Theory of correlation transfer and correlation structure Part II: recurrent networks

CNS*2012 tutorial

July 21st, Decatur, Atlanta | Moritz Helias

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Why study correlations in the brain?

- variable response of cortical neurons to repeated stimuli
- neurons share variability, causing correlations
- typical count correlation in primates $0.01 - 0.25$

  Cohen & Kohn (2011)
- affects the information in the population signal

  Zohary et al. (1994); Shadlen & Newsome (1998)
- correlations are modulated by attention

  Cohen & Maunsell (2009)
- correlations reflect behavior

  Kilavik et al. (2009)
- correlation analysis has been used to infer connectivity

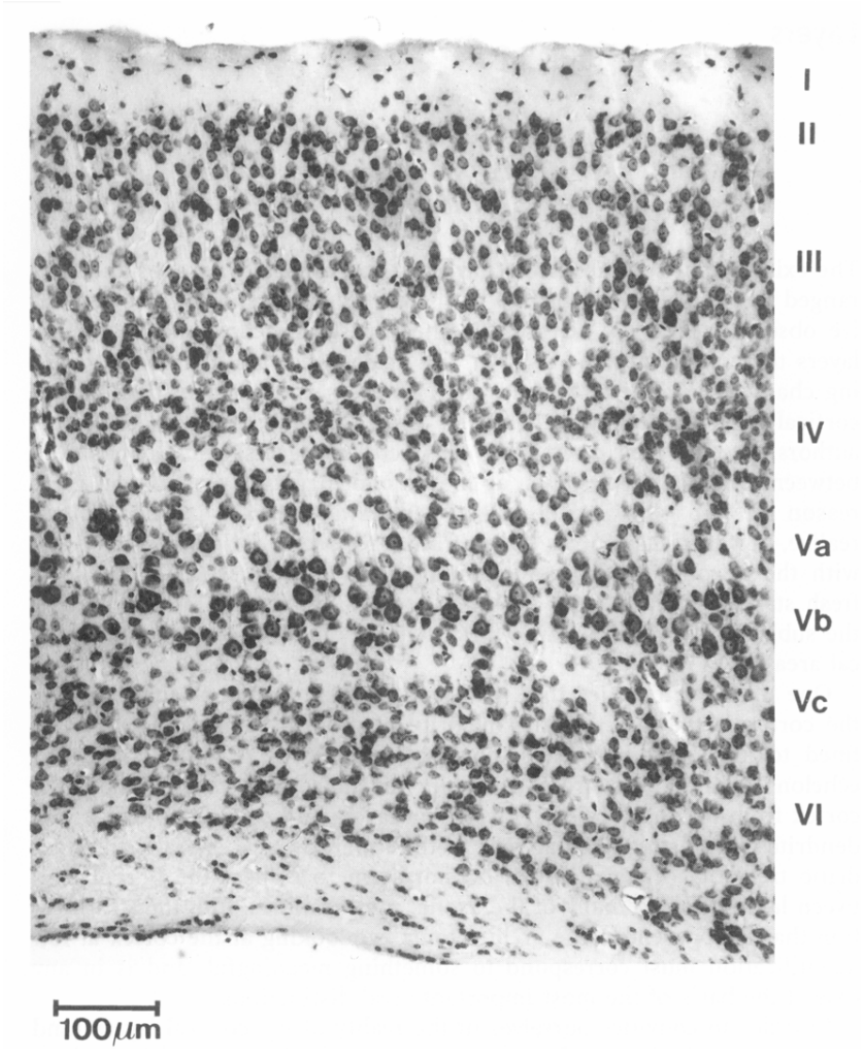
  Aertsen (1989), Alonso (1998)
- synaptic plasticity is sensitive to correlations

  Bi & Poo (1998)

Outline

- in vivo correlations & random networks
- theory of correlations in binary random networks
  - binary neuron model
  - mean-field solution
  - balanced state
  - self-consistency equation for correlations
  - correlation suppression
- theory of correlations in spiking networks
  - leaky integrate-and-fire model
  - linear response theory
  - population averages
  - exposing negative feedback by Schur transform
  - fluctuation suppression $\leftrightarrow$ decorrelation
  - structure of correlations

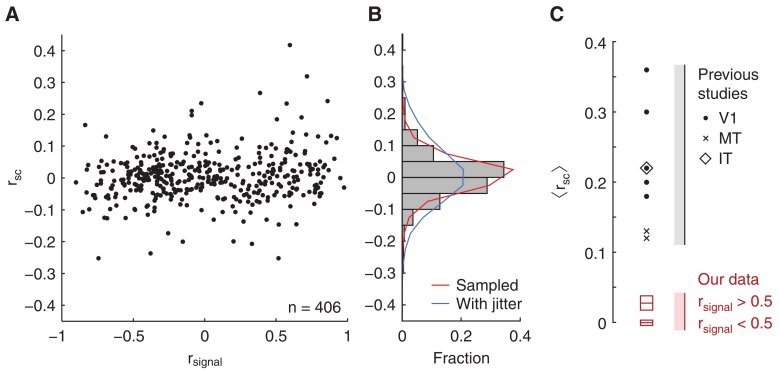
Local cortical network



- $N \simeq 10^5$ neurons / mm^3
- $K \simeq 10^4$ synapses / neuron
- connection prob. $\simeq 10$ percent
- layered structure
- layer-specific connectivity
- different cell types
- most importantly: exc. and inh. cells
- different morphologies

abstraction of neurons as points connected by synapses

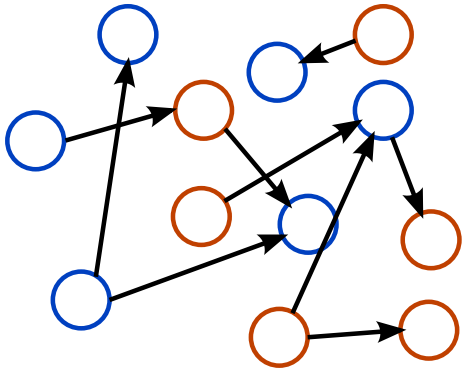
Asynchronous firing

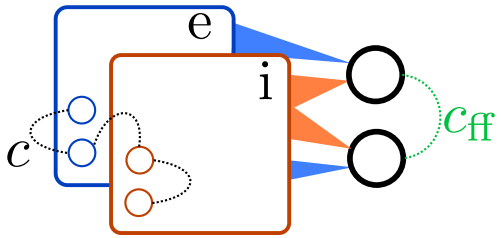


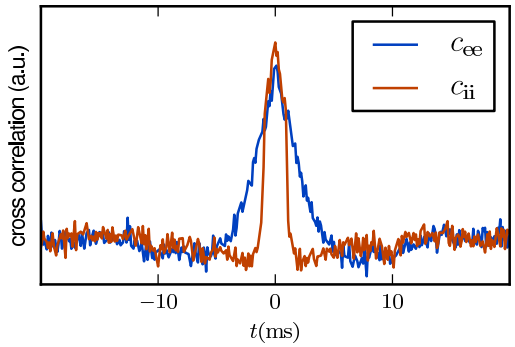
- noise correlations r_{sc} smaller than expected given the amount of common input ($p_c = 0.1$) and despite signal correlations r_{signal}
- trial averaged response $m = \langle x \rangle_{\mathrm{trials}}$
- count (noise) correlation $r_{\mathrm{sc}} = \langle \langle z_1 z_2 \rangle_{\mathrm{trials}} \rangle_{\Theta}$ with $z = \frac{x-m}{\sqrt{\langle (x-m)^2 \rangle_{\mathrm{trials}}}}$
- signal corelation $r_{\mathrm{signal}} = \langle y_1 y_2 \rangle_{\Theta}$ with $y = \frac{m-n}{\sqrt{\langle (m-n)^2 \rangle_{\Theta}}}$ and $n = \langle m \rangle_{\Theta}$

Ecker A, Berens P, Keliris GA, Bethge M, Logothetis NK, Tolias AS (2010): Science 327: 584

Small correlations

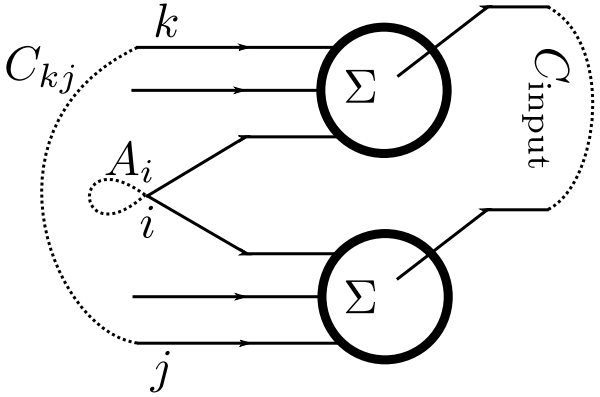


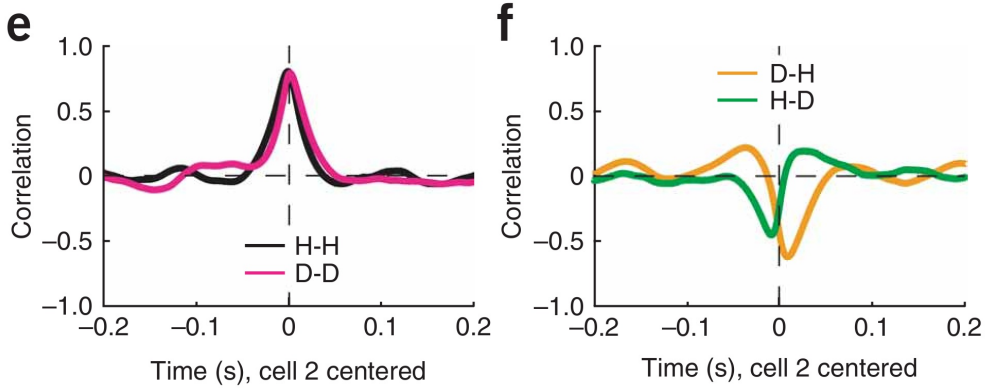




- correlations smaller than expected from common input
- connectivity $p_c = 0.1 \rightarrow 10$ percent common presynaptic partners
- correlations differ for ee and for ii pairs
  (even if symmetric connectivity assumed in simulations)
- naive picture suggests $c = c_{\mathrm{ff}}$

Structure of correlation between input currents

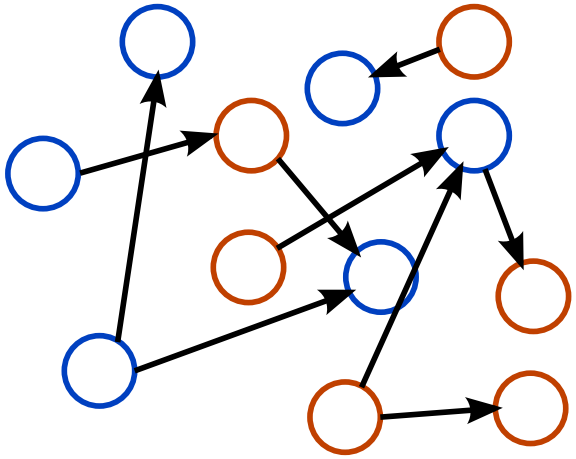


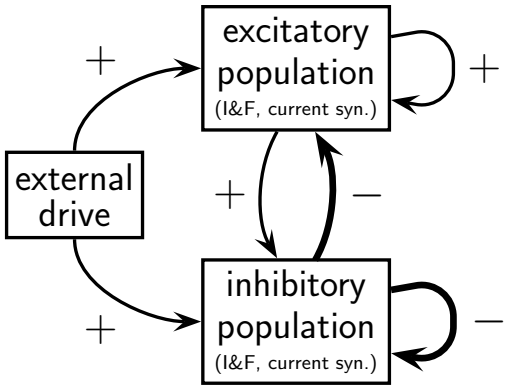


- measurement of excitatory and inhibitory currents separately
- positive contributions by ee and ii correlations
- biphasic contribution by ei correlation

Okun M and Lampl I, Nature neuroscience 11(5) (2008)

Aim: Understand correlations in recurrent random networks





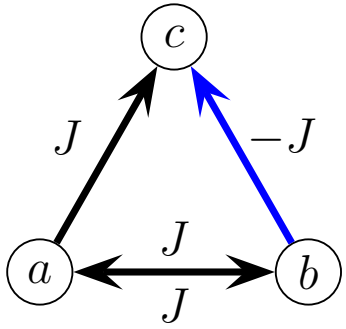
- N excitatory and γN inhibitory neurons
- neurons all have same internal dynamics
- random connectivity with connection probability $p = K/N$
- each exc. synapse has strength J, inh. has strength $-gJ$
- well studied model of local cortical network

van Vreeswijk & Sompolinsky 1996, Amit & Brunel 1997, Brunel 2000

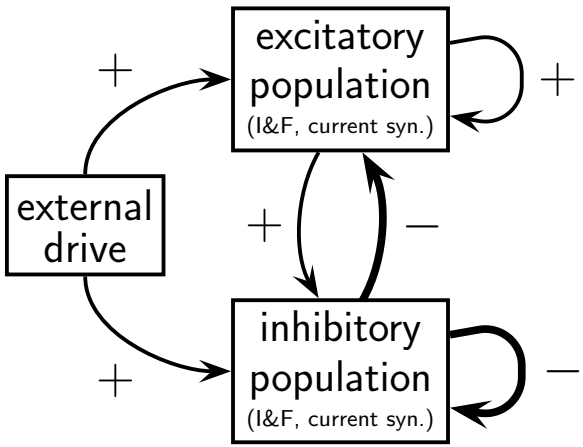
Why study E-I networks?

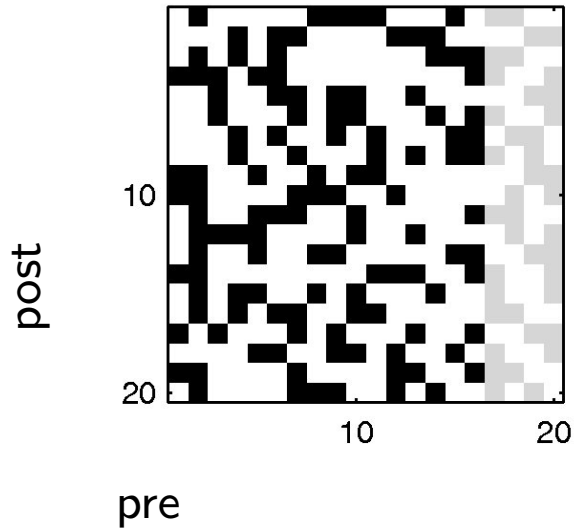
- activity of neurons in vivo: **irregular ($\sim$ Poisson), low rate** $\leftrightarrow$ broad inter-spike-interval distribution
- membrane potential of neurons has **strong fluctuations**
- however, neurons under current injections show regular activity of single cells
- naive view of a network
  - superposition of many synaptic inputs $\Rightarrow$ fluctuations vanish
- E-I networks achieve irregular activity
  - membrane potential close to threshold, **fluctuations drive firing**
- simplest network model that explains emergence of **balanced regime** in a robust manner

Description of networks



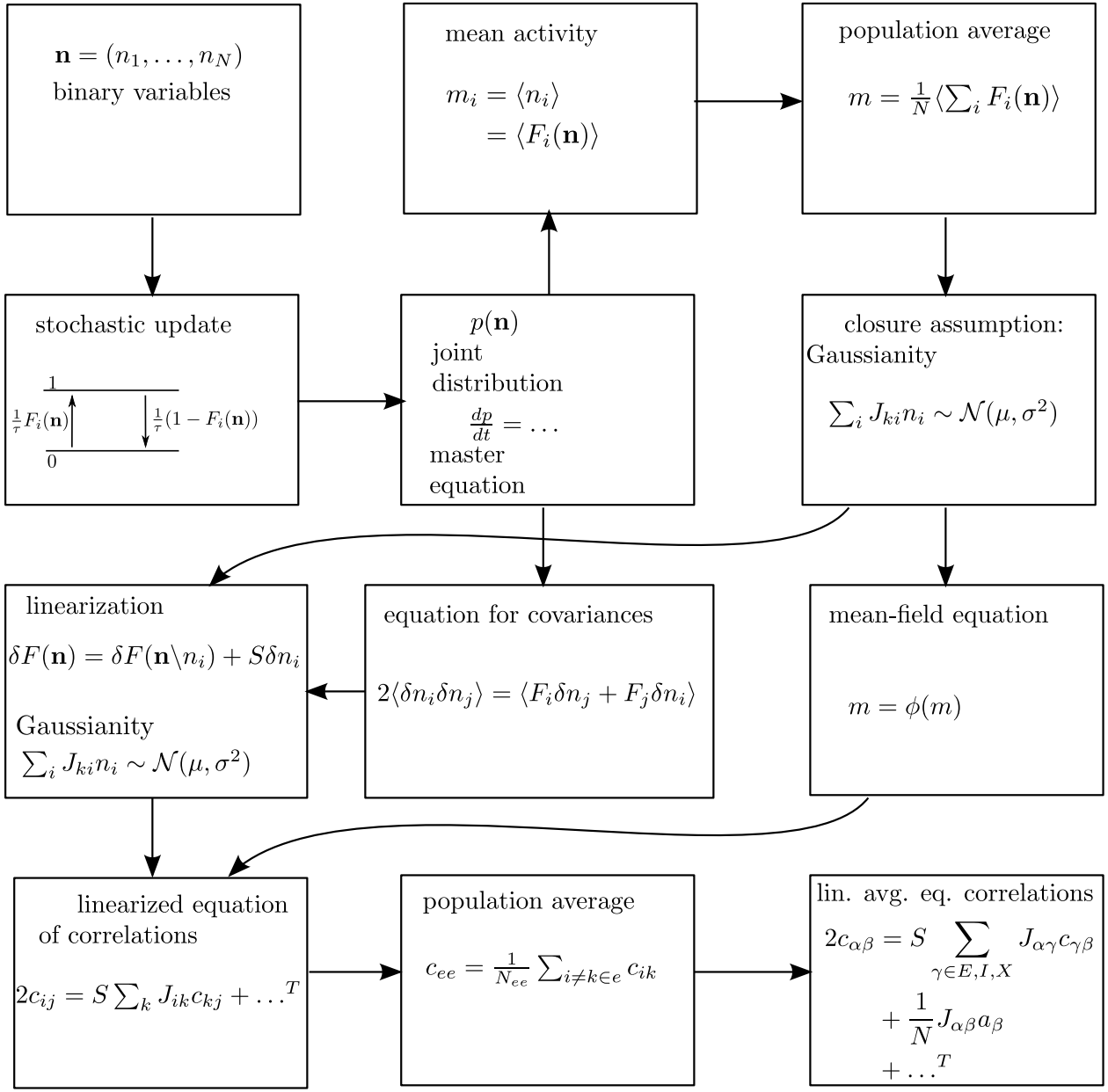
$$\mathbf{J} = \begin{pmatrix} 0 & J & 0 \\ J & 0 & 0 \\ J & -J & 0 \end{pmatrix}$$



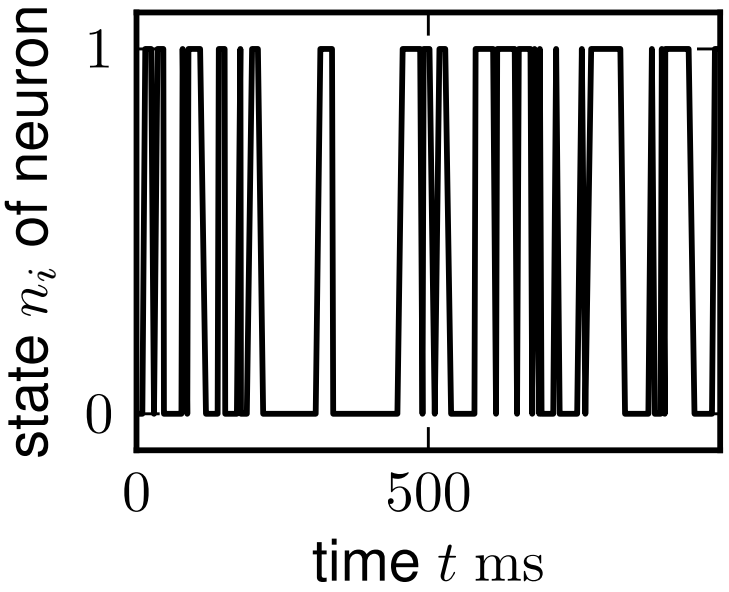


Random network $\Rightarrow$ Erdös-Renyi weight matrix $\mathbf{J} = \{J_{ij}\}$, fixed indegree

(van Vreeswijk & Sompolinsky 1996, 1998, Brunel 2000)


$\mathbf{n} = (n_1, \ldots, n_N)$
binary variables
mean activity
$m_i = \langle n_i \rangle$
$= \langle F_i(\mathbf{n}) \rangle$
population average
$m = \frac{1}{N} \langle \sum_i F_i(\mathbf{n}) \rangle$
stochastic update
1
$\frac{1}{\tau} F_i(\mathbf{n})$
$\frac{1}{\tau}(1 - F_i(\mathbf{n}))$
0
$p(\mathbf{n})$
joint
distribution
$\frac{dp}{dt} = \ldots$
master
equation
closure assumption:
Gaussianity
$\sum_i J_{ki} n_i \sim \mathcal{N}(\mu, \sigma^2)$
linearization
$\delta F(\mathbf{n}) = \delta F(\mathbf{n} \backslash n_i) + S \delta n_i$
Gaussianity
$\sum_i J_{ki} n_i \sim \mathcal{N}(\mu, \sigma^2)$
equation for covariances
$2\langle \delta n_i \delta n_j \rangle = \langle F_i \delta n_j + F_j \delta n_i \rangle$
mean-field equation
$m = \phi(m)$
linearized equation
of correlations
$2c_{ij} = S \sum_k J_{ik} c_{kj} + \ldots^T$
population average
$c_{ee} = \frac{1}{N_{ee}} \sum_{i \neq k \in e} c_{ik}$
lin. avg. eq. correlations
$2c_{\alpha\beta} = S \sum_{\gamma \in E,I,X} J_{\alpha\gamma} c_{\gamma\beta}$
$+ \frac{1}{N} J_{\alpha\beta} a_\beta$
$+ \ldots^T$

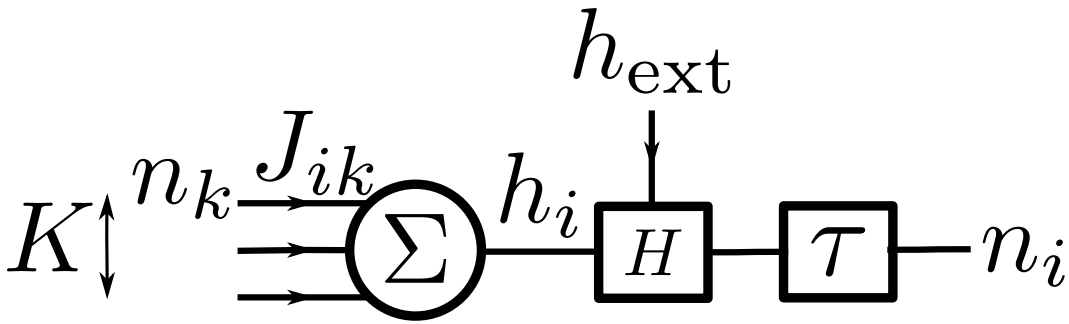
Binary neuron model



- binary state of neuron
  $n_i \in \{0, 1\}$

- classical model used in neuroscience to
  - explain irregular, low activity state Vreeswijk & Sompolinsky 1996, 1998
  - explain pairwise correlations Ginzburg & Sompolinsky 1994
  - develop theory for higher order correlations Buice et al. 2009
  - show active decorrelation in recurrent networks Hertz et. al., 2010, Renart et al. 2010

Binary neuron model

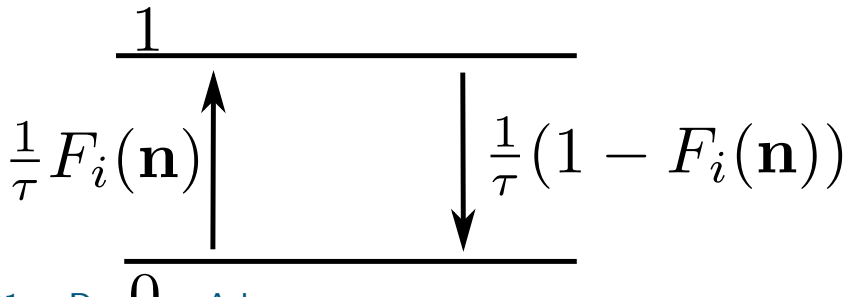


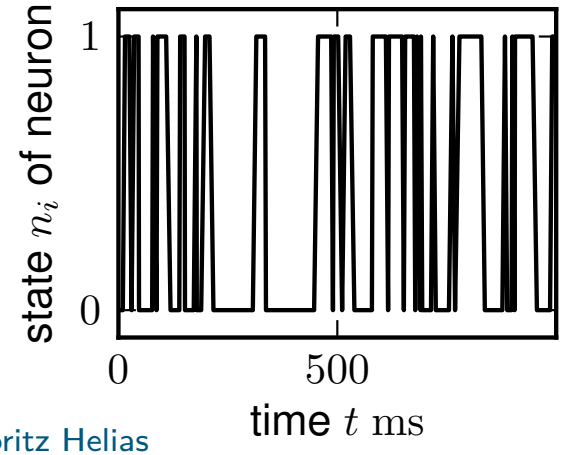
- $\mathbf{n} = (n_1, n_2, \ldots, n_N) \in \{0,1\}^N$ state of whole network
- summed input to neuron i (local field) $h_i = \sum_k J_{ik} n_k + h_{\text{ext}}$
- external input h_{ext} from other areas
- non-linearity $H(h_i) = \begin{cases} 1 & \text{for } h_i > 0 \\ 0 & \text{else} \end{cases}$ controls transition

Binary neuron model

- stochastic update with probability dt/τ in interval dt

  "Poisson jump process" Feller II (1965), Hopfield (1982)
  - prob. of up-state $F_i(\mathbf{n}) = H(h_i)$
  - prob. of down-state $1 - F_i(\mathbf{n})$
- implementations of asynchronous update
  - neuron chosen at exponential intervals of mean duration τ
  - classical: dicretized time, system's state propagated by randomly selecting next neuron for update
    interval between updates is identified with dt
    $\rightarrow$ interpretation $\tau = dtN$





Binary variables

- time point of update chosen randomly
- state $n_i \in \{0, 1\}$ is a random variable
- neuron i assumes state n_i with probability $p_i(n_i)$
- expectation value $\langle\rangle$ over initial conditions and stochastic update time points
- mean

$$m_i = \langle n_i \rangle = p_i(0)\, 0 + p_i(1)\, 1 = p_i(1)$$

- variance

$$a_i = \langle \underbrace{n_i^2}_{\equiv n_i} \rangle - m_i^2 = m_i - m_i^2 = m_i(1 - m_i)$$

- variance uniquely determined by the mean

Mean-field solution

- enables to determine global features, e.g. firing rate
- typically assumes vanishing correlation
- starting point to study correlations

Effective rate dynamics

- occupation of states determined by conservation equation
  master equation of probability $p_i(n_i)$ for neuron i in state n_i

$$\frac{d}{dt}p_i(1) = \underbrace{-\frac{1}{\tau}\left(1 - F_i(\mathbf{n})\right) p_i(1)}_{\text{was up, leaves up-state}} + \underbrace{\frac{1}{\tau} F_i(\mathbf{n})\, p_i(0)}_{\text{was down, enters up-state}}$$

$$p_i(0) + p_i(1) = 1$$

$$\tau\frac{d}{dt}p_i(1) = -p_i(1) + F_i(\mathbf{n})$$

- expected state $m_i = p_i(1)\,1 + p_i(0)\,0 = p(1)$ fulfills same differential equation

$$\tau\frac{d}{dt}m_i = -m_i + F_i(\mathbf{n})$$

Buice et al. (2009)

Homogeneous random network

- assume single population of neurons
- homogeneous network:
  - each neuron has K inputs drawn randomly
  - synaptic weight $J_{ik} = J$ each
  - **input statistics is identical for each neuron**
- $\tau \frac{d}{dt} m_i = -m_i + F_i(\mathbf{n})$ depends on (possibly) all other $\mathbf{n}$
- **idea of mean-field theory**:
  express the statistics of $\mathbf{n}$ (approximately) by the population expectation value $m = \frac{1}{N} \sum_{i=1}^{N} m_i$

Mean-field dynamics

- mean activity $m = \frac{1}{N} \sum_{i=1}^{N} m_i$
- three assumptions:
  - n_k, n_l pairwise *independent* **(1)**
  - *large number* K of inputs per neuron **(2)**
  - *homogeneity* of mean activity $\langle n_i \rangle = m$ **(3)**
- **(1)** $\Rightarrow$ correlations vanish $0 = \langle n_i n_j \rangle - \langle n_i \rangle \langle n_j \rangle$
- **(1)** k of K inputs are active with binomial prob. $B(K, m, k)$
- **(2)** $K \gg 1 \Rightarrow kJ \sim \mathcal{N}(\mu, \sigma)$
- **(3)** with $\mu = JKm \qquad \sigma^2 = J^2 Km(1-m)$
- assumptions allow *closure* of the problem:
  express distribution of $\mathbf{n}$ by mean value m alone

van Vreeswijk & Sompolinsky (1998)

Mean-field dynamics

- study gain function $F_i(h_i)$ of single neuron i
- $h_i = kJ \sim \mathcal{N}(\mu, \sigma)$

  with $\mu = JKm$ and $\sigma^2 = J^2 Km(1-m)$

$$\begin{aligned}
\langle F_i(\mathbf{n}) \rangle &= \left\langle H\left(\sum_j J n_j + h_{\text{ext}}\right)\right\rangle \\
&\overset{\mathbf{1}}{\simeq} \sum_{k=0}^{K} B(K, m, k)\, H(kJ + h_{\text{ext}}) \\
&\overset{\mathbf{2}}{\simeq} \int \mathcal{N}(x)\, H(\sigma x + \mu + h_{\text{ext}})\, dx = \frac{1}{2}\,\text{erfc}\left(-\frac{\mu + h_{\text{ext}}}{\sqrt{2}\sigma}\right)
\end{aligned}$$

Mean-field dynamics

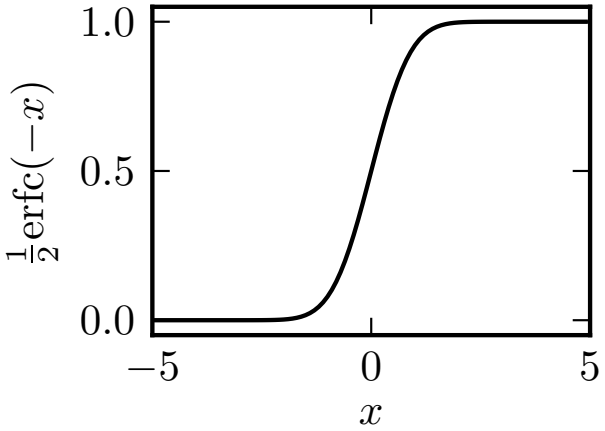
$$\begin{aligned} \tau \frac{dm}{dt} + m &= \frac{1}{2}\,\mathrm{erfc}\left(-\frac{\mu(m) + h_{\mathrm{ext}}}{\sqrt{2}\sigma(m)}\right) \equiv \Phi(m, h_{\mathrm{ext}}) \\ \mu(m) &= JKm \\ \sigma^2(m) &= J^2 Km(1-m) \end{aligned}$$

stationarity $\frac{dm}{dt} = 0$ leads to **self-consistency equation**

$$m = \Phi(m, h_{\mathrm{ext}})$$

Fixed-point rate

$$
\begin{aligned}
m &= \Phi(m, h_{\text{ext}}) \\
&\equiv \frac{1}{2}\,\text{erfc}\left(-\frac{\mu(m)+h_{\text{ext}}}{\sqrt{2}\sigma(m)}\right)
\end{aligned}
$$



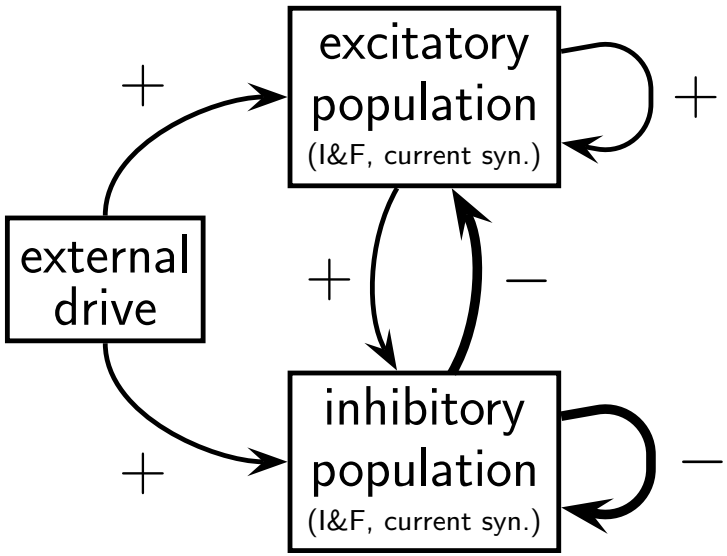
- mean $\mu = JKm \propto K$
  fluctuations $\sigma = |J|\sqrt{Km(1-m)} \propto \sqrt{K}$
- large K: function Φ has sharp transition at $\mu(m) + h_{\text{ext}} \simeq 0$
- $\Rightarrow$ solution $0 < m < 1$ exists near transition

mean input needs to cancel approximately

$$\mu(m) = KJm \simeq -h_{\text{ext}}$$

van Vreeswijk & Sompolinsky 1996, 1998

Balanced network



- two subpopulations
  - N exc neurons
  - γN inh neurons
- random connectivity
  - J_{EE}, J_{IE} exc synpases
  - J_{EI}, J_{II} inh synapses
- fixed number of incoming synapses per neuron
  - K exc synpases
  - γK inh synapses

Mean-field equations

- population averaged activity $m_x = \frac{1}{N_x} \sum_{i \in x} m_i$ for $x \in \{E, I\}$
- derivation can be generalized in straight forward manner
- in general different mean and fluctuations in input to E and I

set of two equation to be solved simultaneously for $x \in \{E, I\}$:

$$
\begin{aligned}
\tau \frac{dm_x}{dt} &= -m_x + \Phi_x(m_E, m_I) \\
\Phi_x(m_E, m_I) &= \frac{1}{2} \operatorname{erfc}\left(-\frac{\mu_x(m_E, m_I) + h_{\text{ext}}}{\sqrt{2}\sigma_x(m_E, m_I)} \right) \\
\mu_x &= K(J_{xE} m_E - \gamma J_{xI} m_I) \\
\sigma_x^2 &= K(J_{xE}^2 m_E(1 - m_E) + \gamma J_{xI}^2 m_I(1 - m_I))
\end{aligned}
$$

Balance condition

- equilibrium rate

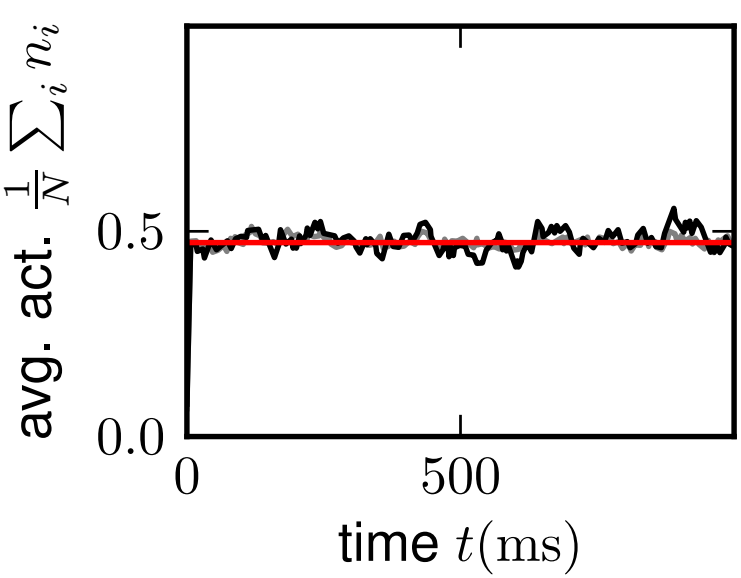
$$m_x = \Phi_x(m_E, m_I) \quad = \quad \frac{1}{2}\,\mathrm{erfc}\left(-\frac{\mu_x(m_E, m_I) + h_{\mathrm{ext}}}{\sqrt{2}\sigma_x(m_E, m_I)}\right)$$

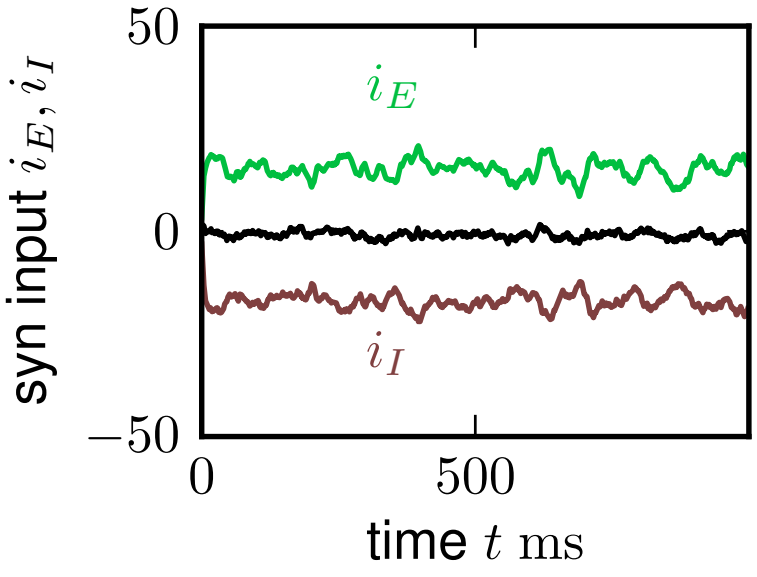
- $\mu_x \propto K$, $\sigma_x \propto \sqrt{K}$
- $K \gg 1$:
  solution with non-saturating rate $0 < m_E, m_I < 1$
  $\Rightarrow$ approximate balance $\mu_x + h_{\mathrm{ext}} \simeq O(\sqrt{K})$
- approximate solution:

$$\begin{aligned} K(J_{EE} m_E + \gamma J_{EI} m_I) + h_{\mathrm{ext}} &\simeq O(\sqrt{K}) \\ K(J_{IE} m_E + \gamma J_{II} m_I) + h_{\mathrm{ext}} &\simeq O(\sqrt{K}) \end{aligned}$$

Balance condition

- mean contributions of E and I to synaptic inputs $\sim$ cancel
- fluctuations in input large compared to threshold
- $\Rightarrow$ irregualar activity of single cell





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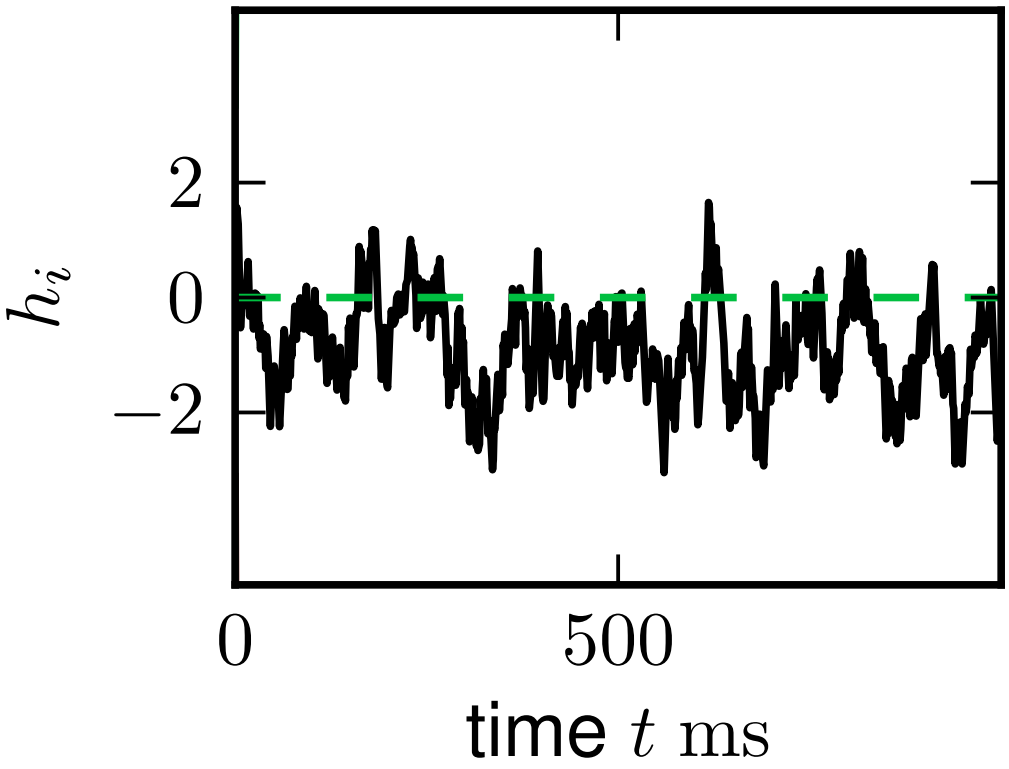
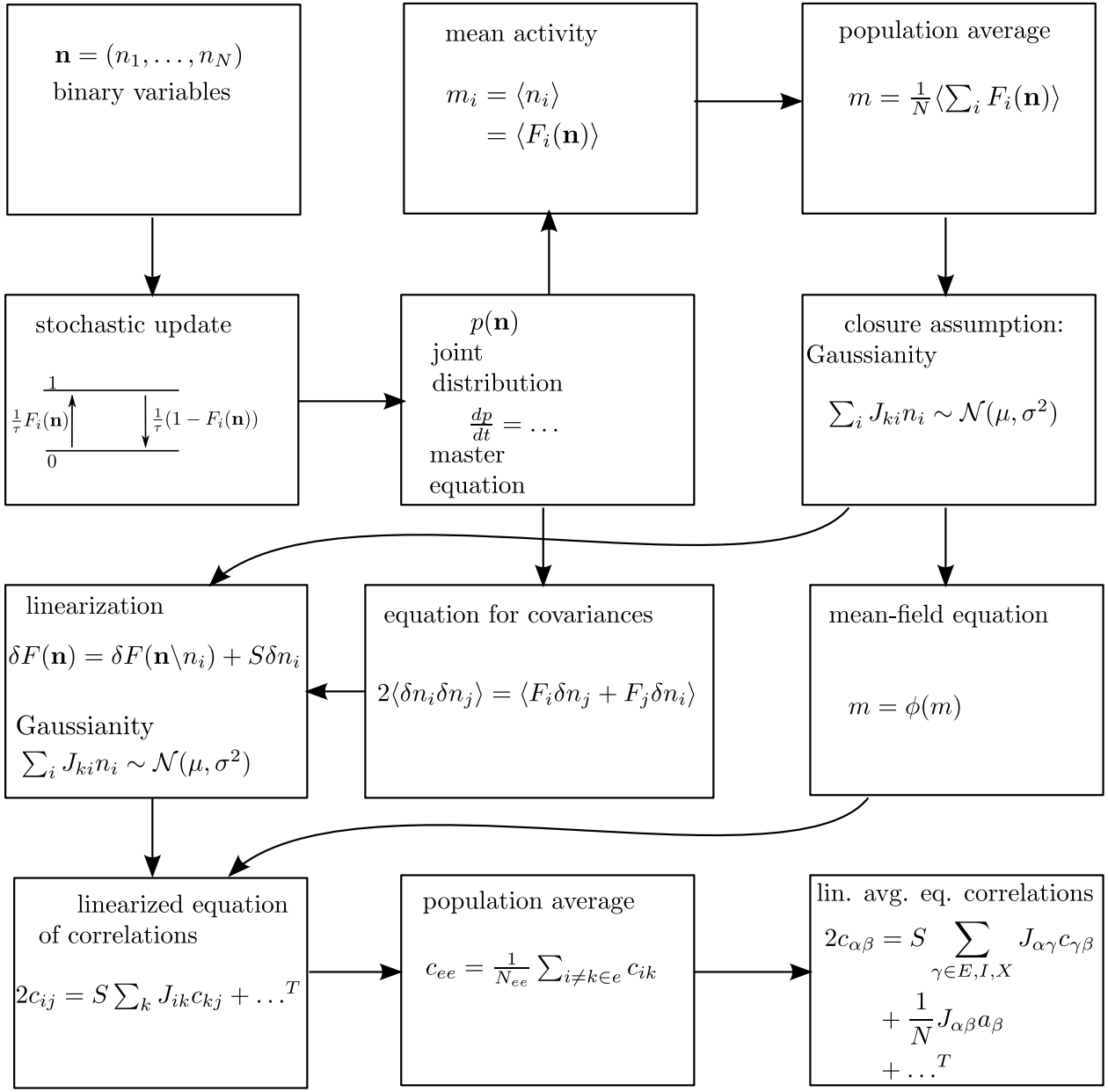


$$h_i = \sum_k J_{ik} n_k + h_{\text{ext}}$$

active, if $h_i > 0$

Summary mean field activity

- Erdös-Renyi networks: simplest model of local connectivity
- assumptions of *homogeneity, indepdendence, and large numbers of synapses* allows closure
- pairwise independence implies vanishing correlation
- binary neuron sufficiently simple for mean-field analysis
- E-I network:
  - balanced state emerges in inhibition-dominated regime
  - mean input to single cell cancels $\Rightarrow$ fluctuations $\gg$ threshold
  - irregular activity like in-vivo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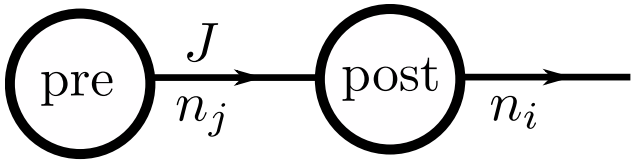
binary variables
mean activity
$m_i = \langle n_i \rangle$
$= \langle F_i(\mathbf{n}) \rangle$
population average
$m = \frac{1}{N} \langle \sum_i F_i(\mathbf{n}) \rangle$
stochastic update
1
$\frac{1}{\tau} F_i(\mathbf{n})$
$\frac{1}{\tau}(1 - F_i(\mathbf{n}))$
0
$p(\mathbf{n})$
joint
distribution
$\frac{dp}{dt} = \ldots$
master
equation
closure assumption:
Gaussianity
$\sum_i J_{ki} n_i \sim \mathcal{N}(\mu, \sigma^2)$
linearization
$\delta F(\mathbf{n}) = \delta F(\mathbf{n} \backslash n_i) + S \delta n_i$
Gaussianity
$\sum_i J_{ki} n_i \sim \mathcal{N}(\mu, \sigma^2)$
equation for covariances
$2\langle \delta n_i \delta n_j \rangle = \langle F_i \delta n_j + F_j \delta n_i \rangle$
mean-field equation
$m = \phi(m)$
linearized equation
of correlations
$2c_{ij} = S \sum_k J_{ik} c_{kj} + \ldots^T$
population average
$c_{ee} = \frac{1}{N_{ee}} \sum_{i \neq k \in e} c_{ik}$
lin. avg. eq. correlations
$2c_{\alpha\beta} = S \sum_{\gamma \in E,I,X} J_{\alpha\gamma} c_{\gamma\beta}$
$+ \frac{1}{N} J_{\alpha\beta} a_\beta$
$+ \ldots^T$

Correlation by a single connection



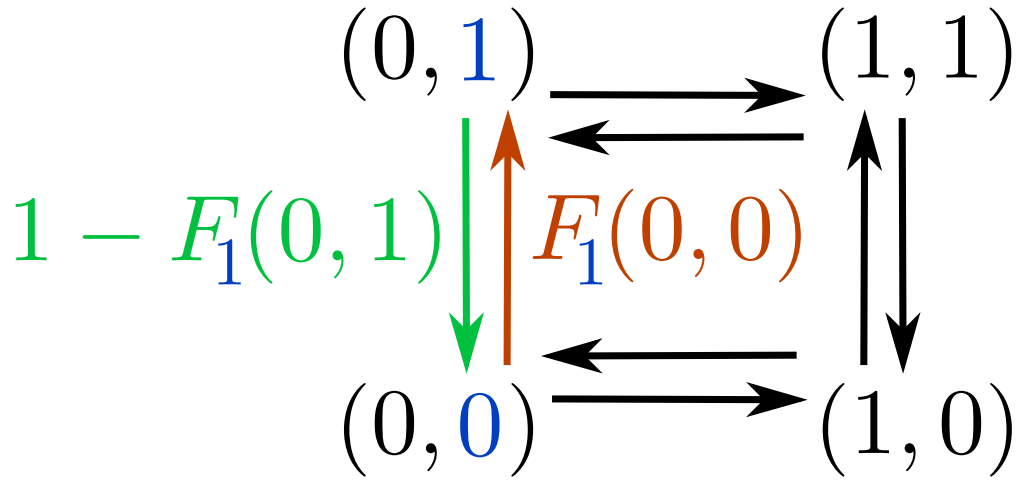
- definition of correlation:
  coactivity minus expectation assuming independence

$$\begin{aligned} c_{ij} &= \langle n_i n_j \rangle - \langle n_i \rangle \langle n_j \rangle \\ &= \langle \delta n_i \delta n_j \rangle \end{aligned}$$

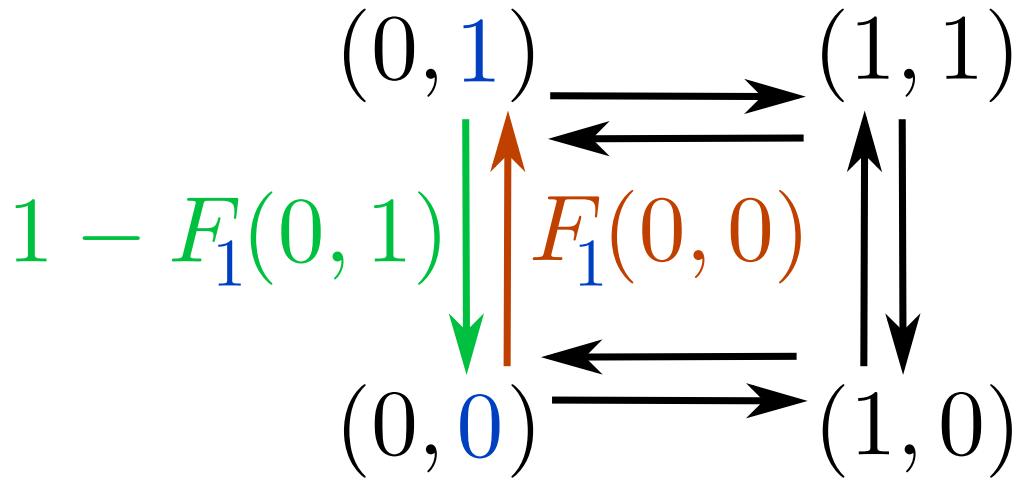
- $\equiv$ cofluctuation around expectation $\delta n_i = n_i - \langle n_i \rangle$
- simplest case: effect of a single synaptic connection
- activities n_i and n_j are correlated due to connection $j \to i$, $c_{ij} > 0$

Conservation of probability

- all states for a network of 2 neurons
  $\mathbf{n} = (n_1, n_2) \in \{0,1\} \times \{0,1\}$
- the network is always in a state $\Rightarrow$ conservation of probability
- at each point in time at most one neuron makes a transition
  $\Rightarrow$ no diagonal arrows
- the loss of probability in the original state is the gain in the target state



Conservation of probability



- notation: $\mathbf{n}_{i+} = (n_1, n_2, \ldots, \underbrace{1}_{\text{pos } i}, \ldots, n_N)$ $\mathbf{n}_{i-}$ similar

$$\frac{dp(\mathbf{n})}{dt} = \frac{1}{\tau} \sum_{i=1}^{N} (2n_i - 1) \left(p(\mathbf{n}_{i-}) \, F_i(\mathbf{n}_{i-}) - p(\mathbf{n}_{i+}) \, (1 - F_i(\mathbf{n}_{i+})) \right)$$

- $(2n_i - 1) = 1$ if $n_i = 1, -1$ else indicates direction of flux entering or exiting, respectively

Mean activity

multiply previous eq. by n_k and sum over all possible states $\mathbf{n}$

$$
\begin{aligned}
0 &= \sum_{\mathbf{n}} n_k \sum_{i=1}^{N} \underbrace{(2n_i - 1)}_{1 \text{ if } n_i=1,-1 \text{ else}} \left(p(\mathbf{n}_{i-})F_i(\mathbf{n}_{i-}) - p(\mathbf{n}_{i+})(1 - F_i(\mathbf{n}_{i+}))\right) \\
&= \sum_{\mathbf{n}\setminus n_k} p(\mathbf{n}_{k-})F_k(\mathbf{n}_{k-}) - p(\mathbf{n}_{k+})(1 - F_k(\mathbf{n}_{k+}))
\end{aligned}
$$

rearrange

$$
\begin{aligned}
\langle n_k \rangle &= \sum_{\mathbf{n}} n_k p(\mathbf{n}) = \sum_{\mathbf{n}\setminus n_k} p(\mathbf{n}_{k+}) \\
&= \sum_{\mathbf{n}\setminus n_k} p(\mathbf{n}_{k-})F_k(\mathbf{n}_{k-}) + p(\mathbf{n}_{k+})F_k(\mathbf{n}_{k+}) \\
&= \langle F_k(\mathbf{n}) \rangle
\end{aligned}
$$

mean activity of k = mean of gain function $\quad m_k = \langle n_k \rangle = \langle F_k(\mathbf{n}) \rangle$

Equation for correlations

same approach as for the mean: multiply equation of equilibrium probability flux by $n_k n_l$, sum over all states

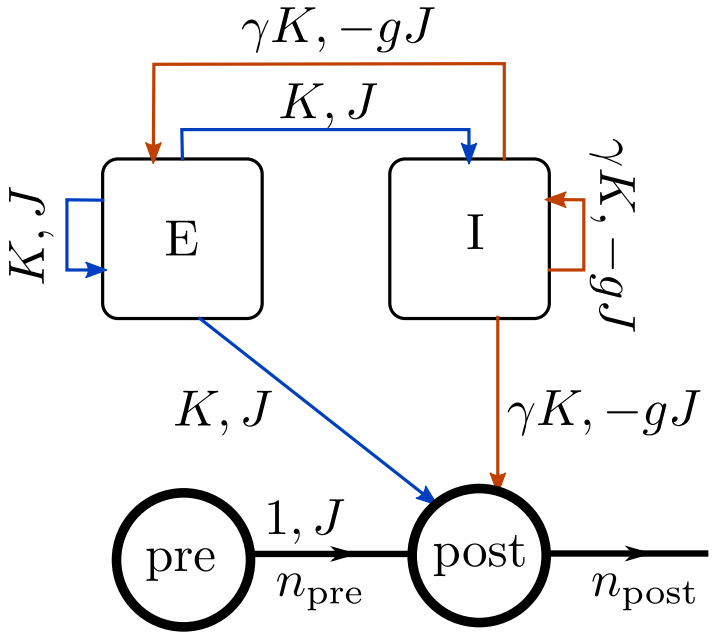
$$0 = \sum_{\mathbf{n}} n_k n_l \sum_{i=1}^{N} \underbrace{(2n_i - 1)}_{1 \text{ if } n_i=1,-1 \text{ else}} \left(p(\mathbf{n}_{i-})F_i(\mathbf{n}_{i-}) - p(\mathbf{n}_{i+})(1 - F_i(\mathbf{n}_{i+}))\right)$$

only two terms remain, where $i = k$ or $i = l$, rearranging yields

$$\begin{aligned} c_{kl} &= \frac{1}{2}\langle F_k(\mathbf{n})\delta n_l\rangle + \frac{1}{2}\langle F_l(\mathbf{n})\delta n_k\rangle \\ \text{with } \delta n_i &= n_i - \langle n_i\rangle \end{aligned}$$

correlations are caused by fluctuations δn_l affecting the activation function of neuron k and vice versa

Correlation by a single connection



- neuron post receives input from network
- in addition input from another, independent neuron pre
- correlation due to the single connection $\mathrm{pre} \to \mathrm{post}$
  $c_{\mathrm{post,pre}} = \frac{1}{2}\langle F_{\mathrm{post}}(\mathbf{n})\delta n_{\mathrm{pre}}\rangle$
- second term $\langle F_{\mathrm{pre}}(\mathbf{n})\delta n_{\mathrm{post}}\rangle$ vanishes, because post has no effect on pre

Correlation by a single connection

- input from network to pre in mean-field approximation is a Gaussian noise $x \sim \mathcal{N}(\mu, \sigma^2)$
- total input to neuron post is $h_{\mathrm{post}} = x + J n_{\mathrm{pre}}$

$$
\begin{aligned}
c_{\mathrm{post,pre}} &= \frac{1}{2}\langle H(x + J n_{\mathrm{pre}})\delta n_{\mathrm{pre}}\rangle_{x,n_{\mathrm{pre}}} \\
&= \frac{1}{2}\langle H(x + J) n_{\mathrm{pre}}\delta n_{\mathrm{pre}} + H(x)(1 - n_{\mathrm{pre}})\delta n_{\mathrm{pre}}\rangle_{x,n_{\mathrm{pre}}} \\
&= \frac{1}{2}\langle H(x + J) - H(x)\rangle_x \, \langle n_{\mathrm{pre}}\delta n_{\mathrm{pre}}\rangle_{n_{\mathrm{pre}}}
\end{aligned}
$$

- fluctuations of pre neuron drive correlations
  $c \propto$ autocovariance $\langle n_{\mathrm{pre}}\delta n_{\mathrm{pre}}\rangle = \langle \delta n_{\mathrm{pre}}\delta n_{\mathrm{pre}}\rangle = a_{\mathrm{pre}}$

Ginzburg & Sompolinsky (1994)

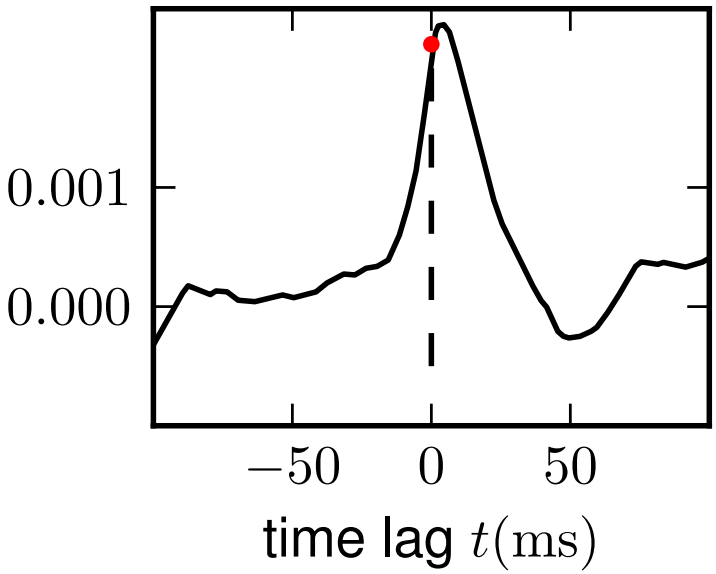
Susceptibility

- J has small impact compared to 'noise' from network $x \sim \mathcal{N}(\mu, \sigma)$
- Taylor expansion in J

$$\begin{aligned} \langle H(x+J) - H(x) \rangle_x &= S(\mu,\sigma)J + O(\epsilon^2) \\ S(\mu,\sigma) &= \left.\frac{\partial}{\partial \epsilon}\right|_{\epsilon=0} \langle H(x+\epsilon) - H(x) \rangle_x \\ &= \frac{1}{\sqrt{2\pi}\sigma} e^{-\frac{\mu^2}{2\sigma^2}} \end{aligned}$$

- susceptibility S quantifies to linear order sensitivity post's activity to small fluctuation in input
- susceptibility $S(\mu, \sigma)$ depends on *neuron properties* and on *network state* (μ, σ)

Correlation by a single connection: comparison to simulation



nest::
simulated()

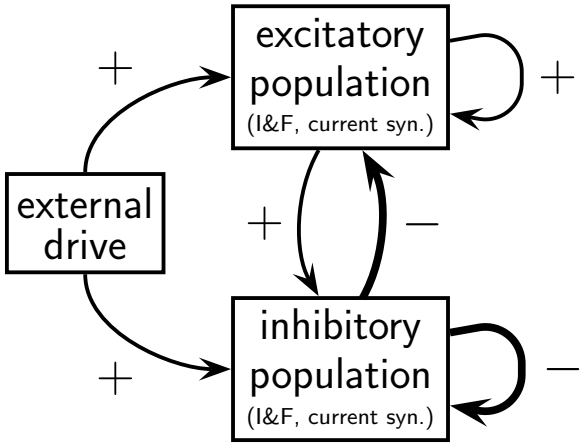
$$c_{\mathrm{post,pre}} = \frac{J}{2} S(\mu,\sigma)\; a_{\mathrm{pre}}$$

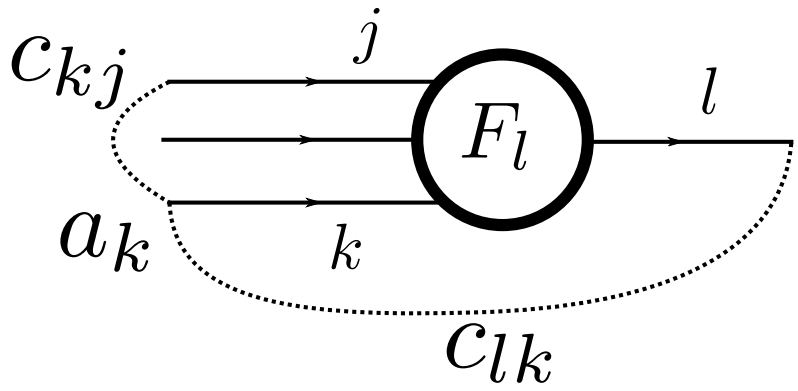
$$a_{\mathrm{pre}} = \langle n_{\mathrm{pre}} \rangle (1 - \langle n_{\mathrm{pre}} \rangle)$$

- a_{pre} strength of pre fluctuation
- $\frac{J}{2}\, S(\mu,\sigma)$ transmission of fluctuation from input to output
- theory (red dot) and simulation (black curve) agree

Ginzburg & Sompolinsky 1994, simulated with NEST, www.nest-initiative.org

Correlations in a recurrent network





$$c_{lk} = \frac{1}{2}\langle F_l(\mathbf{n})\delta n_k\rangle + \frac{1}{2}\langle F_k(\mathbf{n})\delta n_l\rangle$$

- complicated, because in $\langle F_k(\mathbf{n})\delta n_l\rangle$ neuron l might be correlated with any other neuron in $\mathbf{n}$ projecting to target k

Correlations in a recurrent network

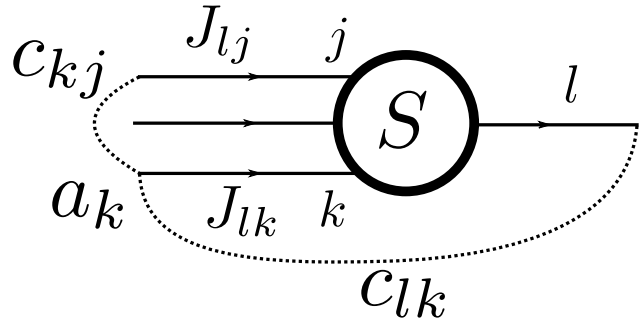
$$\begin{aligned}\langle F_l(\mathbf{n})\delta n_k\rangle &= \langle H(h_{l\setminus n_j}+J_{lj})n_j\delta n_k + H(h_{l\setminus n_j})(1-n_j)\delta n_k\rangle \\ &= \langle [H(h_{l\setminus n_j}+J_{lj}) - H(h_{l\setminus n_j})]\; n_j\delta n_k\rangle \\ &+ \langle H(h_{l\setminus n_j})\delta n_k\rangle\end{aligned}$$

first term: repeating for $i \neq j \rightarrow$ third order correlation, neglected

$$\langle [H(x+J_{lj}) - H(x)]\rangle_x \langle n_j\delta n_k\rangle_{\mathbf{n}} \simeq S(\mu,\sigma)J_{lj}c_{jk}$$

second term: independent of j; j was chosen arbitrarily, so

$$c_{lk} = \frac{S(\mu,\sigma)}{2}\sum_j (J_{kj}c_{jl} + J_{lj}c_{jk})$$



$$c_{ii} = a_i$$

autocovariances a_i drive cross-covariances c_{lk}

Population-averaged correlations

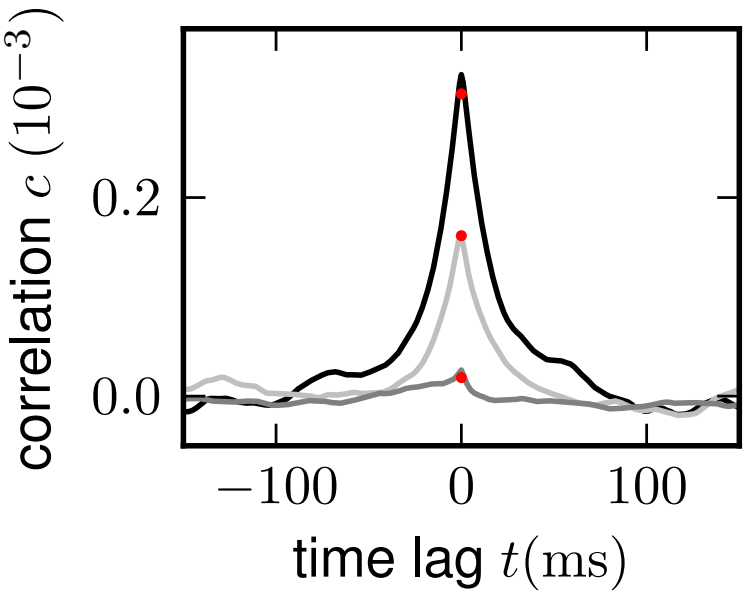
- often the correlation averaged over many pairs is interesting
- introduce avg. correlation $c_{ee} = \frac{1}{N_e^2} \sum_{k \neq l \in \mathcal{E}} c_{kl}$
  (other 3 pairings analogous)
- inserting $c_{kl} = \frac{S(\mu,\sigma)}{2} \sum_i \left(J_{ki} c_{il} + J_{li} c_{ik} \right)$ we obtain

$$
\begin{aligned}
c_{ee} &= \frac{K\,J\,S(\mu,\sigma)}{2} \left(\frac{2}{N} a + 2c_{ee} - 2\gamma g c_{ie} \right) \\
c_{ii} &= \frac{K\,J\,S(\mu,\sigma)}{2} \left(-\frac{2}{N} g a - 2\gamma g c_{ii} + 2c_{ei} \right) \\
c_{ei} = c_{ie} &= \frac{1}{2} \left(c_{ee} + c_{ii} \right) \\
a &= (1 - \langle n \rangle) \langle n \rangle
\end{aligned}
$$

can be solved by elementary methods

Ginzburg & Somplolinsky 1994

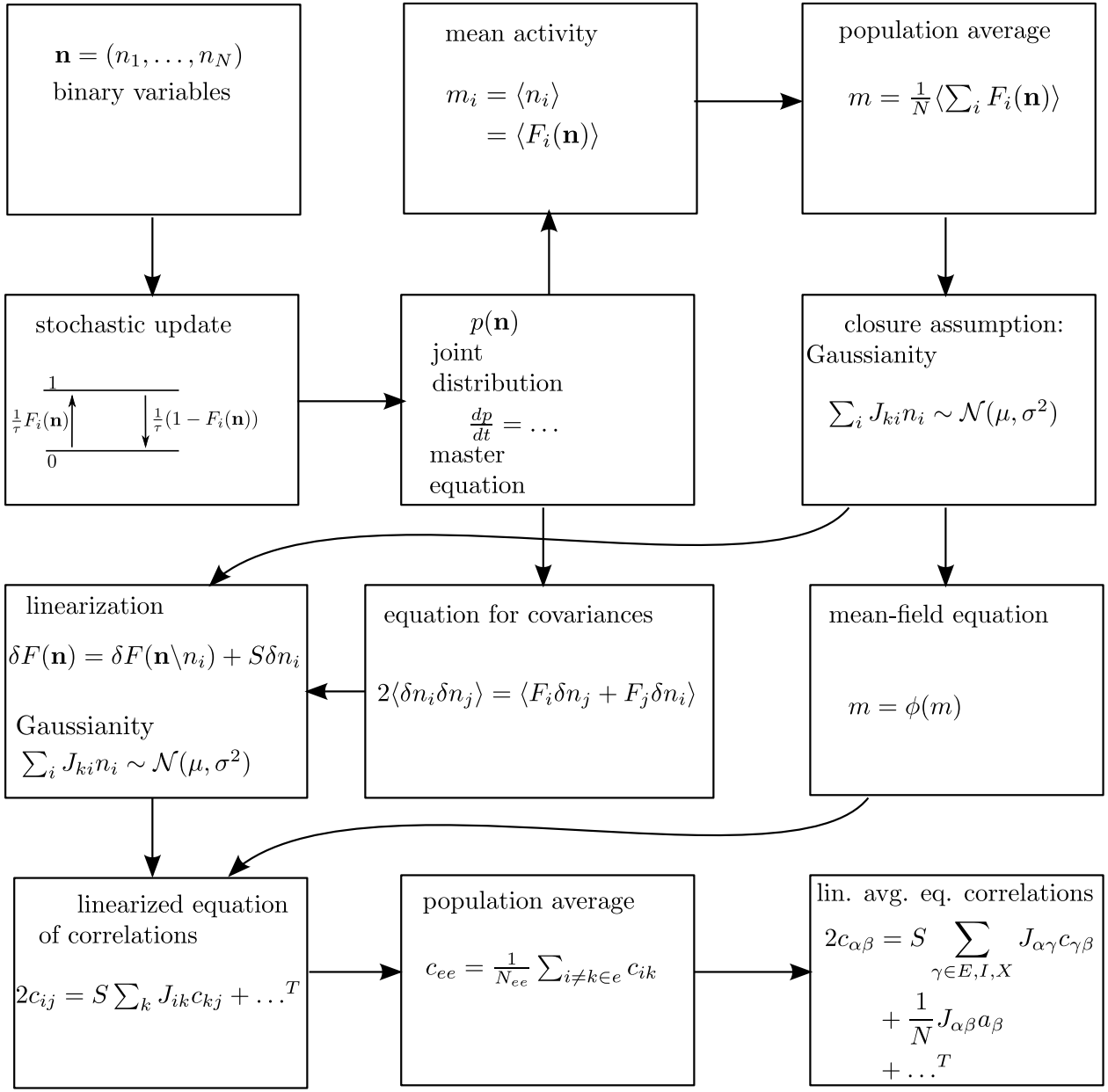
Population-averaged correlations: comparison to simulation



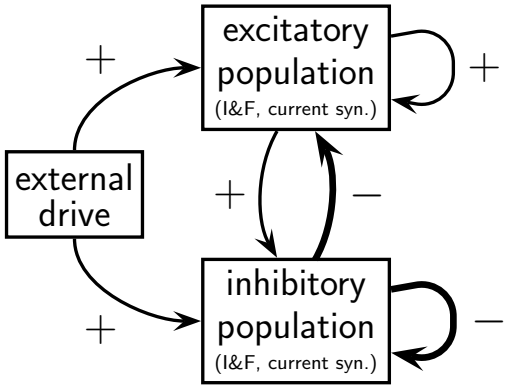
nest::
simulated()

- binary neuron implemented in NEST www.nest-initiative.org
- implementation uses exponentially distributed update intervals

- theoretical prediction (red dot) agrees with simulation
- strength of correlations depends on type of neuron (black: c_{ee}, gray c_{ii}, light gray c_{ei})


$\mathbf{n} = (n_1, \ldots, n_N)$
binary variables
mean activity
$m_i = \langle n_i \rangle$
$= \langle F_i(\mathbf{n}) \rangle$
population average
$m = \frac{1}{N} \langle \sum_i F_i(\mathbf{n}) \rangle$
stochastic update
1
$\frac{1}{\tau} F_i(\mathbf{n})$
$\frac{1}{\tau}(1 - F_i(\mathbf{n}))$
0
$p(\mathbf{n})$
joint
distribution
$\frac{dp}{dt} = \ldots$
master
equation
closure assumption:
Gaussianity
$\sum_i J_{ki} n_i \sim \mathcal{N}(\mu, \sigma^2)$
linearization
$\delta F(\mathbf{n}) = \delta F(\mathbf{n} \backslash n_i) + S \delta n_i$
Gaussianity
$\sum_i J_{ki} n_i \sim \mathcal{N}(\mu, \sigma^2)$
equation for covariances
$2\langle \delta n_i \delta n_j \rangle = \langle F_i \delta n_j + F_j \delta n_i \rangle$
mean-field equation
$m = \phi(m)$
linearized equation
of correlations
$2c_{ij} = S \sum_k J_{ik} c_{kj} + \ldots^T$
population average
$c_{ee} = \frac{1}{N_{ee}} \sum_{i \neq k \in e} c_{ik}$
lin. avg. eq. correlations
$2c_{\alpha\beta} = S \sum_{\gamma \in E,I,X} J_{\alpha\gamma} c_{\gamma\beta}$
$+ \frac{1}{N} J_{\alpha\beta} a_\beta$
$+ \ldots^T$

The balanced condition revisited



- three populations $\alpha \in \{E, I, X\}$ of N neurons each
- finite, external population
- random connection propbability p
- shared external sources

- balanced condition fixes population averaged activities m_α
- effective coupling from pop β to neuron in α is

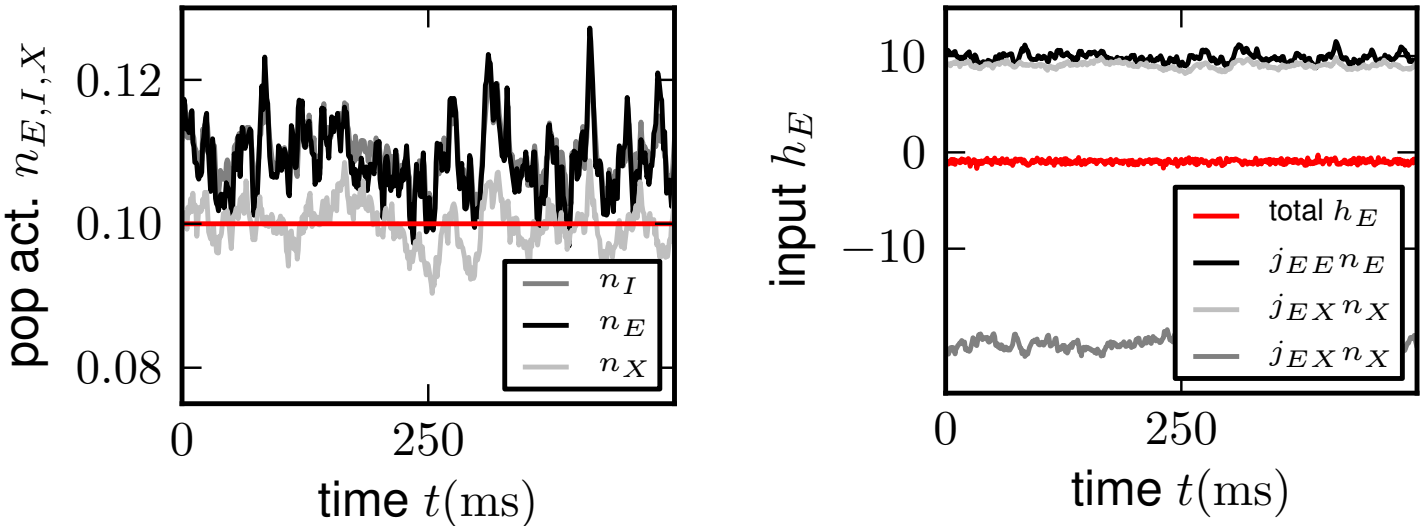
$$j_{\alpha\beta} = KJ_{\alpha\beta} \qquad \mathrm{K} = \mathrm{pN}$$

- mean input to neuron of population α must approx. cancel

$$h_\alpha = \sum_\beta j_{\alpha\beta} m_\beta \simeq 0$$

van Vreeswijk & Sompolinsky (1996), Amit & Brunel (1997), Renart et al. (2010)

Fast tracking – balance on a fast time scale



- cancellation of mean input approx determines rates
- observation: cancelation on input side also holds on fast time scale

$$\delta h_\alpha = \sum_\beta j_{\alpha\beta}\delta n_\beta \simeq 0$$

- imposes relation between population fluctuations

$\delta n_\alpha = \frac{1}{N}\sum_{i\in\alpha} n_i - m_\alpha$ Renart et al. (2010)

Population fluctuations – population averaged correlations

- population fluctuations $\delta n_\alpha = \frac{1}{N}\sum_{i\in\alpha}\delta n_i$

$$\begin{aligned}\langle \delta n_\beta \delta n_\gamma\rangle &= \frac{1}{N^2}\sum_{i\in\beta,j\in\gamma}\langle \delta n_i \delta n_j\rangle \\ &= \delta_{\beta\gamma}\frac{1}{N^2}\sum_{i\in\beta}\langle \delta n_i^2\rangle + \frac{1}{N^2}\sum_{i\in\beta,j\in\gamma,i\neq j}\langle \delta n_i \delta n_j\rangle \\ &= \delta_{\beta\gamma}\frac{1}{N}a_\beta + c_{\beta\gamma}\end{aligned}$$

- are linked to average autocovariance a_β and pairwise averaged cross covariance $c_{\beta\gamma}$

Suppression of input correlation in balanced state

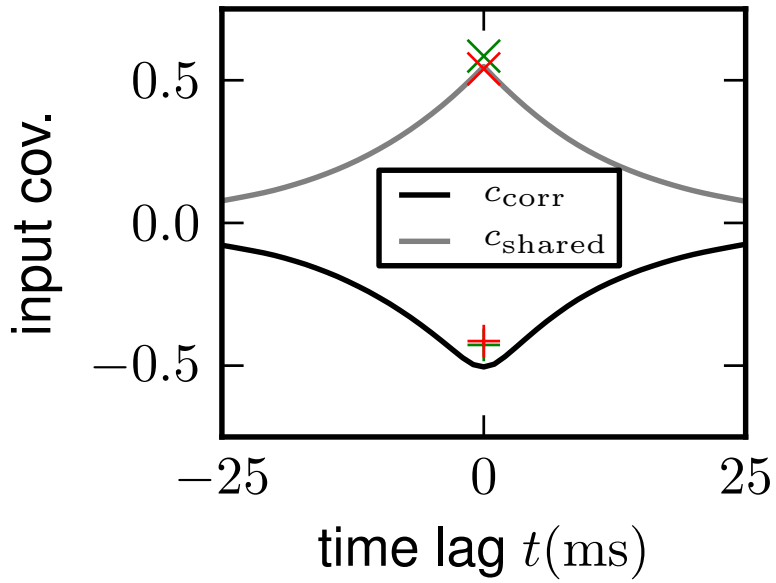
- observation: balance condition also holds approximately on fast time scale, $\delta h \simeq 0$

$$0 \simeq \langle \delta h_\alpha^2 \rangle = \sum_{\beta\gamma} j_{\alpha\beta} j_{\alpha\gamma} \langle \delta n_\beta \delta n_\gamma \rangle$$

- with previous result $\langle \delta n_\beta \delta n_\gamma \rangle = \delta_{\beta\gamma} \frac{1}{N} a_\beta + c_{\beta\gamma}$ and $j_{\alpha\beta} = J_{\alpha\beta} K = J_{\alpha\beta} pN$

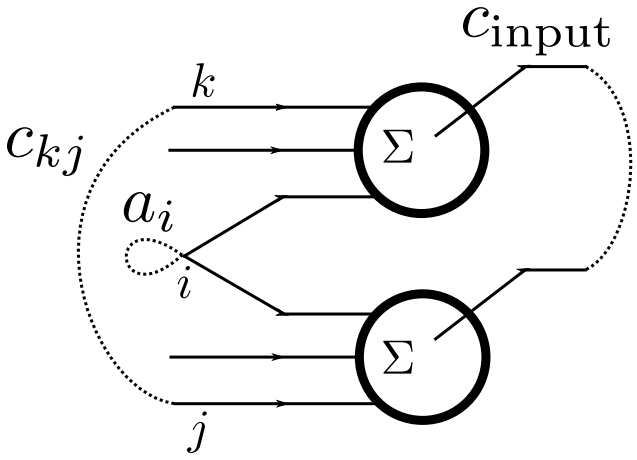
$$0 \simeq \langle \delta h_\alpha^2 \rangle = pK \sum_\beta J_{\alpha\beta}^2 a_\beta + K^2 \sum_{\beta\gamma} J_{\alpha\beta} J_{\alpha\gamma} c_{\beta\gamma}$$

Suppression of input correlation in balanced state



$$0 \simeq pK \sum_{\beta} J_{\alpha\beta}^2 a_\beta + K^2 \sum_{\beta\gamma} J_{\alpha\beta} J_{\alpha\gamma} c_{\beta\gamma}$$

$$= c_{\mathrm{shared}} + c_{\mathrm{corr}}.$$

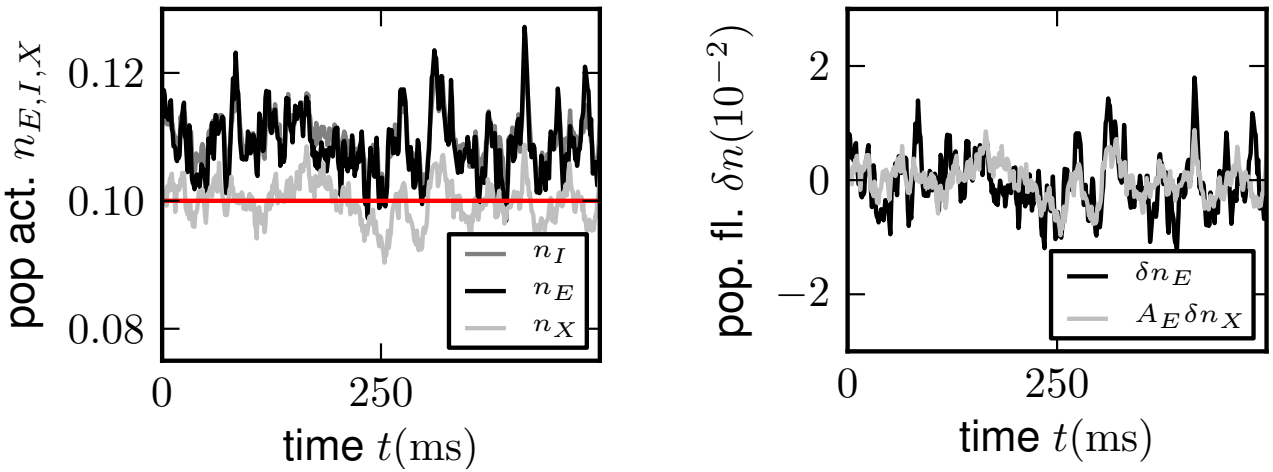


Does fast tracking determine correlations?

- cancellation $\delta h_\alpha \simeq 0$ relates population fluctuations δn_α

$$0 \simeq \delta h_\alpha = \sum_\beta j_{\alpha\beta} \delta n_\beta \qquad \text{define matrix} \qquad \mathbf{j} = \begin{pmatrix} j_{EE} & j_{EI} \\ j_{IE} & j_{II} \end{pmatrix}$$

$$\begin{pmatrix} \delta n_E \\ \delta n_I \end{pmatrix} = -\mathbf{j}^{-1} \begin{pmatrix} j_{EX} \\ j_{IX} \end{pmatrix} \delta n_X = \begin{pmatrix} A_E \\ A_I \end{pmatrix} \delta n_X$$



Hertz et al 2010, Renart et al. 2010

Does fast tracking determine correlations?

- apply connection between population fluctuation and auto-/crosscovariance

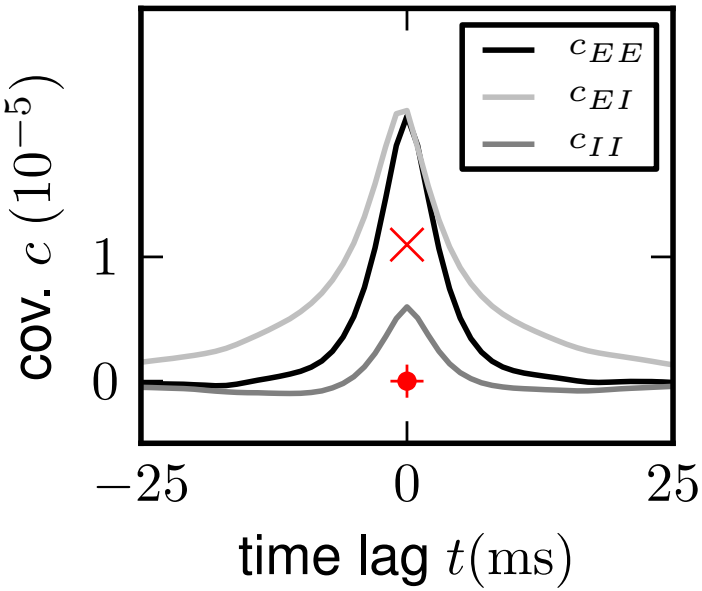
$$\langle \delta n_\beta \delta n_\gamma \rangle = \delta_{\beta\gamma} \frac{1}{N} a_\beta + c_{\beta\gamma} \qquad \langle \delta n_X^2 \rangle = \frac{a_X}{N}$$

- use fast tracking condition

$$\begin{pmatrix} \delta n_E \\ \delta n_I \end{pmatrix} = \begin{pmatrix} A_E \\ A_I \end{pmatrix} \delta n_X$$

$$c_{\alpha\alpha} = A_\alpha^2 \frac{a_X}{N} - \frac{a_\alpha}{N}$$

$$c_{\alpha\beta} = A_\alpha A_\beta \frac{a_X}{N}$$



Renart et al. 2010

Two components of correlations: intrinsic fluctuations and external drive

$$2c_{\alpha\beta} = S\left(\sum_{\gamma\in\{E,I,X\}}(j_{\alpha\gamma}c_{\gamma\beta} + j_{\beta\gamma}c_{\gamma\alpha}) + \frac{1}{N}j_{\alpha\beta}a_\beta + \frac{1}{N}j_{\beta\alpha}a_\alpha\right)$$

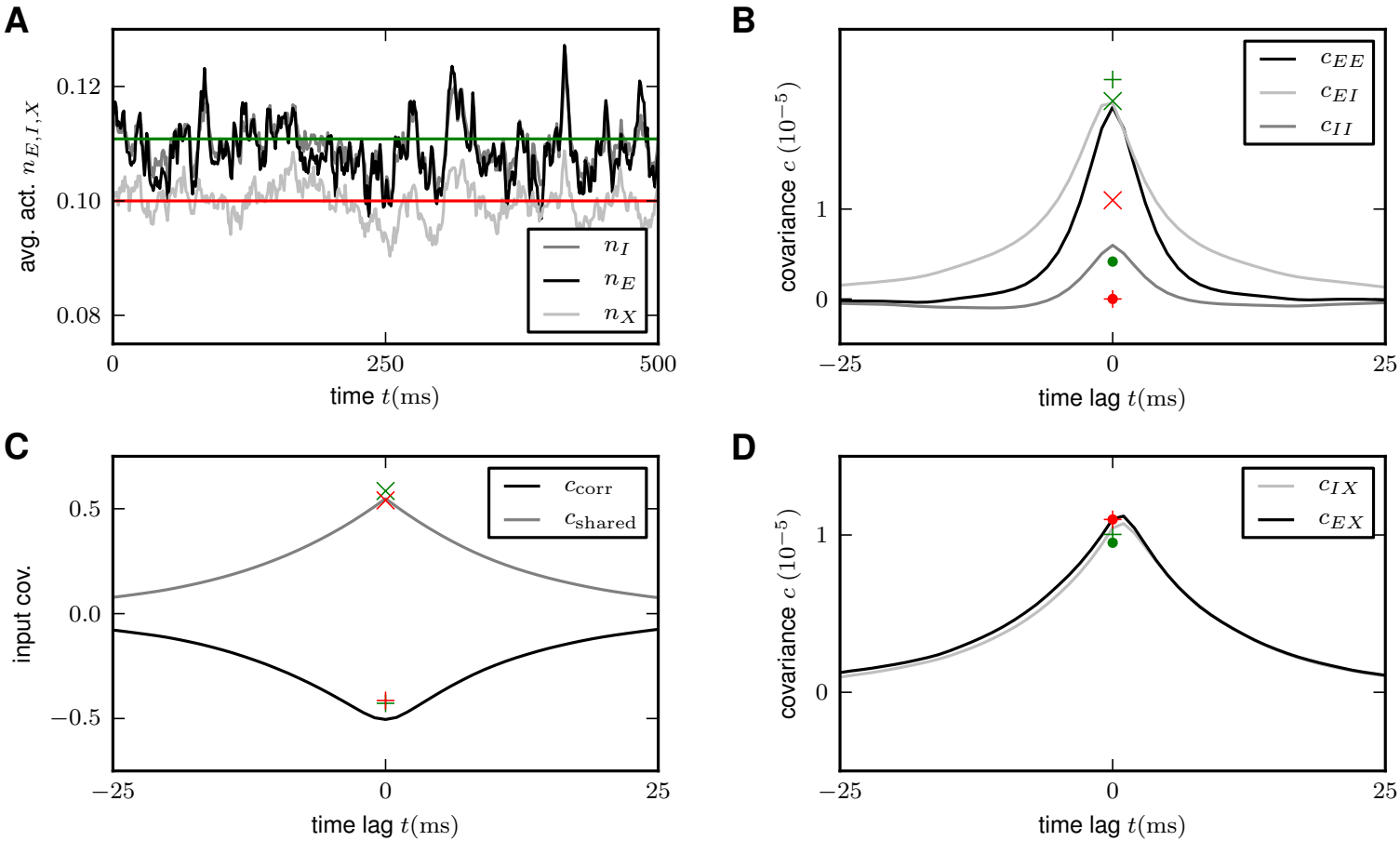
Ginzburg & Sompolinsky (1994)

$$A\begin{pmatrix} c_{EE} \\ c_{EI} \\ c_{II}\end{pmatrix} = B\begin{pmatrix} \frac{a_E}{N} \\ \frac{a_I}{N}\end{pmatrix} + C\begin{pmatrix} c_{EX} \\ c_{IX}\end{pmatrix}$$

$$D\begin{pmatrix} c_{EX} \\ c_{IX}\end{pmatrix} = E\frac{a_X}{N}$$

- 2 source terms drive covariance: external a_X and intrinsic fluctuations a_E, a_I
- covariance has scale $1/N$ compared to autocovariance

Cancellation condition constrains correlations



- good approximation of simulated correlations
- correlation structure constrained by cancellation in input

Summary

- correlations can be understood analytically in binary networks
  - mean field solution determines 'working point' (rates)
  - fluctuations around working point accounted for to linear order
  - recurrent equation relating auto- and crosscorrelations
- balance in networks $\equiv$ suppression on input correlation
- constrains, but does not determine correlation structure
- correlation structure obeys cancelation condition
- correlations driven by two 'sources'
  - autocovariance of neurons within the network
  - autocovariance of external drive

Further reading

- I Ginzburg, H Sompolinsky (1994)
  Theory of correlations in stochastic neural networks
  Phys Rev E 50 (4)
- Amit & Brunel (1997)
  Model of global spontaneous sctivity and local structured activity during delay periods in the cerebral cortex, Cerebral Cortex 7: 237–252
- C A van Vreeswijk and H Sompolinsky (1998)
  Chaotic Balanced State in a Model of Cortical Circuits.
  Neural Comp. 10:1321-1372.
- M A Buice, J D Cowan, C C Chow (2010)
  Systematic fluctuation expansion for neural network activity equations
  Neural Comput 22, 377–426
- J Hertz, Cross-Correlations in High-Conductance States of a Model Cortical Network, Neural Computation 22, 427–447
- A Renart, J De La Rocha, L Hollander, N Parga, A Reyes, KD Harris (2010)
  The Asynchronous state in cortical circuits
  Science 327, 587 Science 2010

How to treat correlations in spiking networks?

- determine state of network in mean-field theory
- linearization of neural response around working point
- map to equivalent linear system
- average
  - either actitivity over populations
  - or pairwise correlations over equivalent pairs
- solve resulting (recurrent) equation in frequency domain

Leaky integrate-and-fire dynamics

$$\tau_m \frac{dV_i(t)}{dt} + V_i(t) = RI_i(t)$$

$$R\left(\tau_s \frac{dI_i(t)}{dt} + I_i(t)\right) = \tau_m \sum_{j=1}^{N} J_{ij} s_j(t-d) \equiv b_i(t)$$

$$\text{if } V > V_\theta \quad \text{then} \quad V \leftarrow V_r, \text{spike}$$

Fourcaud & Brunel (2002)

neuron i spikes at time points t_i^k, "spike train":

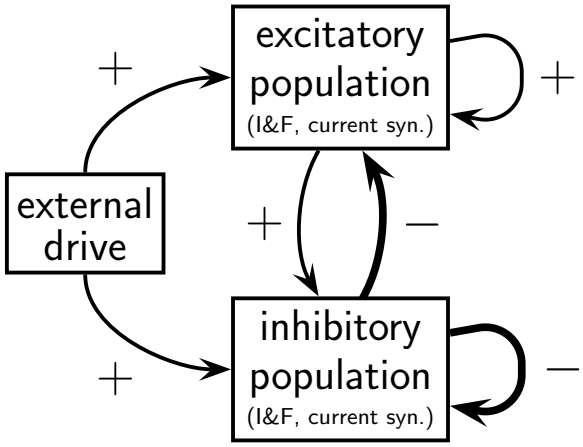
$$s_i(t) = \sum_k \delta(t - t_i^k)$$

we aim to understand correlations between spike trains

$$c_{ij}(\tau) = \langle \delta s_i(t+\tau) \delta s_j(t) \rangle$$

$$\delta s_i(t) = s_i(t) - \langle s_i \rangle$$

Homogeneous random network



- N exc., γN inh. neurons
- identical internal dynamics
- random connectivity, K exc inputs, γK inh inputs
- amplitude J of exc synapse, $-gJ$ of inh synapse

- identical statistics of summed input to each neuron suggests equal rate r of all neurons

$$b_i(t) = \tau_m \sum_j J_{ij} s_j(t)$$

$$= \tau_m J \underbrace{\sum_{j \in \text{exc. srcs}}}_{K} s_j(t) - \tau_m g J \underbrace{\sum_{k \in \text{inh. srcs}}}_{\gamma K} s_k(t) + \tau_m J s_{\text{ext.}}(t)$$

Amit & Brunel 1997, Brunel & Hakim 1999, Brunel 2000

Mean-field solution: closure assumption

- population average in network $\nu(t) = \frac{1}{N(1+\gamma)} \sum_i s_i(t)$
- homogeneity: all neurons $s_j(t)$ have same rate $\nu(t)$
- assume vanishing correlation:
  sum of K Poisson processes with rate ν = Poisson, rate $K\nu$
- mean $K\nu$ = variance $K\nu$
- diffusion approximation $J \ll \theta$

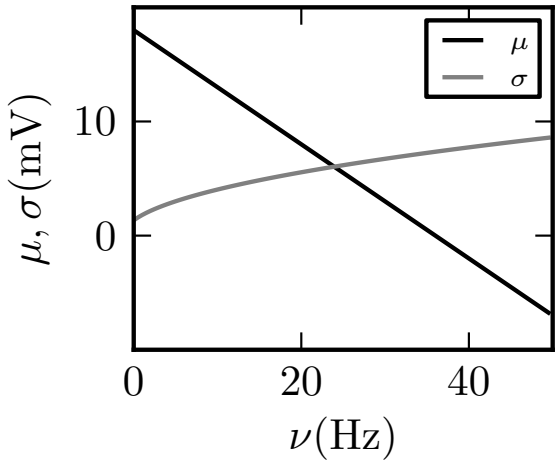
$$b(t) \simeq \mu + \sigma\xi(t)$$

with

$$\mu = \tau_m JK(1-\gamma g)\,\nu + J\nu_{\text{ext.}}$$

$$\sigma = J\sqrt{\tau_m K(1+\gamma g^2)\,\nu + \tau_m \nu_{\text{ext.}}}$$

$\xi(t)$ = unit var. Gaussian white noise



Amit & Brunel 1997, Brunel & Hakim 1999, Brunel 2000

Mean-field solution: self-consistent rate

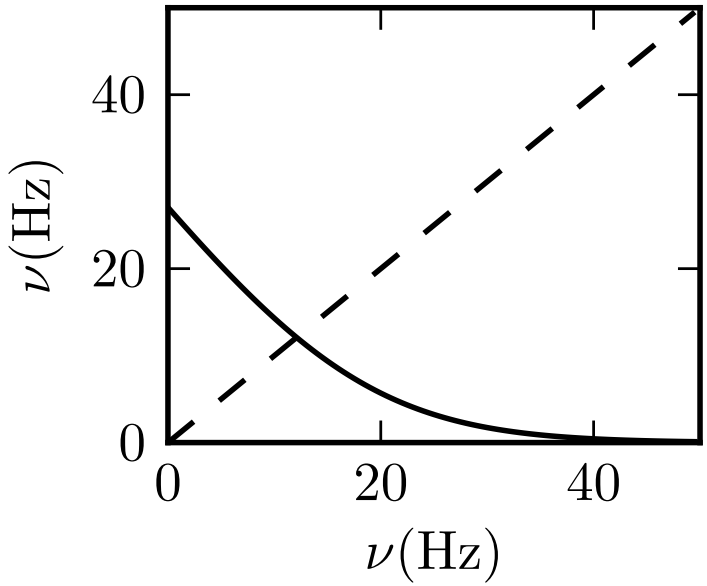
- in diffusion limit, firing rate of LIF neuron can be calculated

$$\nu^{-1} = \tau_r + \tau_m \sqrt{\pi} \int_{y_r}^{y_\theta} f(y)\, dy$$

with

$$f(y) = e^{y^2}(1 + \mathrm{erf}(y))$$

$$y_{\theta,r} = \frac{\{V_\theta, V_r\} - \mu}{\sigma} + \frac{\alpha}{2}\sqrt{\frac{\tau_s}{\tau_m}}$$

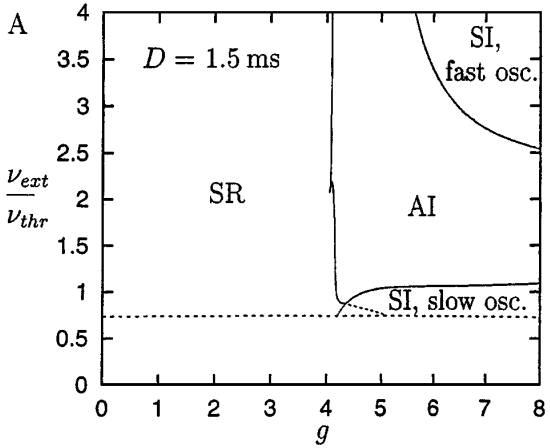


$$\nu = \phi(\mu(\nu), \sigma^2(\nu))$$

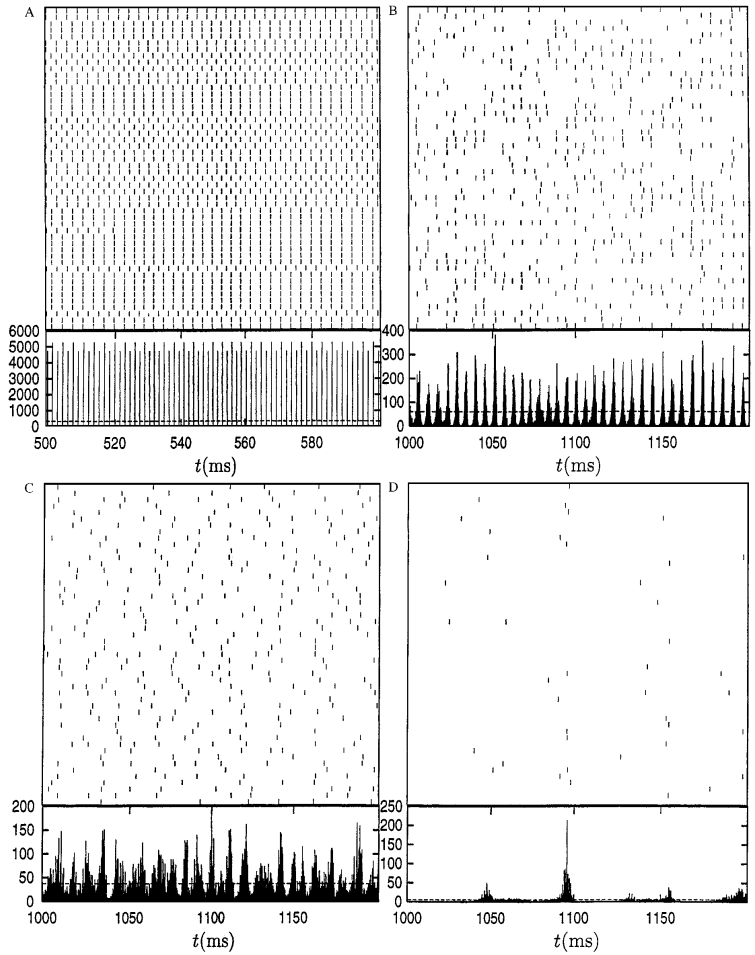
Siegert 1954, Brunel 2000, Brunel Fourcaud 2003, Moreno Bote et al. 2006

Phase diagram

- several states exist
- phase diagram can be obtained by perturbative methods + stability analysis
- here focus on asynchronous irregular activity similar to in-vivo



Brunel 2000



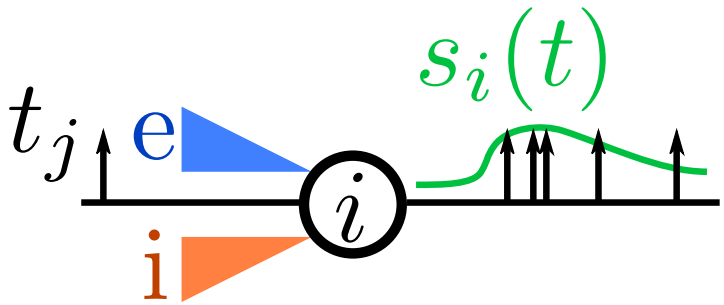
Linearization

spike train: functional $s_i(t) = G_t^i(\mathbf{s})$ depends on past spikes $\mathbf{s}(t'), t' < t$

$$G_t^i(\mathbf{s}) = G_t^i(\mathbf{s}\backslash s_j) + \int_{-\infty}^{t} \frac{\partial G_t^i(\mathbf{s})}{\partial s_j(t')}\, s_j(t')\, dt'$$

with the functional derivative defined as

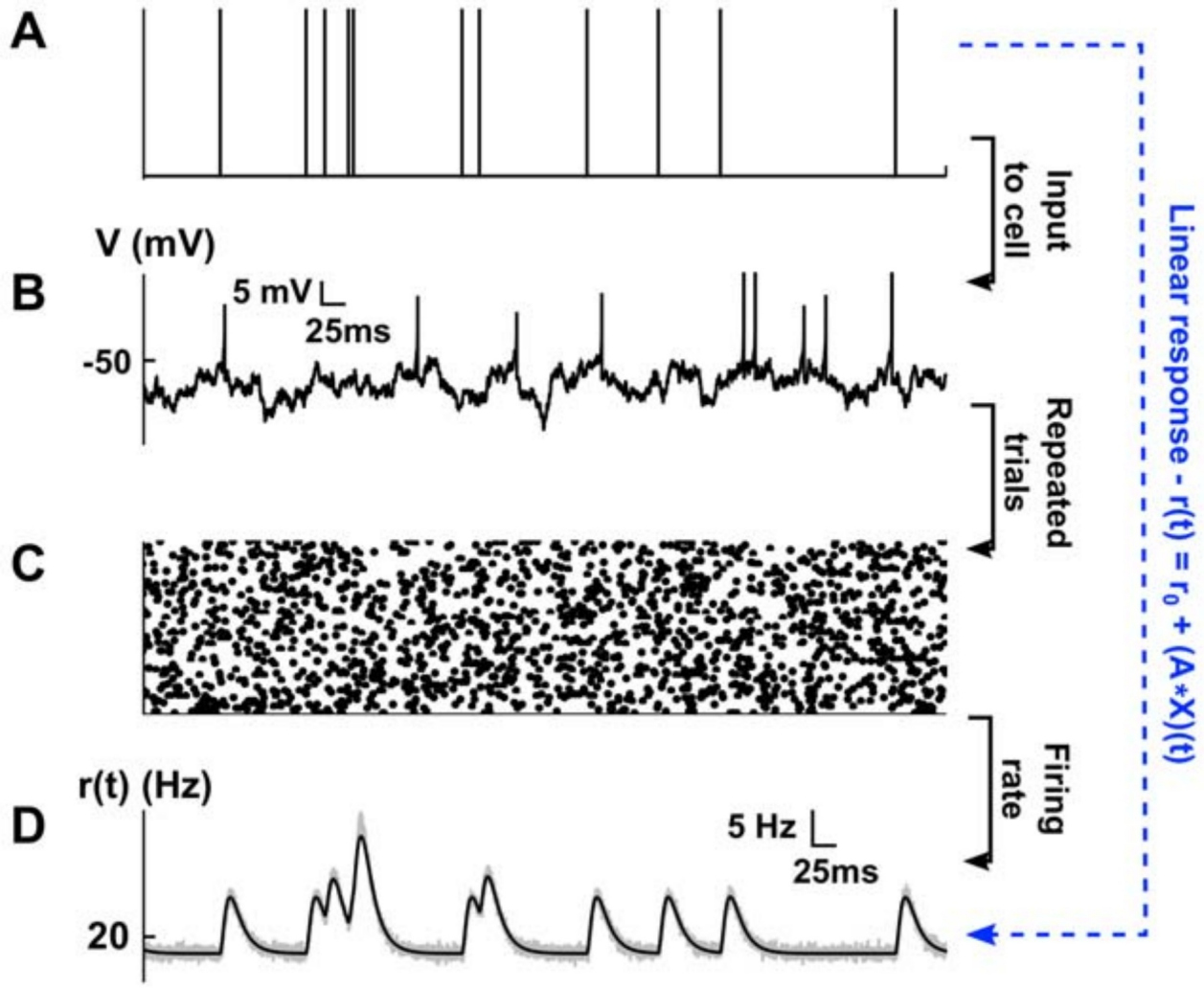
$$\frac{\partial G_t^i(\mathbf{s})}{\partial s_j(t')} = \lim_{\epsilon\to 0} \frac{1}{\epsilon}\left(G_t^i(\mathbf{s} + \epsilon \mathbf{e}_j \delta(\circ - t') - G_t^i(\mathbf{s})\right) \equiv h_{ij}(\mathbf{s}\backslash s_j, t, t')$$



- small perturbation by single spike of neuron j
- response $s_i(t)$ to first order linear in perturbation

Pernice et al. 2011, 2012, Trousdale et al. 2012, Tetzlaff et al. 2012

Relation to spike-triggered average



Trousdale et al. 2012

Linearized convolution equation for correlations

for $t > u$

$$
\begin{aligned}
c_{ik}(t,u) &= \langle s_i(t)\,\delta s_k(u)\rangle = \langle G_t^i(\mathbf{s})\,\delta s_k(u)\rangle \\
&= \langle G_t^i(\mathbf{s}\backslash s_j)\,\delta s_k(u)\rangle \\
&+ \int_{-\infty}^{t} \langle h_{ij}(\mathbf{s}\backslash s_j, t, t')\, s_j(t')\delta s_k(u)\rangle\; dt'
\end{aligned}
$$

- first term: functional independent of s_j
- second term: expansion for s_l causes third order terms $s_l s_j s_k$ neglected here $\rightarrow$ assumption of independence of h_{ij} and s_j, s_k
- choice j was arbitrary, so to linear order

$$
c_{ik}(t,u) \simeq \sum_j \int_{-\infty}^{t} \langle h_{ij}(\mathbf{s}\backslash s_j, t, t')\rangle\, c_{jk}(t',u)\; dt'
$$

Properties of the response kernel

- average over remaining inputs $\mathbf{s}\backslash s_j$:
  replace by equivalent Gaussian noise $\langle\rangle_{\mathbf{s}\backslash s_j} \to \langle\rangle_{x\sim\mathcal{N}(\mu,\sigma)}$

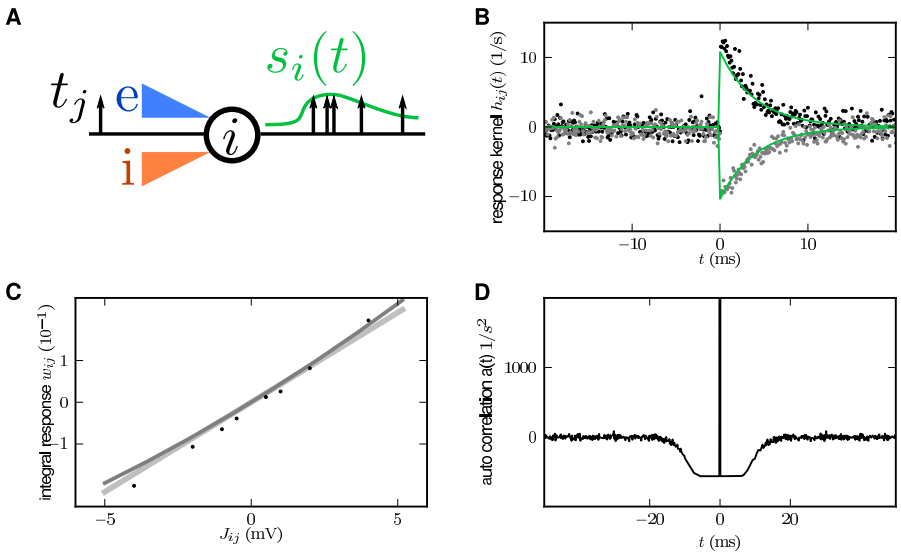
$$h_{ij}(t,t') \simeq \lim_{\epsilon\to 0} \frac{1}{\epsilon} \left\langle G_t^i(x + \epsilon J_{ij}\delta(\circ - t')) - G_t^i(x) \right\rangle_x$$

- linear approximation of neuron $j's$ influence on neuron i
  $\to$ impulse response
- stationarity: kernel only depends on time difference $h_{ij}(t-t')$
- step response $w_{ij}(t) = \int_{-\infty}^{\infty} h_{ij}(t')\,\theta(t-t')\,dt' = \int_0^t h_{ij}(t')\,dt'$
- dc susceptibility $w_{ij}(\infty) \equiv$ change of equilibrium rate due to step in input j after long time

$$H(\infty) = \nu(\mu + J_{ij}, \sigma + J_{ij}^2) - \nu(\mu,\sigma)$$

Helias et al. (2010), Tetzlaff et al. (2012)

Interpretation of the kernel



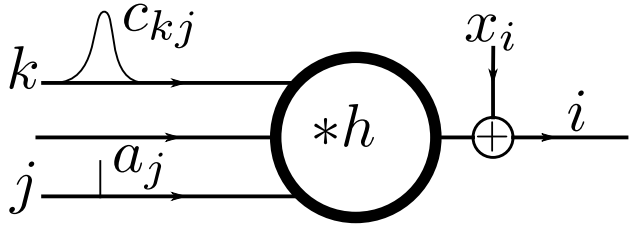
dc susceptibility $w_{ij} \equiv H_{ij}(\infty) \equiv$ change of equilibrium rate due to step ϵ in input j after long time

- $w_{ij} = \lim_{\epsilon \to 0} \frac{\nu(\mu+\epsilon J_{ij}, \sigma^2+\epsilon J_{ij}^2) - \nu(\mu,\sigma^2)}{\epsilon}$
- linearize $\nu(\mu, \sigma^2)$ for small ϵ

$$w_{ij} = \sqrt{\pi}(\tau_{\mathrm{m}}\nu_i)^2 \frac{J_{ij}}{\sigma_i} \left(f(y_\theta)(1 + \frac{y_\theta}{2\sigma_i} J_{ij}) - f(y_r)(1 + \frac{y_r}{2\sigma_i} J_{ij}) \right)$$

Equivalent linear dynamics

spiking dynamics:



$$\langle \delta s_i \rangle = 0$$

$$c_{ij}(\tau) = \langle \delta s_i(t+\tau)\delta s_j \rangle = \begin{cases} \sum_k h_{ik} * (c_{kj} + \delta_{jk} a_j)(\tau) & i \neq j \\ a_i(\tau) = \delta(\tau)\nu_i & i = j \end{cases}$$

continuous, linear dynamics equivalent up to second moment:

$$y_i(t) = \sum_k (h_{ik} * y_k)(t) + x_i(t)$$

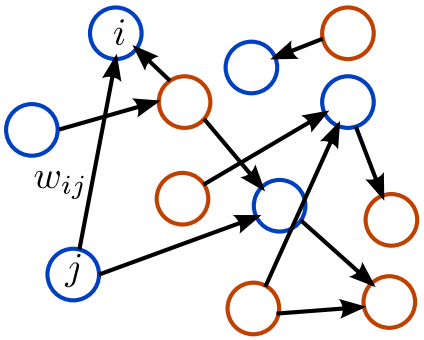
$$\langle x_i(t) \rangle = 0 \qquad \langle x_i(t+\tau)x_j(t) \rangle = \delta(\tau)\delta_{ij}\nu_i$$

$$c_{ij}(\tau) = \langle y_i(t+\tau)y_j(t) \rangle$$

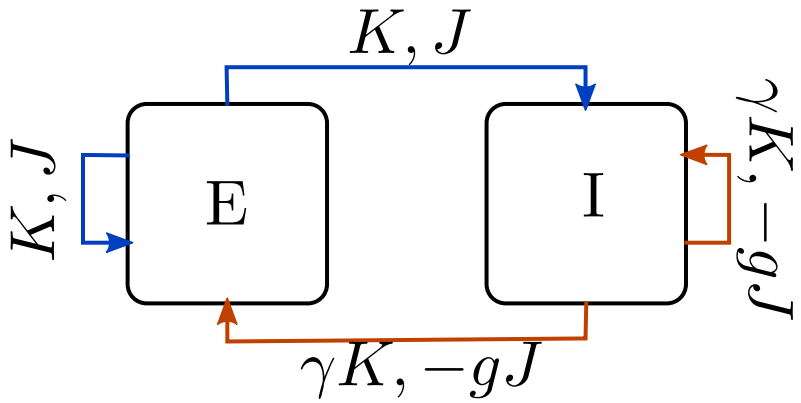
fulfills same convolution equation

Lindner et al. 2005, Pernice et al. 2012, Trousdale et. al 2012, Tetzlaff et al. 2012

Population averaged system



avg. $\Rightarrow$



N-dim

$$\mathbf{y} = \mathbf{W} h * \mathbf{y} + \mathbf{x}$$

2-dim

$$\begin{pmatrix} y_\mathsf{E} \\ y_\mathsf{I} \end{pmatrix} = Kw \begin{pmatrix} 1 & -\gamma g \\ 1 & -\gamma g \end{pmatrix} h * \begin{pmatrix} y_\mathsf{E} \\ y_\mathsf{I} \end{pmatrix} + \begin{pmatrix} x_\mathsf{E} \\ x_\mathsf{I} \end{pmatrix}$$

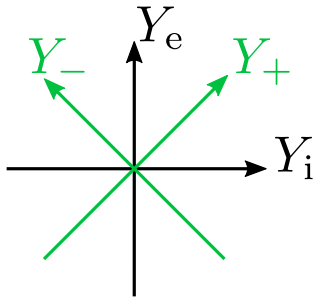
- introduce population averaged activity

  $y_\mathsf{E} = \frac{1}{N} \sum_{i \in \mathcal{E}} y_i \qquad y_\mathsf{I} = \frac{1}{\gamma N} \sum_{i \in \mathcal{I}} y_i$

- effective coupling: number of synapses $\times$ weight

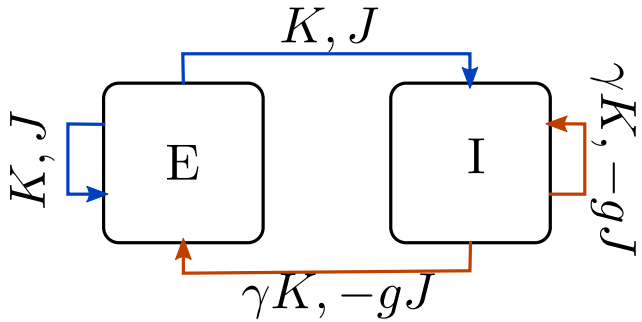
Schur transformation exposes negative feedback

$$\mathbf{Y}(\omega) = \mathbf{W}H(\omega)\mathbf{Y}(\omega) + \mathbf{X}(\omega)$$

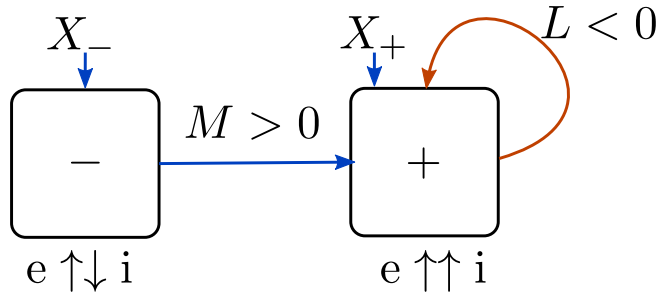


$$\begin{pmatrix} Y_\mathrm{E} \\ Y_\mathrm{I} \end{pmatrix} = \frac{1}{\sqrt{2}} \begin{pmatrix} 1 \\ 1 \end{pmatrix} Y_+ + \frac{1}{\sqrt{2}} \begin{pmatrix} 1 \\ -1 \end{pmatrix} Y_-$$

Schur basis $\equiv$ orthonormalized eigenbasis



Schur $\Rightarrow$



$$\tilde{\mathbf{W}} = Kw \begin{pmatrix} 1 & -\gamma g \\ 1 & -\gamma g \end{pmatrix}$$

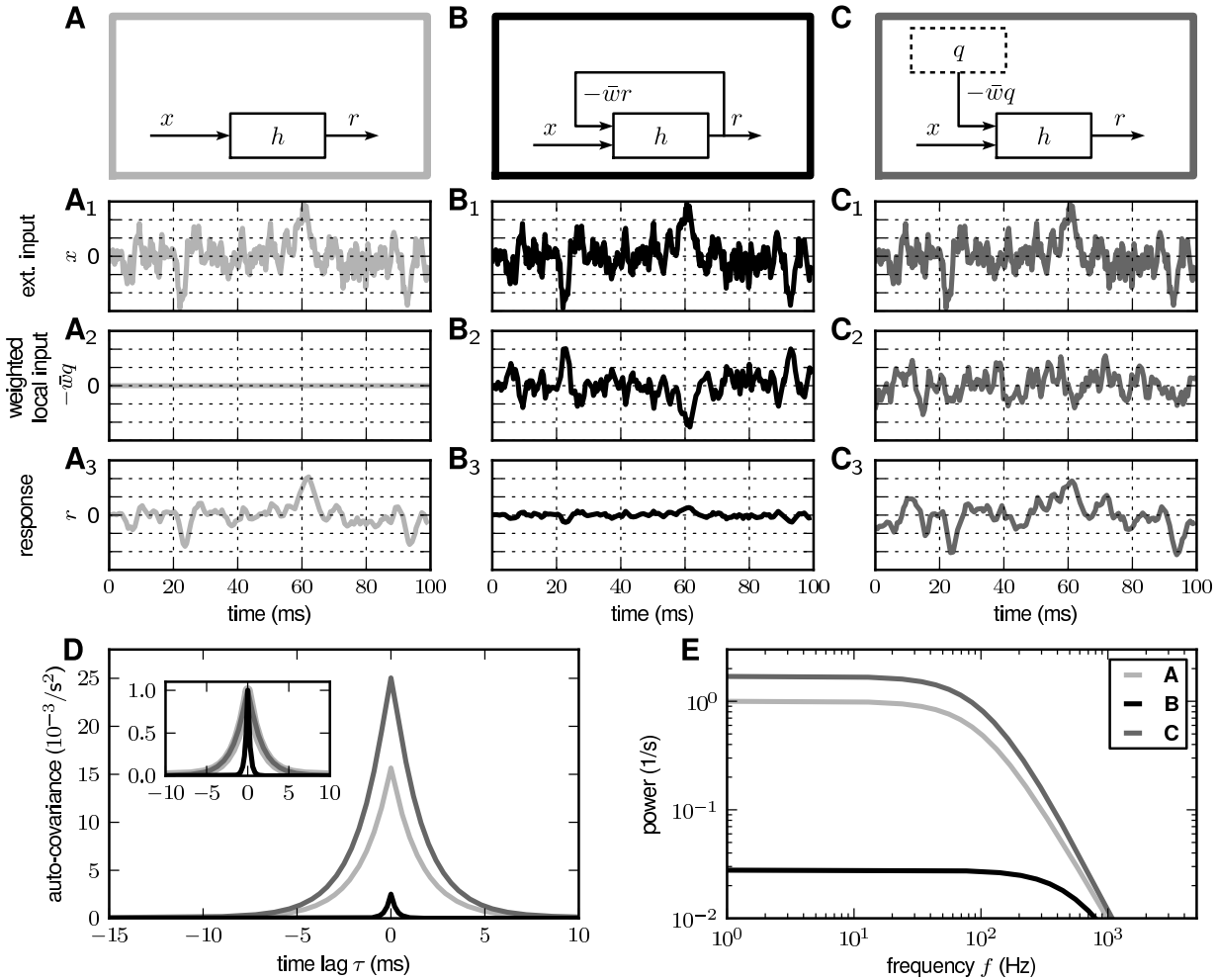
$$\hat{\mathbf{W}} = \begin{pmatrix} L & M \\ 0 & 0 \end{pmatrix}$$

$$L = Kw(1 - \gamma g)$$
$$M = Kw(1 + \gamma g)$$

$$Y_- = HX_- \qquad Y_+ = \frac{M}{1 - LH} HX_- + X_+$$

Tetzlaff et al. 2012

Negative feedback cancels fluctuations



Tetzlaff et al. 2012

fluctuation suppression has same cause in E-I as in I networks

Small fluctuations $\leftrightarrow$ small correlations

small population fluctuations of population α

$$\langle y_\alpha^2 \rangle = \frac{1}{N_\alpha^2} \sum_{i,j} \langle y_i y_j \rangle$$
$$= \frac{1}{N_\alpha} a_\alpha + c_{\alpha\alpha}$$

imply small pairwise averaged correlations $c_{\alpha\alpha}$
at fixed autocorrelation a_α

$$a_\alpha = \frac{1}{N_\alpha} \sum_{i} \langle y_i y_i \rangle$$

$$c_{\alpha\alpha} = \frac{1}{N_\alpha^2} \sum_{i \neq j} \langle y_i y_j \rangle$$

Tetzlaff et al. (2012)

Pairwise correlations

$$c_{ij}(\tau) = \sum_{k\neq j} w_{ik} h * (c_{kj} + \delta_{kj}\nu_j\delta(\circ))$$

average correlation between excitatory pairs of neurons:

$c_{EE}(\tau) = \frac{1}{N^2}\sum_{i\neq j\in\mathcal{E}} c_{ij}(\tau)$ $\qquad c_{II}, c_{EI}, c_{IE}\ldots$

$$\mathbf{c} = \begin{pmatrix} c_{EE} & c_{EI} \\ c_{IE} & c_{II} \end{pmatrix} = \underbrace{Kw \begin{pmatrix} 1 & -\gamma g \\ 1 & -\gamma g \end{pmatrix}}_{\tilde{\mathbf{W}}} h * \mathbf{c} + r\frac{Kw}{N}\begin{pmatrix} 1 & -g \\ 1 & -g \end{pmatrix} h * \delta$$

$$= \tilde{\mathbf{W}} h * \left(\mathbf{c} + \underbrace{\frac{\nu}{N}\begin{pmatrix} 1 & 0 \\ 0 & 1/\gamma \end{pmatrix}}_{\equiv \mathbf{D}} \delta \right)$$

Averaged correlations $\leftrightarrow$ correlation of average

$$\mathbf{c} = \tilde{\mathbf{W}} h * \underbrace{(\mathbf{c} + \mathbf{D}\delta)}_{\equiv \bar{\mathbf{c}}} \qquad \text{introduce} \qquad \bar{\mathbf{c}} = \mathbf{c} + \mathbf{D}\delta$$

$\bar{\mathbf{c}}$ equivalent to population fluctuations

$$\bar{c}_{\mathrm{EE}}(\tau) = \underbrace{c_{\mathrm{EE}}(\tau)}_{i \neq j} + \underbrace{\frac{\nu}{N}\delta(\tau)}_{i=j} \qquad a_{\mathrm{E}}(\tau) \simeq \frac{\nu}{N}\delta(\tau)$$

$$\simeq \frac{1}{N^2} \sum_{i,j \in \mathcal{E}} \langle y_i(t+\tau) y_j(t) \rangle = \langle y_{\mathrm{E}}(t+\tau) y_{\mathrm{E}}(t) \rangle$$

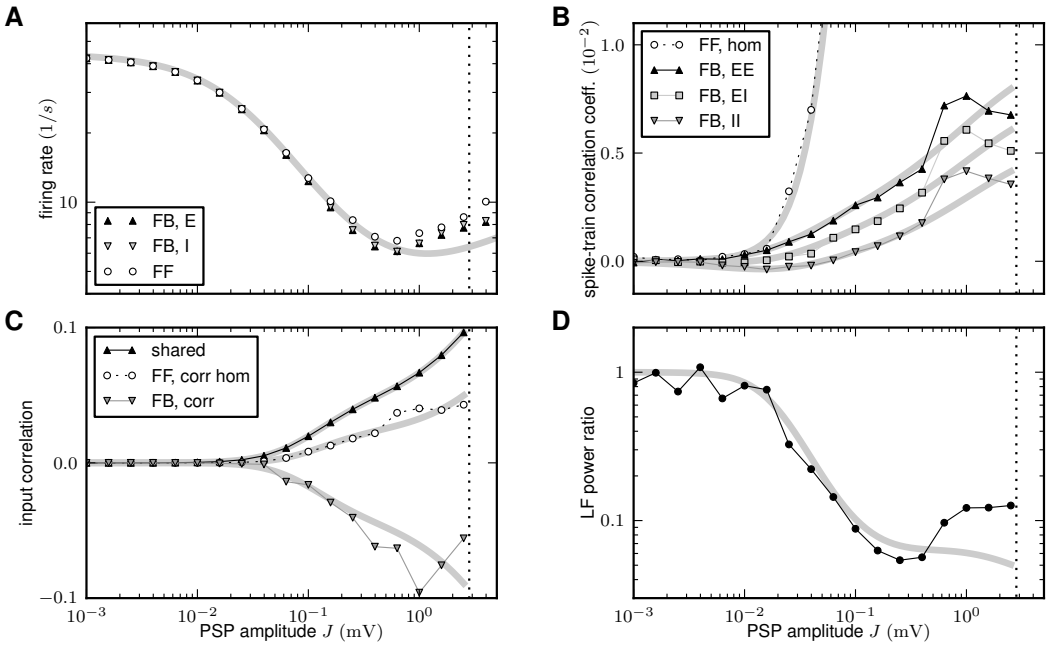
$$\mathbf{Y}(\omega) = \tilde{\mathbf{W}} H(\omega) \mathbf{Y}(\omega) + \sqrt{\mathbf{D}}\mathbf{X}(\omega)$$

$$= \mathbf{P}(\omega)\sqrt{\mathbf{D}}X(\omega) \qquad \text{with} \quad \mathbf{P}(\omega) = (\mathbf{1} - H(\omega)\tilde{\mathbf{W}})^{-1}$$

$$\bar{\mathbf{C}}(\omega) = \langle \mathbf{Y}(\omega)\mathbf{Y}^T(-\omega) \rangle = \mathbf{P}(\omega)\, \mathbf{D}\, \mathbf{P}^T(-\omega)$$

Hawkes (1971), Pernice et al. (2011, 2012), Trousdale et al. (2012), Tetzlaff et al. (2012)

Structure of correlations



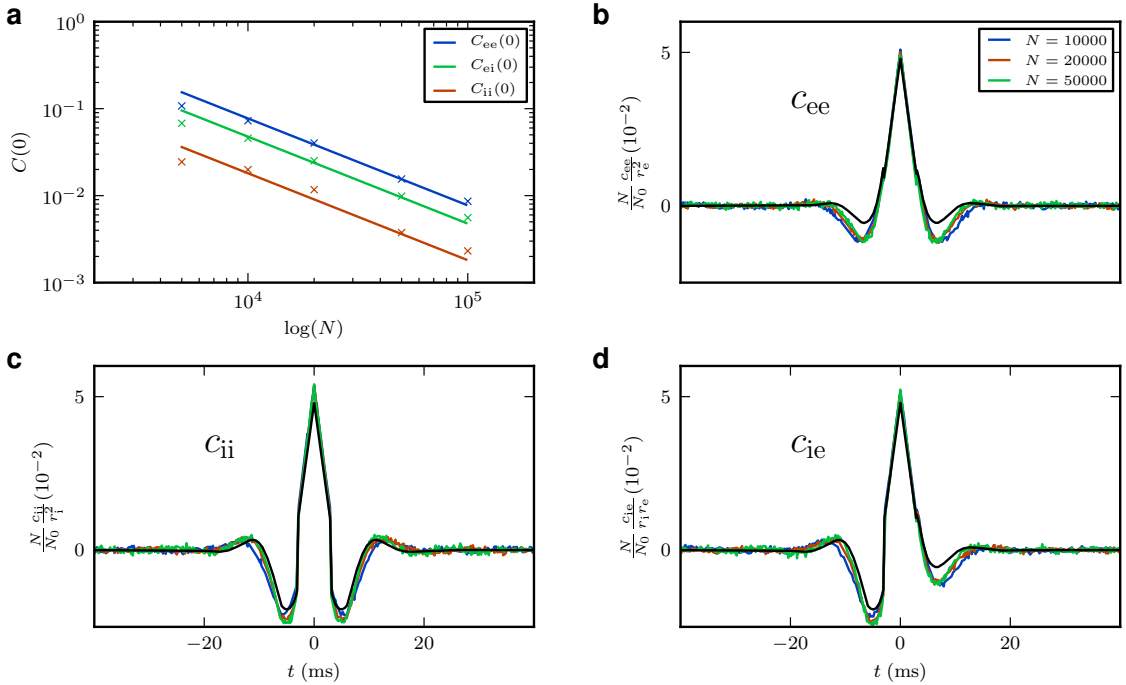
- $C_{EE} > C_{EI} > C_{II}$
- due to direct connections: A 'drives' C
- suppresssion by feedback $(1-L)^{-1}$

Tetzlaff et al. (2012)

$$C_{EE/II} = \frac{C_{shared}}{(1-L)^2} + \frac{2KwA}{1-L} \begin{cases} \frac{1}{N_E} & \text{for EE} \\ \frac{-\gamma g}{N_I} & \text{for II} \end{cases}$$

$$C_{EI} = \frac{1}{2}(C_{EE} + C_{II}) \quad \text{with} \quad C_{shared} = Kw^2 \left(\frac{1}{N_E} + \frac{\gamma g^2}{N_I} \right) A.$$

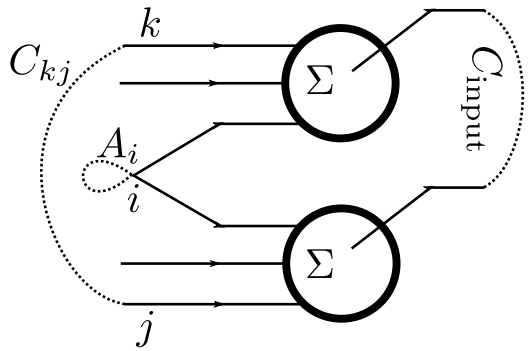
What about infinite brains?



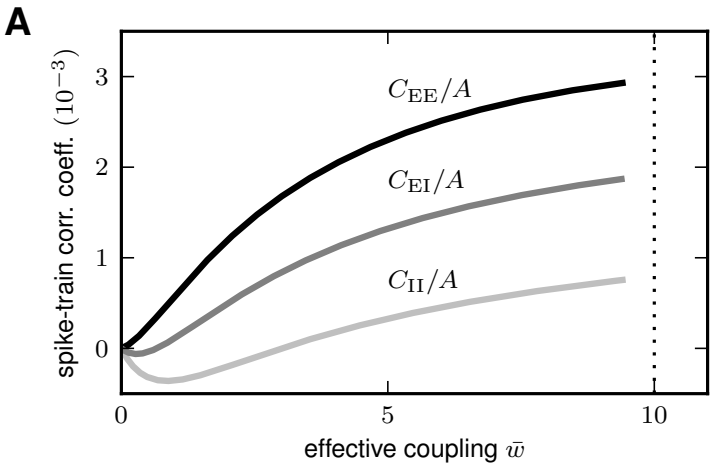
- scaling: $w \propto 1/N \propto 1/K$
- adjust external noise to maintain working point (fluctuations)
- negative compound feedback: $Kw(1 - \gamma g) \equiv L = \text{const.}$
- asymmetry remains in limit of infinitely large networks

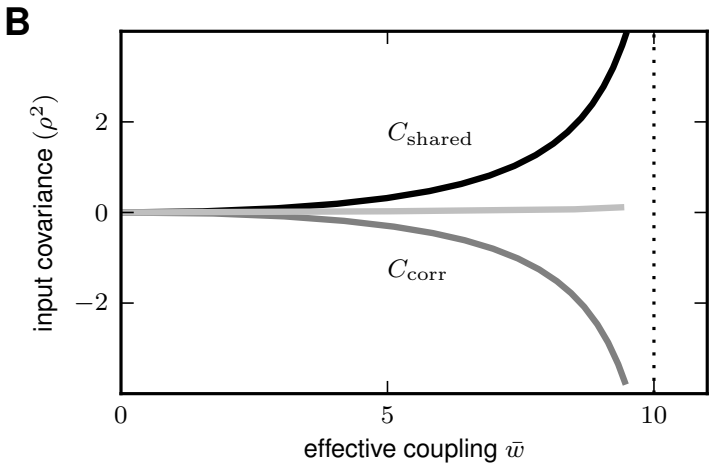
Helias et al. (submitted)

Cancelation of input correlation



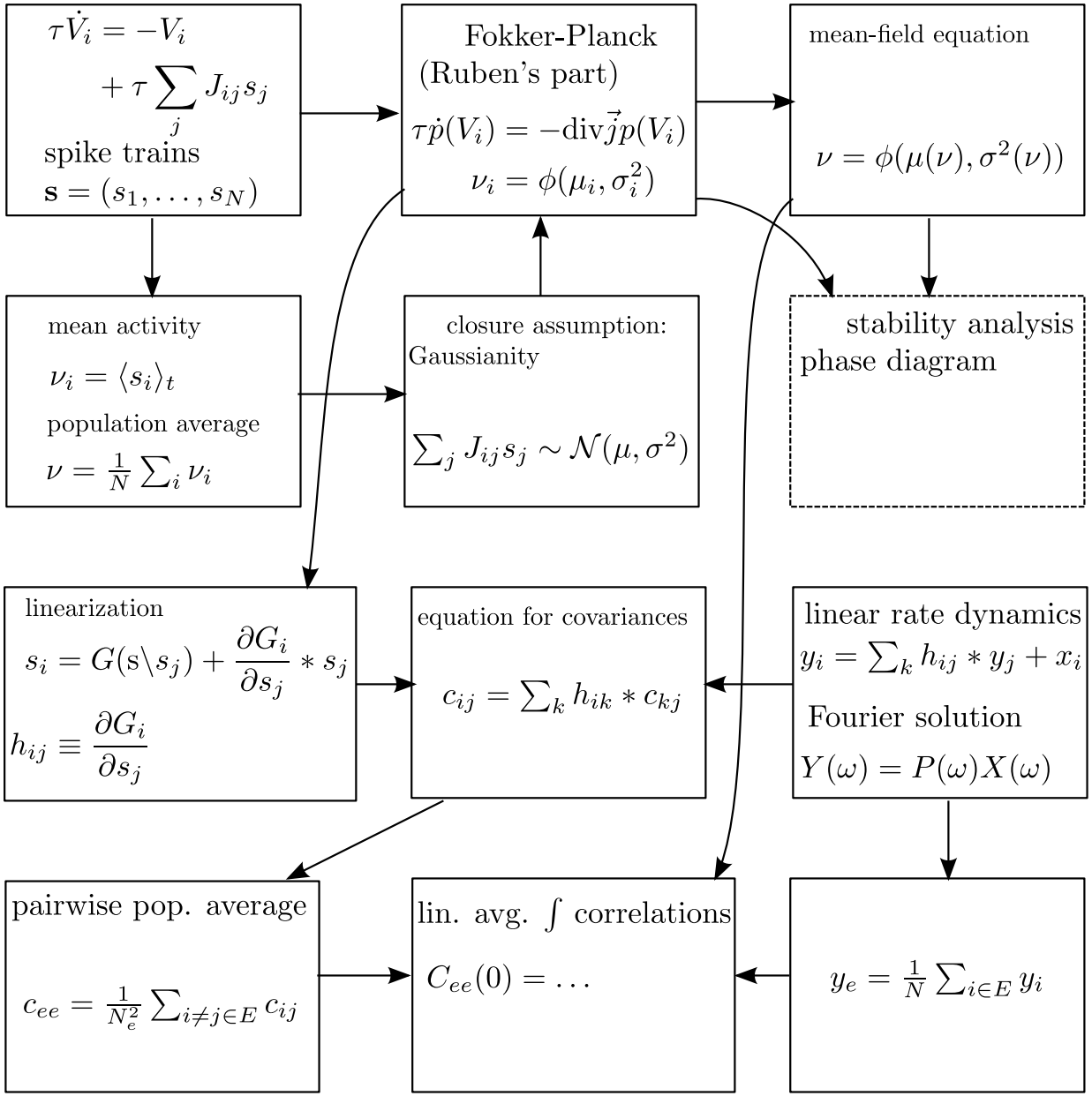
$$
\begin{aligned}
C_{\text{input}} &= C_{\text{shared}} + C_{\text{corr}} \\
C_{\text{shared}} &= p_c K w^2 (1 + \gamma g^2) A \\
C_{\text{corr}} &= (Kw)^2 (C_{\text{EE}} - 2\gamma g C_{\text{EI}} + (\gamma g)^2 C_{\text{II}})
\end{aligned}
$$





- $C_{\text{shared}} > 0$, $C_{\text{corr}} < 0$ partially cancel
- EI network: $C_{\text{EE}} > C_{\text{EI}} > C_{\text{II}} \Rightarrow C_{\text{corr}} < 0$
- I network: $C_{\text{II}} < 0$, same cancelation

Tetzlaff et al. 2012


$\tau\dot{V}_i = -V_i + \tau\sum_j J_{ij}s_j$
spike trains
$\mathbf{s} = (s_1, \ldots, s_N)$
Fokker-Planck
(Ruben's part)
$\tau\dot{p}(V_i) = -\mathrm{div}\vec{j}p(V_i)$
$\nu_i = \phi(\mu_i, \sigma_i^2)$
mean-field equation
$\nu = \phi(\mu(\nu), \sigma^2(\nu))$
mean activity
$\nu_i = \langle s_i \rangle_t$
population average
$\nu = \frac{1}{N}\sum_i \nu_i$
closure assumption:
Gaussianity
$\sum_j J_{ij}s_j \sim \mathcal{N}(\mu, \sigma^2)$
stability analysis
phase diagram
linearization
$s_i = G(\mathrm{s}\backslash s_j) + \frac{\partial G_i}{\partial s_j} * s_j$
$h_{ij} \equiv \frac{\partial G_i}{\partial s_j}$
equation for covariances
$c_{ij} = \sum_k h_{ik} * c_{kj}$
linear rate dynamics
$y_i = \sum_k h_{ij} * y_j + x_i$
Fourier solution
$Y(\omega) = P(\omega)X(\omega)$
pairwise pop. average
$c_{ee} = \frac{1}{N_e^2}\sum_{i\neq j\in E} c_{ij}$
lin. avg. $\int$ correlations
$C_{ee}(0) = \ldots$
$y_e = \frac{1}{N}\sum_{i\in E} y_i$

Correlations in structured networks

$$\mathbf{C}(\omega) = \langle \mathbf{Y}(\omega)\mathbf{Y}(-\omega) \rangle = \mathbf{P}(\omega)\ \mathbf{D}\ \mathbf{P}^T(-\omega)$$

propagator $\mathbf{P}(\omega) = [\mathbf{1} - \underbrace{H(\omega)\mathbf{W}}_{G(\omega)}]^{-1}$ can be expanded

iff absolute value of spectrum is bounded by unity

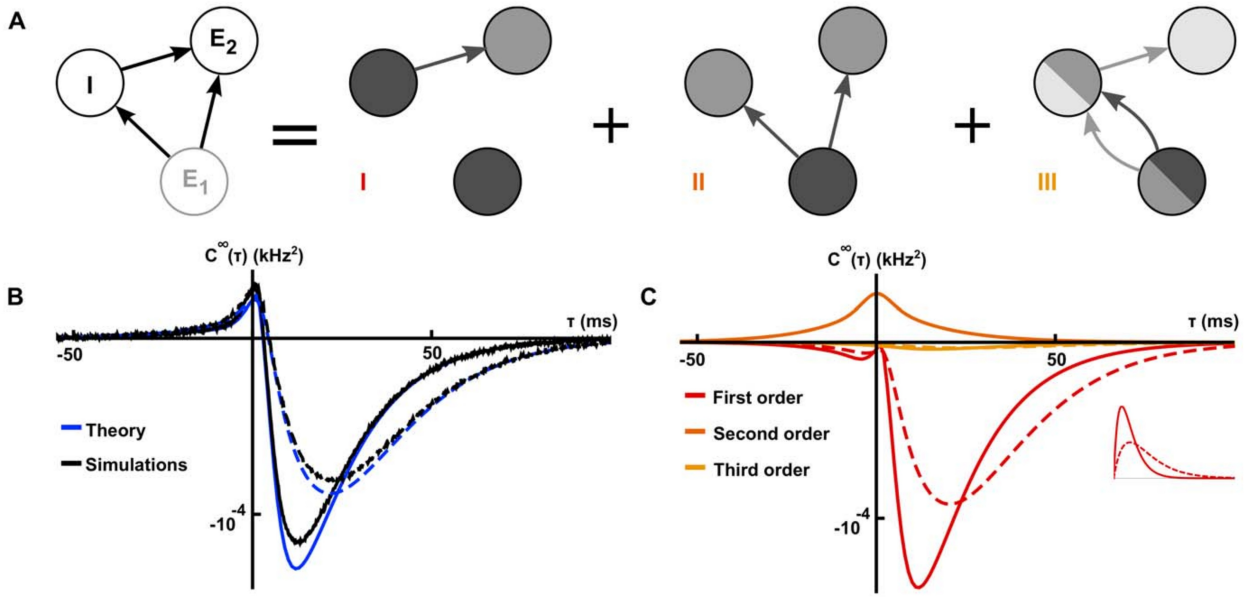
$$\mathbf{W}v_i = \lambda_i v_i \qquad \text{iff } |H(\omega)\lambda_i| \ < 1 \ \forall\ i, \omega$$

$$\rightarrow \mathbf{P}(\omega) = \sum_{n=0}^{\infty} \mathbf{G}(\omega)^n$$

$$\mathbf{C}(\omega) = \sum_{n,m} \mathbf{G}^n(\omega)\ \mathbf{D}\ (\mathbf{G}^T)^m(-\omega)$$

Pernice et al. (2011), (2012), Trousdale et al. (2012)

Correlations in structured networks



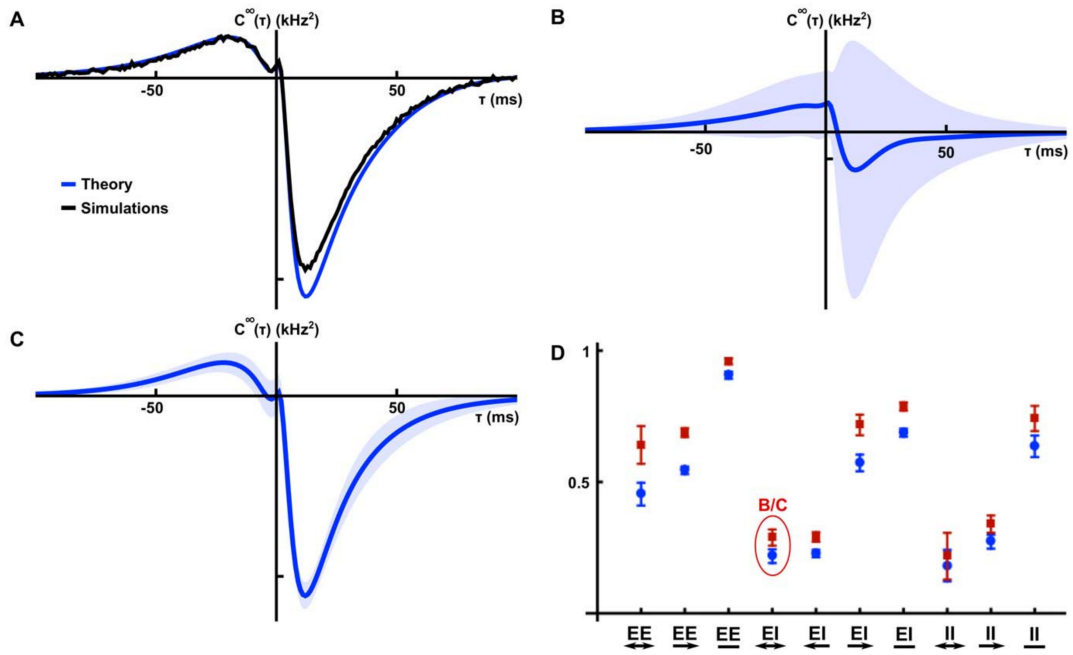
- for nilpotent coupling matrix $G^3 = 0 \quad \mathbf{P} = 1 + \mathbf{G} + \mathbf{G}^2$

$$\mathbf{C} = \underbrace{\mathbf{D}\mathbf{G}^T + \mathbf{G}\mathbf{D}}_{\text{order I}} + \underbrace{\mathbf{G}\mathbf{D}\mathbf{G}^T + \mathbf{D}(\mathbf{G}^T)^2 + \mathbf{G}^2\mathbf{D}}_{\text{order II}}$$

$$+ \underbrace{\mathbf{G}\mathbf{D}(\mathbf{G}^T)^2 + \mathbf{G}^2\mathbf{D}\mathbf{G}^T}_{\text{order III}}$$

Trousdale et al. 2012

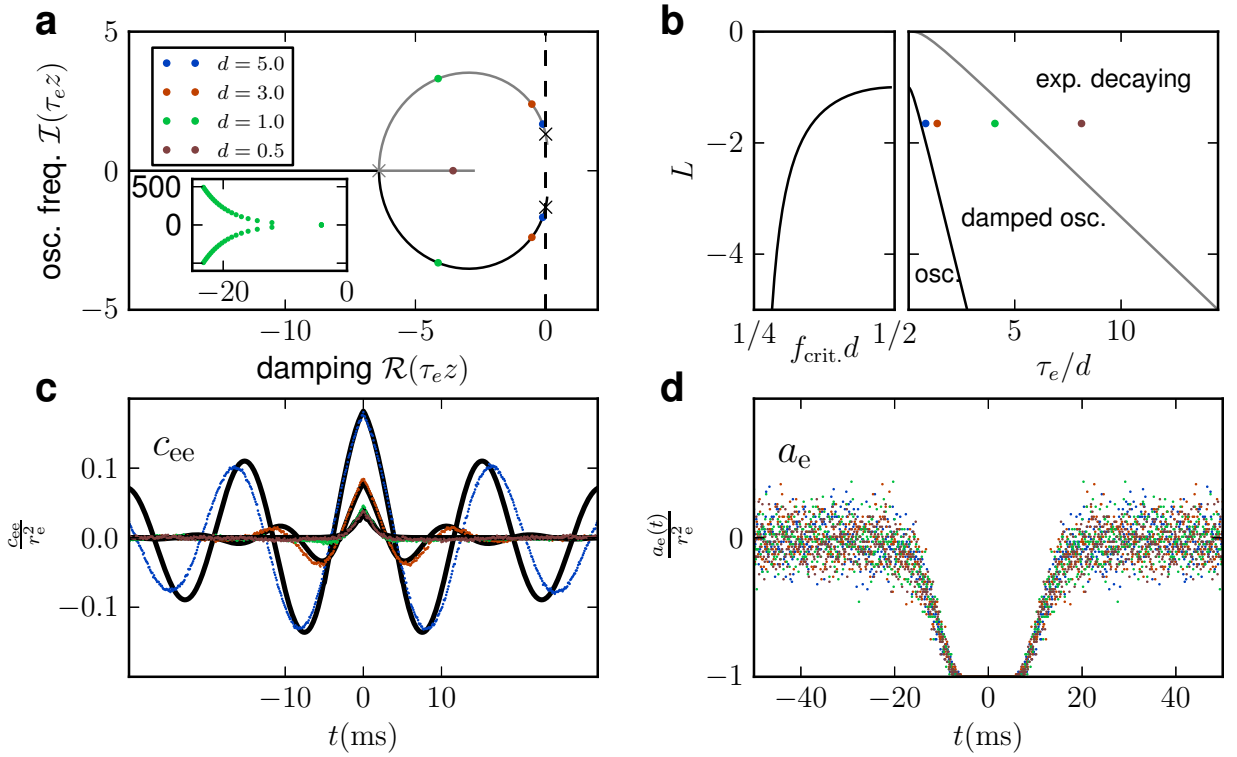
Contribution of first order term in random networks



- covariance between pairs fluctuates around population mean
- mostly due to first order terms $\mathbf{GD}, \mathbf{DG}^T$ (direct connections)

Trousdale et al. 2012

Delays, oscillations, temporal shape . . .



Helias et al.

(submitted)

investigating frequency dependence of $C(\omega)$ explains

- delayed synaptic coupling $\rightarrow$ fast global oscillations Brunel 2000
- temporal shape of correlation functions
- scaling invariant properties of network dynamics

Summary

- qualitatively similar approach as for binary neurons: mean-field solution, linearization, Fourier transform
- equivalence of linearized LIF, linear Poisson, linear rate equations
- correlations smaller than expected by shared input
- suppression of correlations $\equiv$ suppression of population fluctuations
- negative feedback is underlying reason
  $\curvearrowright$ same phenomenon in E-I and in I networks
- obserable as cancellation of input correlations
- structured networks: expansion of propagator yields intuition

Further reading

- Amit & Brunel (1997), Model of global spontaneous sctivity and local structured activity during delay periods in the cerebral cortex, Cerebral Cortex 7: 237–252
- N Brunel and V Hakim (1999), Fast global oscillations in networks of integrate-and-fire neurons with low firing rates, Neural Computation, 11, 1621–1671
- N Brunel (2000), Dynamics of sparsely connected networks of excitatory and inhibitory spiking neurons, J Comput Neurosci. 8(3):183-208.
- N Fourcaud, N Brunel (2002), Dynamics of the Firing Probability of Noisy Integrate-and-Fire Neurons. Neural Comput 14, 2057–2110
- A G Hawkes (1971), Point spectra of some mutually exciting point processes
  Royal Stat. Soc. 33(3): 438-443
- M Helias, M Deger, S Rotter, M Diesmann (2010), Instantaneous Non-Linear Processing by Pulse-Coupled Threshold Units. PLoS Comput Biol 6(9): e1000929. doi:10.1371/journal.pcbi.1000929
- T Tetzlaff, M Helias, GT Einevoll, M Diesmann (2012), Decorrelation of neural-network activity by inhibitory feedback
  PLoS Comp Biol (in press), arXiv:1204.4393v1 [q-bio.NC]
- J Trousdale, Y Hu, E Shea-Brown, and K Josić (2012), Impact of Network Structure and Cellular Response on Spike Time Correlations.
  PLoS Comput Biol 8(3), e1002408.
- V Pernice, B Staude, S Cardanobile, S Rotter (2011), How Structure Determines Correlations in Neuronal Networks.
  PLoS Comput Biol 7(5): e1002059. doi:10.1371/journal.pcbi.1002059
- V Pernice, B Staude, S Cardanobile, S Rotter (2012), Recurrent interactions in spiking networks with arbitrary topology.
  Phys Rev E 85, 031916
- M Helias, T Tetzlaff, M Diesmann (2012), Echoes in correlated neural systems (submitted), arXiv:1207.0298v2 [q-bio.NC]