_I\tilde{J}_{IE_1})^*\tilde{C}^0_{E_1}}_{\mathrm{II}}
$$

$$
+ \underbrace{(\tilde{A}_{E_2}\tilde{J}_{E_2E_1})|\tilde{A}_I\tilde{J}_{IE_1}|^2\tilde{C}^0_{E_1}}_{\mathrm{III}}
$$

Example - microcircuits

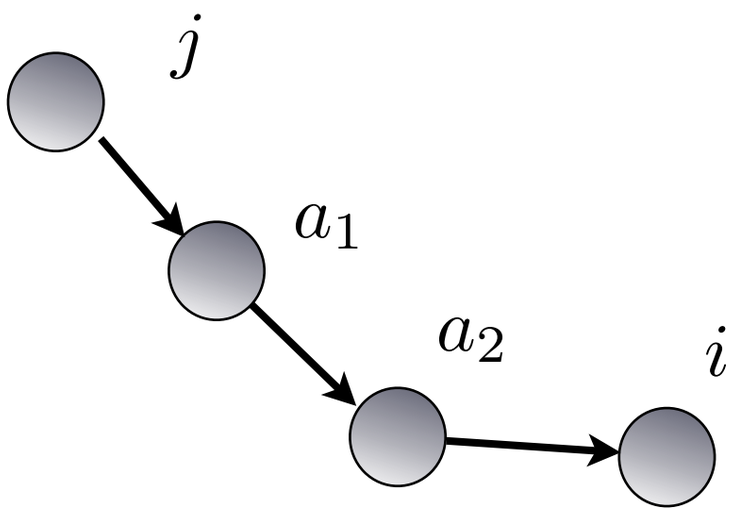




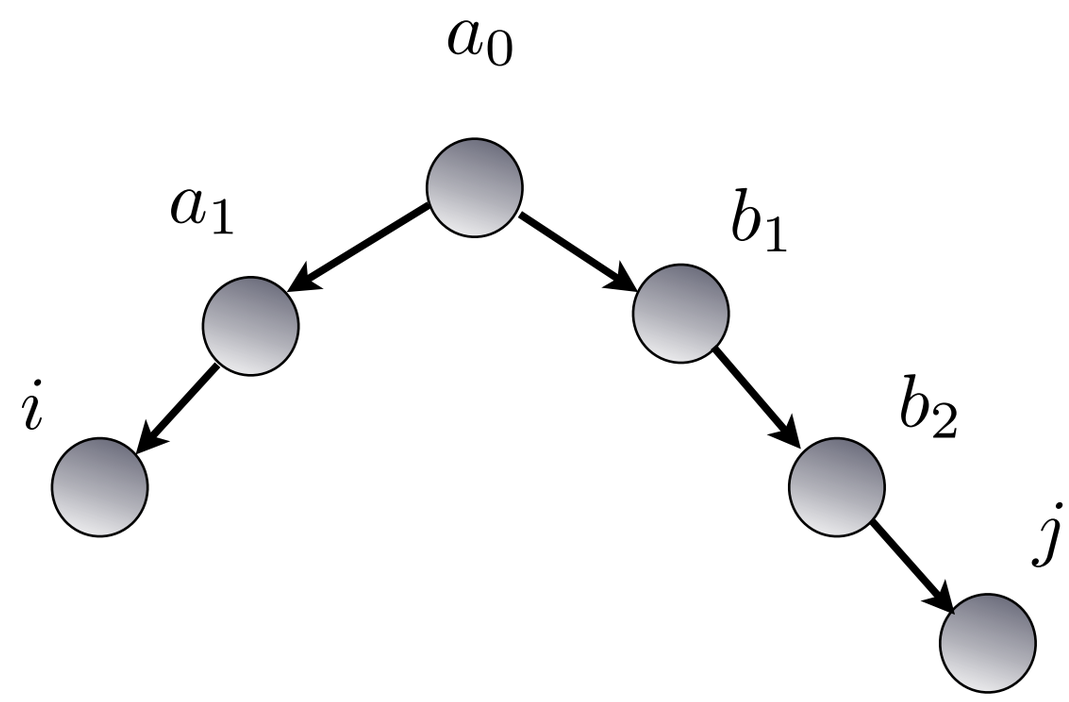


Expansion in terms of paths through the graph

$$\tilde{\mathbf{C}}^{\infty}(\omega) = \lim_{n\to\infty} \tilde{\mathbf{C}}^{n}(\omega) = (\mathbf{I} - \tilde{\mathbf{K}}(\omega))^{-1}\tilde{\mathbf{C}}^{0}(\omega)(\mathbf{I} - \tilde{\mathbf{K}}^{*}(\omega))^{-1}$$



$$\tilde{\mathbf{K}}_{ia_{n-1}}\tilde{\mathbf{K}}_{a_{n-1}a_{n-2}}\cdots\tilde{\mathbf{K}}_{a_1 j}\tilde{\mathbf{C}}^{0}_{jj}$$



$$\tilde{\mathbf{K}}_{ia_{n-1}}\tilde{\mathbf{K}}_{a_{n-1}a_{n-2}}\cdots\tilde{\mathbf{K}}_{a_1 a_0}\tilde{\mathbf{C}}^{0}_{a_0 a_0}\tilde{\mathbf{K}}^{*}_{a_0 b_1}\cdots\tilde{\mathbf{K}}^{*}_{b_{m-2}b_{m-1}}\tilde{\mathbf{K}}^{*}_{b_{m-1}j}$$

Network of all-to-all coupled cells

If we have N_E excitatory and N_I inhibitory cells

$$\tilde{\mathbf{K}} = \tilde{A}\tilde{\mathbf{J}}, \qquad \text{where} \qquad \tilde{\mathbf{J}} = \begin{pmatrix} \tilde{J}_E \mathbf{1}_{N_E N_E} & \tilde{J}_I \mathbf{1}_{N_E N_I} \\ \tilde{J}_E \mathbf{1}_{N_I N_E} & \tilde{J}_I \mathbf{1}_{N_I N_I} \end{pmatrix}$$

Then the cross-correlation is

$$\tilde{\mathbf{C}}^{\infty}_{E,I} = \tilde{C}^0 \left[\tilde{A}\frac{\tilde{\mu}_I}{N_I} + \tilde{A}^* \frac{\tilde{\mu}_E^*}{N_E} + |\tilde{A}|^2 \tilde{\mu}_c \right]$$

Mutual coupling

$$\tilde{\mu}_I(\omega) = N_I \tilde{J}_I(\omega)$$

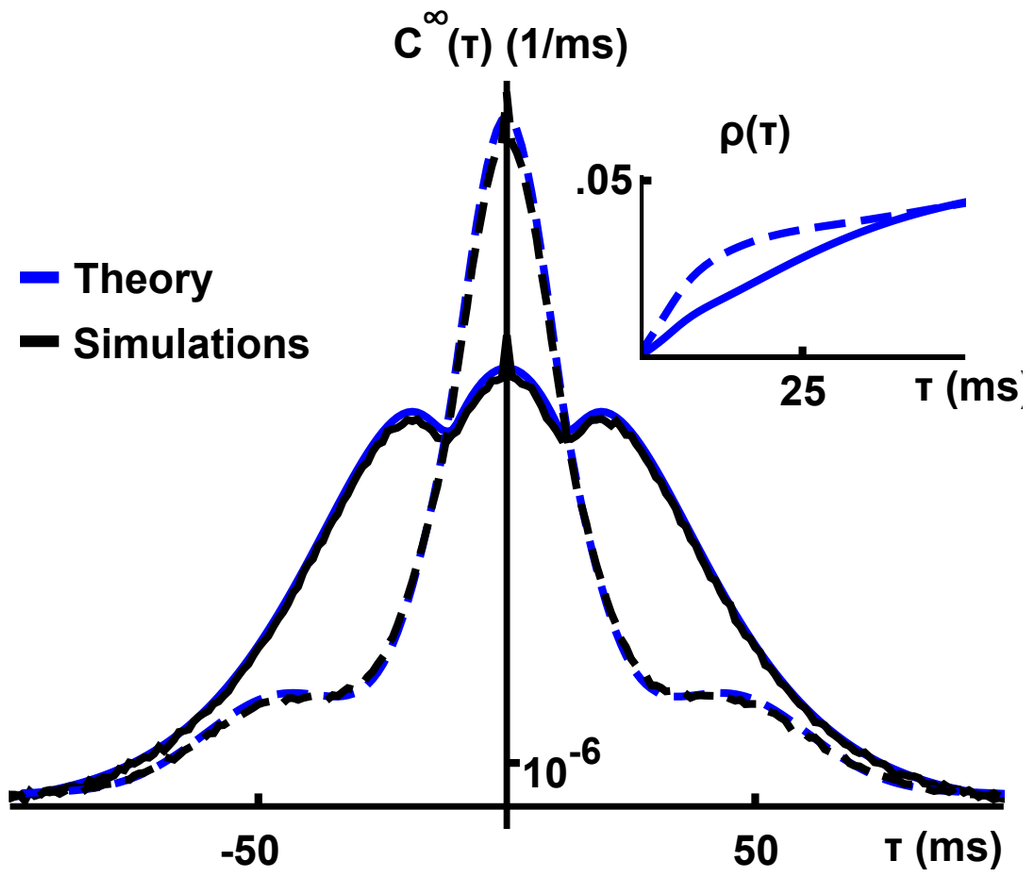
$$\tilde{\mu}_E(\omega) = N_E \tilde{J}_E(\omega)$$

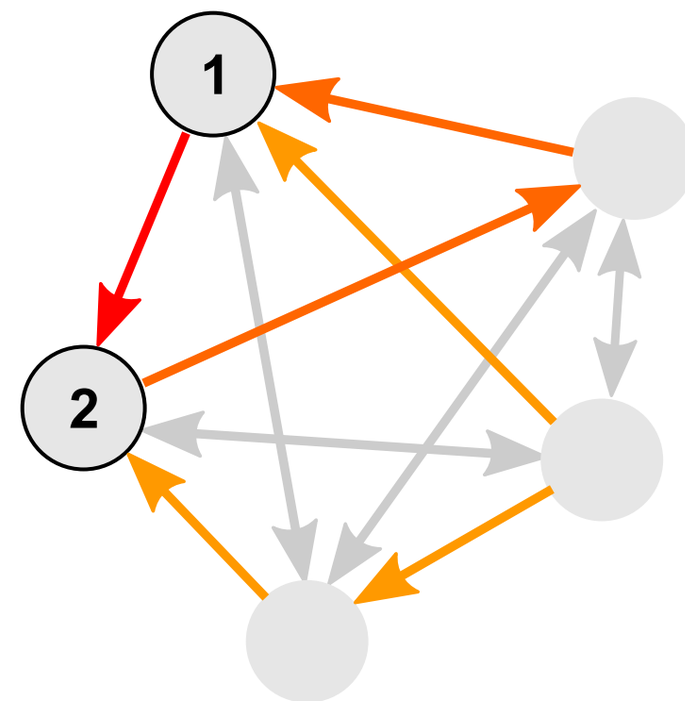
Common input

$$\tilde{\mu}_c(\omega) = N_E |\tilde{J}_E(\omega)|^2 + N_I |\tilde{J}_I(\omega)|^2$$

No Contributions of longer paths!

Unbalanced network



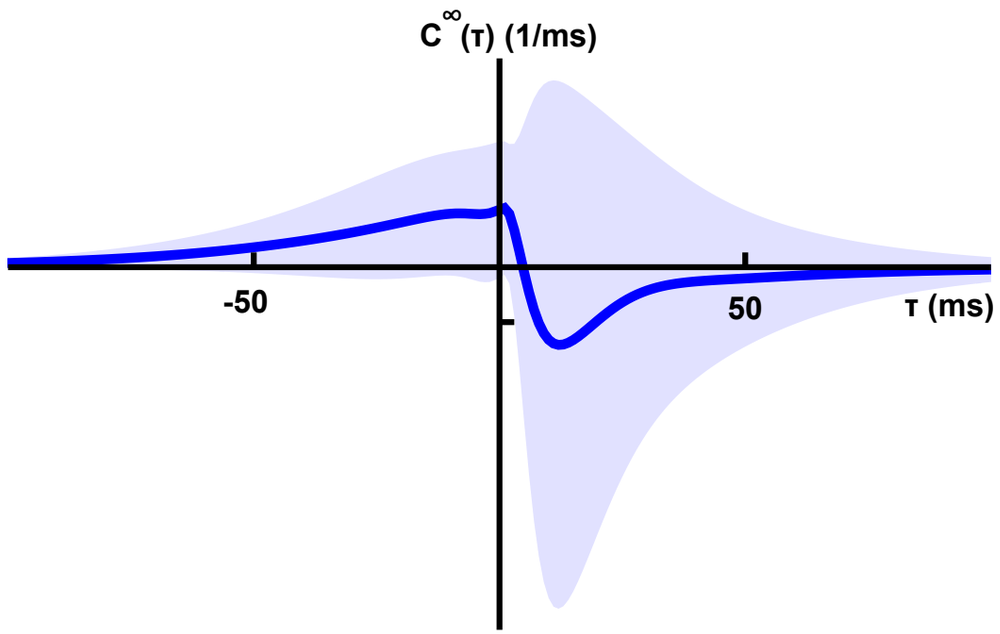


$$C_{12} = C^{0}[K^{*} + K^{2} + K(K^{*})^{2} + \ldots]$$

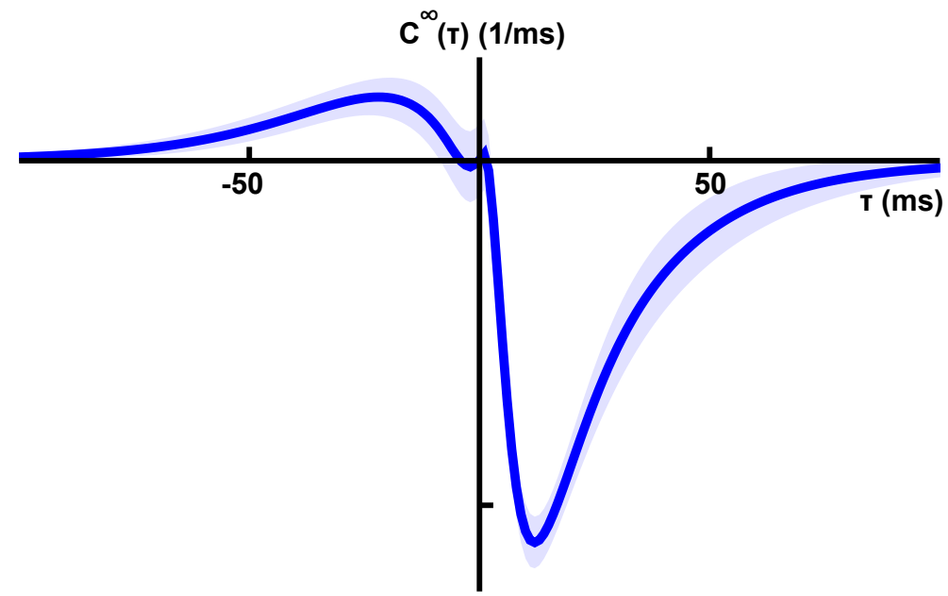
Cross-correlation between two excitatory cells

Cross-correlations in random networks

Analytically obtained mean



Unconditioned



Conditioned on reciprocal coupling

Conclusion

- Linear response theory can be used to understand the statistical structure of population activity

- The transfer of input correlations to output correlations is different for membrane voltages and spikes. This could impact how we interpret population recordings.

- Cross-correlation functions can be understood in terms of contributions from paths through the network. Thus architecture and population activity can be related.

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