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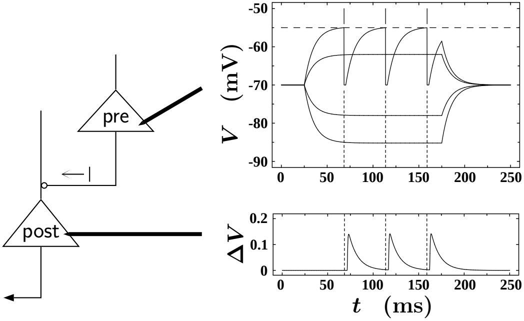
Biological neuronal networks - from structure to activity

February 21, 2017 | Moritz Helias

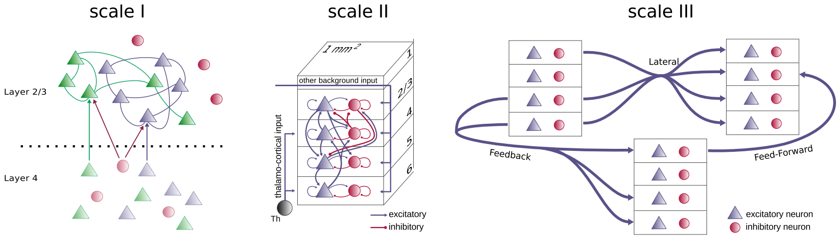
Theory of multi-scale neuronal networks
Institute of Neuroscience and Medicine (INM-6)
Institute for Advanced Simulation (IAS-6)
Jülich Research Centre and JARA, Jülich, Germany

Neuronal interaction on microscopic scale



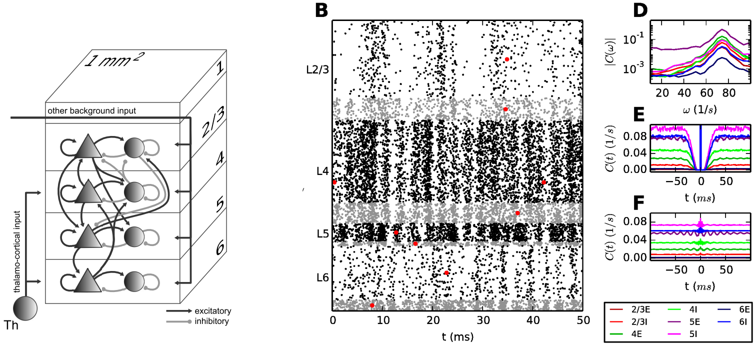
- dynamics evolves in continuous time
- interaction through short electrical pulses (“spikes”)
- contact points: synapses

Structure and dynamics on different spatial scales



scale	I (microscopic)	II (local circuit)	III (multi-area)
connectivity	cell-assemblies	layer-specific	long-range
observable	pairwise correlations	fast oscillations	slow oscillations

Statistics of neuronal activity



Bos et al. 2016 PloS CB

- asynchronous-irregular spiking of neurons
- different measures of statistics:
  - firing rates
  - inter-spike interval statistics
  - correlations between pairs of neurons
- Which measures are informative of computational performance?

Computation at the edge of chaos

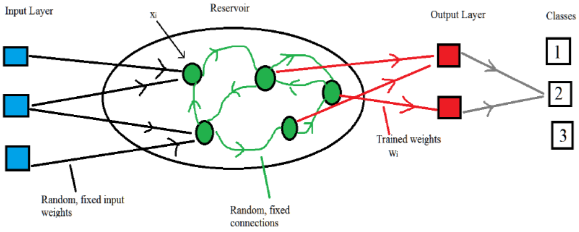


Fig: Malica et al. 2014

- idea of reservoir computing (Maass 2002, Jaeger 2002):

  - recurrently, randomly connected neurons

  - activity produces rich set of basis functions

  - training linear readout alone is sufficient

- edge of chaos (Natschlaeger et al. 2004):

  - binary networks, discrete parallel update

  - optimal computation at transition from regular to chaotic dynamics

Questions

- Is there a transition to chaos in time-continuous externally driven networks?
- Does performance peak at the transition?
- Is the activity statistics compatible with neuronal recordings?

Is there a transition to chaos in time-continuous externally driven networks?

Model definition

- definition of the model

$$\frac{dx_i}{dt} = -x_i + \sum_{j=1}^{N} J_{ij}\varphi(x_j)$$

$$\varphi(x) = \tanh(x), \quad i = 1, \ldots, N \gg 1$$

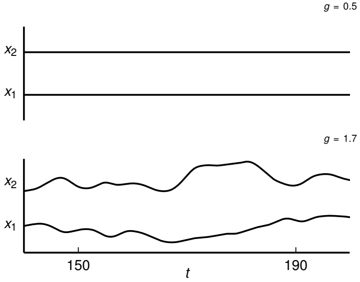
Sompolinsky, Crisanti, Sommer PRL 1988

- simple connectivity structure
  single parameter g:
  Gaussian distributed weights

$$J_{ij} \sim \mathcal{N}(0, g^2/N)$$

- original model:
  - no input signal
  - transition from silence to chaos at $g = 1$
  $\leftrightarrow$ silent fixed point looses stability

(a)



Model definition

- definition of the model

$$\frac{dx_i}{dt} = -x_i + \sum_{j=1}^{N} J_{ij}\varphi(x_j) + \xi_i(t)$$

$$\varphi(x) = \tanh(x), \quad i = 1, \ldots, N \gg 1$$

Goedeke, Schuecker, Helias arXiv 2016

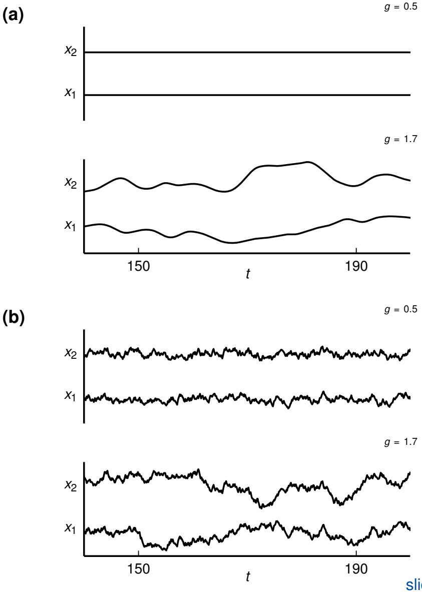
- simple connectivity structure
  single parameter g:
  Gaussian distributed weights

$$J_{ij} \sim \mathcal{N}(0, g^2/N)$$

- unstructured input:
  additive white noise

$$\langle \xi_i(t)\xi_i(s) \rangle = 2\sigma^2 \delta(t-s)$$

- no obvious transition



Generating functional

- definition of the model

$$\frac{dx_i}{dt} = -x_i + \sum_{j=1}^{N} J_{ij}\varphi(x_j) + \xi_i(t)$$

- generating functional (Martin et al. 1973, Janssen 1976, DeDominicis 1978)

$$Z[\mathbf{l}](\mathbf{J}) = \int \mathcal{D}\{\mathbf{x},\tilde{\mathbf{x}}\}\ \exp\left(S_0[\mathbf{x},\tilde{\mathbf{x}}] - \tilde{\mathbf{x}}^{\mathrm{T}}\mathbf{J}\varphi\left(\mathbf{x}\right) + \mathbf{l}^{\mathrm{T}}\mathbf{x}\right)$$

with $S_0[\mathbf{x},\tilde{\mathbf{x}}] = \tilde{\mathbf{x}}^{\mathrm{T}}\left(\partial_t + 1\right)\mathbf{x} + \sigma^2\tilde{\mathbf{x}}^{\mathrm{T}}\tilde{\mathbf{x}}$

Disorder average

- assume self-averaging network properties:
  - quenched randomness in couplings J_{ij}
  - large N limit: expect small variability between realizations

  $\rightarrow$ average $Z(J)$ over J

$$\left\langle \exp\left(\ldots - \tilde{\mathbf{x}}^{\mathrm{T}}\mathbf{J}\varphi\left(\mathbf{x}\right) + \ldots\right)\right\rangle_{J\sim\mathcal{N}(0,N^{-1}g^{2})}$$

$$\bar{Z}[\mathbf{l}] := \langle Z[\mathbf{l}](\mathbf{J})\rangle_{\mathbf{J}} = \int \mathcal{D}\{\mathbf{x},\tilde{\mathbf{x}}\}\,\exp\Big(S_0[\mathbf{x},\tilde{\mathbf{x}}] + \mathbf{l}^{\mathrm{T}}\mathbf{x}\Big)$$

$$\times\,\frac{1}{2}\sum_i \int\int \tilde{x}_i(t)\tilde{x}_i(t')\,\underbrace{\left(\frac{g^2}{N}\sum_j \varphi(x_j(t))\varphi(x_j(t'))\right)}_{\equiv Q_1}\,dt\,dt'$$

Saddle-point approximation

- average generating functional

$$\bar{Z}[\mathbf{l}] := \langle Z[\mathbf{l}](\mathbf{J}) \rangle_{\mathbf{J}} = \int \mathcal{D}\{\mathbf{x}, \tilde{\mathbf{x}}\} \exp\Big(S_0[\mathbf{x}, \tilde{\mathbf{x}}] + \mathbf{l}^{\mathrm{T}} \mathbf{x}$$
$$\times \frac{1}{2} \sum_i \int \int \tilde{x}_i(t) \tilde{x}_i(s) \underbrace{\left(\frac{g^2}{N} \sum_j \varphi(x_j(t)) \varphi(x_j(s)) \right)}_{\equiv Q_1} dt\, ds$$

Saddle-point approximation

- average generating functional

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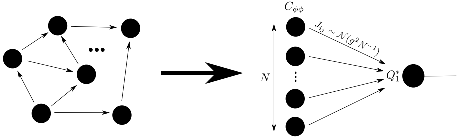
$$\times \frac{1}{2}\sum_i \int\int \tilde{x}_i(t)\tilde{x}_i(s) \underbrace{\left\langle \frac{g^2}{N}\sum_j \varphi(x_j(t))\varphi(x_j(s))\right\rangle}_{\equiv Q_1^*} dt\, ds$$

- decouple 4-point coupling by Hubbard Stratonovich transform
- saddle point approximation in the auxiliary field Q_1
- reduction to single-neuron problem in fluctuating background field ("Hartree-Fock")
- self-consistent statistics

$$\frac{dx}{dt} = -x + \eta(t) + \xi(t).$$
$$\langle \eta(t)\eta(s)\rangle = g^2 \langle \varphi\varphi\rangle(t,s)$$



Self-consistent solution for autocorrelation

- effective equation

$$\frac{dx}{dt} = -x + \eta(t) + \xi(t).$$

$$\langle \eta(t)\eta(s)\rangle = g^2 \langle \varphi\varphi\rangle(t,s)$$

- autocorrelation $c(\tau) = \langle x(t+\tau)x(t)\rangle$

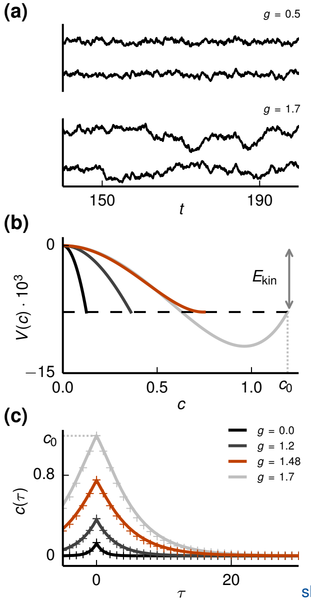
$$\ddot{c}(\tau) = c - g^2\langle\varphi\varphi\rangle(t+\tau,t) - 2\sigma^2\delta(\tau)$$
$$= -V'(c;c_0) - 2\sigma^2\delta(\tau)$$

$\rightarrow$ “Newtonian” equation of motion

- initial “velocity” $\dot{c}(0+) = -\sigma^2$
- c_0 from "energy conservation"

$$\frac{1}{2}\sigma^4 + V(c_0;c_0) = V(0;c_0) = 0$$

- without noise ($\sigma = 0$) model explains self-generated fluctuating activity



Transition to chaos

- replica calculation:
  pair of systems with common noise and slightly different initial conditions
- measure distance at function of time (Derrida & Pommeau 1987)

$$
\begin{aligned}
d(t,t) &= \sum_i \langle [x_i^1(t) - x_i^2(t)]^2 \rangle \\
&= c^{11}(t,t) + c^{22}(t,t) - 2c^{12}(t,t)
\end{aligned}
$$

- idea: maximum Lyapunov exponent $\lambda_{\max}$ related to decay rate of cross-correlation c^{12} between pair of systems
- average of generating functional over coupling matrix and saddle-point approximation (analogous to single system)

$$
\begin{aligned}
(\partial_t + 1)\, x^\alpha(t) &= \xi(t) + \eta^\alpha(t)\,, \quad \alpha \in \{1,2\}\,, \\
\langle \eta^\alpha(s)\, \eta^\beta(t) \rangle &= g^2\, \langle \varphi(x^\alpha(s)) \varphi(x^\beta(t)) \rangle.
\end{aligned}
$$

- two copies coupled by common noise ξ and identical realization of J

Transition to chaos

- consider deviations from fully synchronized state
- expand the cross-correlation around its stationary solution

$$c^{12}(t,s) = c(t-s) + \varepsilon\, k^{(1)}(t,s)$$

- from effective equations derive equation for first order deflection $k^{(1)}(t,s)$
- can be reformulated as Schroedinger equation

$$\left[-\partial_\tau^2 + W(\tau)\right] \psi(\tau) = E\, \psi(\tau),$$

- “ground state energy” E_0 determines the asymptotic growth rate of $k^{(1)}(t,t)$
- Lyapunov exponent

$$\lambda_{\max} = -1 + \sqrt{1 - E_0}$$

- transition to chaos given by ground state with vanishing energy $E_0 = 0$

Transition to chaos

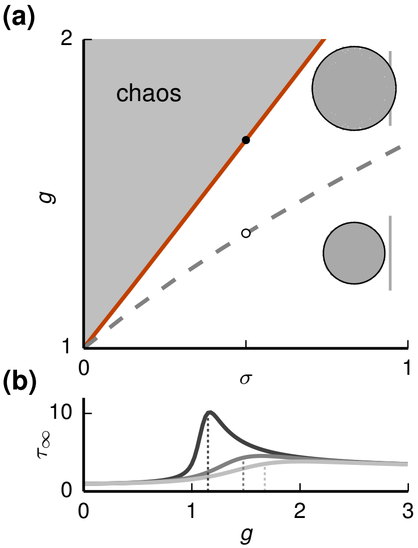
- construct solution from $\dot{c}(\tau)$
- exact condition for transition to chaos

$$g_c^2 \langle \varphi(x)^2 \rangle - c_0 = 0$$

- transition not given by local instability

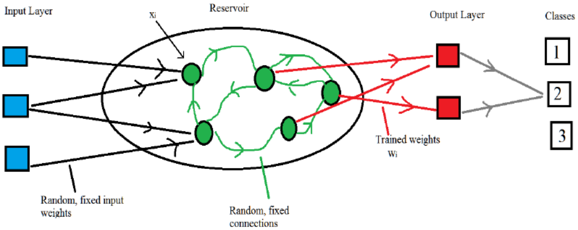
$$g^2 \langle \varphi'(x)^2 \rangle > 1$$

- emergence of **new regime** with
  - locally expanding dynamics
  - asymptotically stable dynamics
- decay time of a.c.f does not diverge at transition
- **Is new regime good for computation?**



Does performance peak at the transition?

Memory capacity



- common stimulus $z(t)$

$$\frac{dx_i}{dt} = -x_i + \sum_{j=1}^{N} J_{ij}\varphi(x_j) + \xi(t) + z(t)$$

- reconstruct $z(t)$ by sparse linear readout $\hat{z}(t) = w^{\mathrm{T}} x(t+\tau)$ at *later* time point $t+\tau$
- memory capacity $M(\tau) = \sup_w 1 - \frac{(z(t)-\hat{z}(t))^2}{\hat{z}^2(t)} \in [0,1]$
  (Dembre et al. 2012)

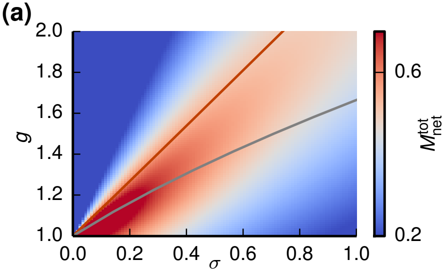
$$M(\tau) = \frac{1}{c_0\langle z^2(t)\rangle} \sum_{i=1}^{N} \langle x_i(t)\, z(t-\tau)\rangle^2$$

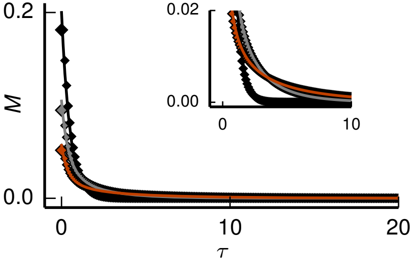
Memory capacity

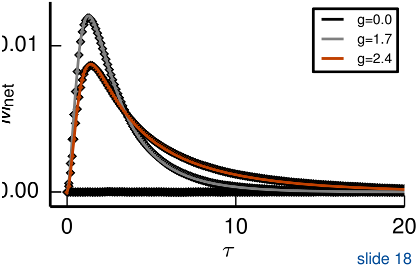
- closed form solution by replica calculation

$$M(\tau) = \frac{1}{c_0} e^{-2\tau} I_0(2g\langle\varphi'\rangle\tau)\,.$$

- memory for larger τ due to synaptic coupling
- decomposition into single neuron and network contribution







Intermediate summary

- activity statistics of large random recurrent driven network accurately predicted by mean-field theory
- transition to chaos exists:
  - at point where autocorrelation has inflection point at $\tau = 0$
- additive input shifts transition to chaos to larger couplings
- emergence of new dynamic regime with:
  - local amplification
  - globally regular dynamics
  - optimal signal memory

Is the activity statistics compatible with neuronal recordings?

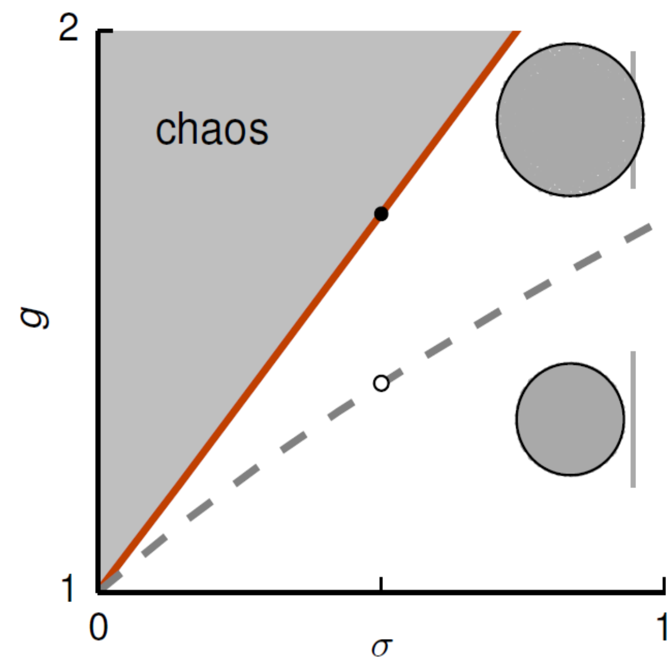
Operational regime of cortical networks

- in which regime are cortical networks operating?
- cannot measure Lyapunov exponent as state of cortical networks cannot be set
- candidate: spectral radius of the connectivity W of the linearized effective dynamics

$$\frac{dx_i}{dt} = -x_i + \sum_{j=1}^{N} J_{ij}\phi(x_j) + \xi_i(t)$$

linearization

$$\frac{dx_i}{dt} = -x_i + \sum_{j=1}^{N} \underbrace{J_{ij}\phi'(x_j^0)}_{W_{ij}} x_j + \xi_i(t)$$



- linear dynamics explains correlation structure in spiking neural networks for asynchronous irregular activity (Grytskyy et al. 2014)
- aim: infer connectivity structure (i.e. the spectral radius) from experimentally observed correlation structure

Linear network dynamics

- time-lag integrated covariances are given by expectation values of zero-frequency Fourier modes (Risken 1996):

$$c_{ij} = \int_{-\infty}^{\infty} c_{ij}(\tau) d\tau = \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} \langle x_i(t+\tau) x_j(t) \rangle_x \, dt \, d\tau = \langle X_i(0) X_j(0) \rangle_x$$

- in linear systems, the generating functional in Fourier domain factorizes into generating functions for each frequency

$$Z[\mathbf{J}] = \det(\mathbf{1} - \mathbf{W}) \int D\mathbf{X} \int D\tilde{\mathbf{X}} \, e^{S(\mathbf{X}, \tilde{\mathbf{X}}) + \mathbf{J}^T \mathbf{X}}$$

  - with action

$$S(\mathbf{X}, \tilde{\mathbf{X}}) = \tilde{\mathbf{X}}^T (-\mathbf{1} + \mathbf{W}) \mathbf{X} + \frac{D}{2} \tilde{\mathbf{X}}^T \tilde{\mathbf{X}}$$

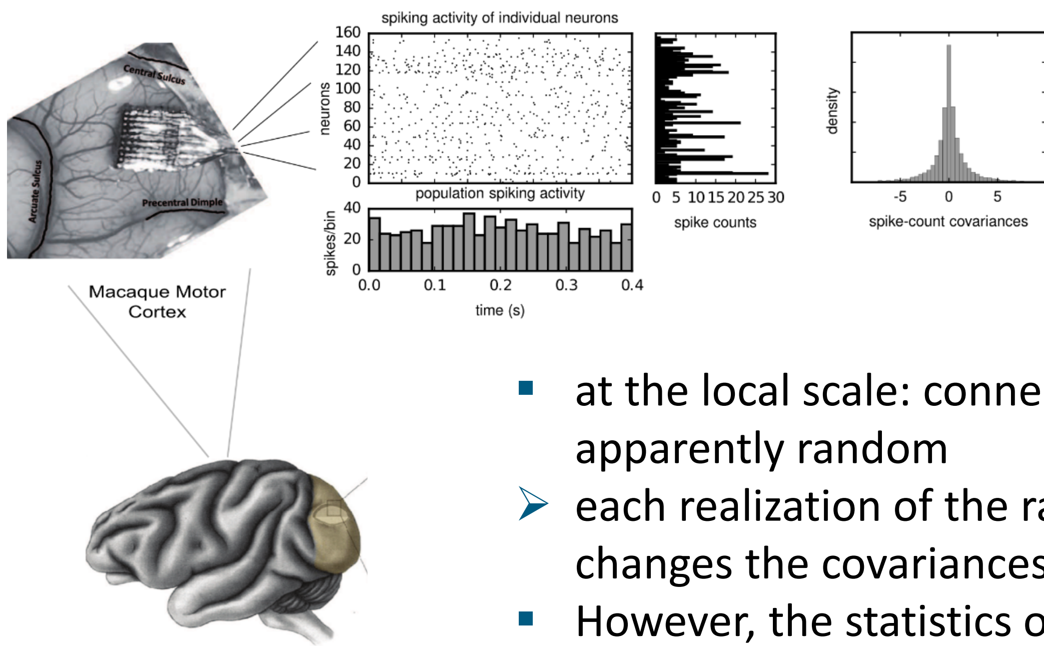
- time-lag integrated covariances given as propagators

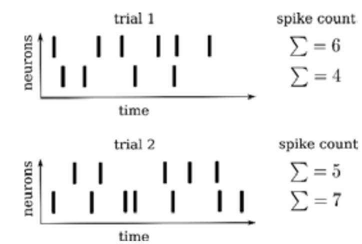
$$c_{ij} = \left[\frac{1}{\mathbf{1} - \mathbf{W}} \mathbf{D} \frac{1}{\mathbf{1} - \mathbf{W}^T} \right]_{ij}$$

Undersampling problem

- relation between covariances between all neurons in the network and all connections
- with present-day recording techniques, there is still a massive undersampling of neural activity

$$c_{ij} = \left[\frac{1}{\mathbf{1}-\mathbf{W}}\,\mathbf{D}\,\frac{1}{\mathbf{1}-\mathbf{W}^T}\right]_{ij}$$

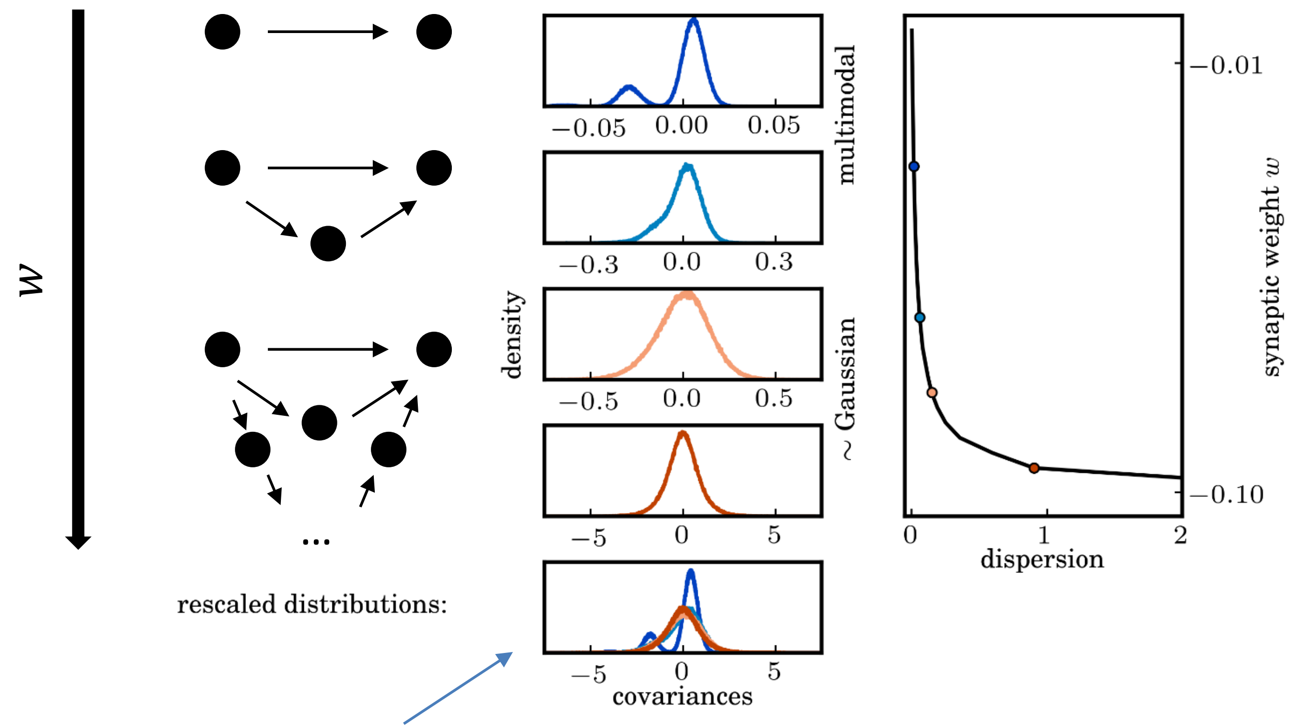




- at the local scale: connections are sparse and look apparently random
- ➢ each realization of the random connectivity matrix changes the covariances between individual neurons
- However, the statistics of covariances can be assumed to be <u>self-averaging</u>

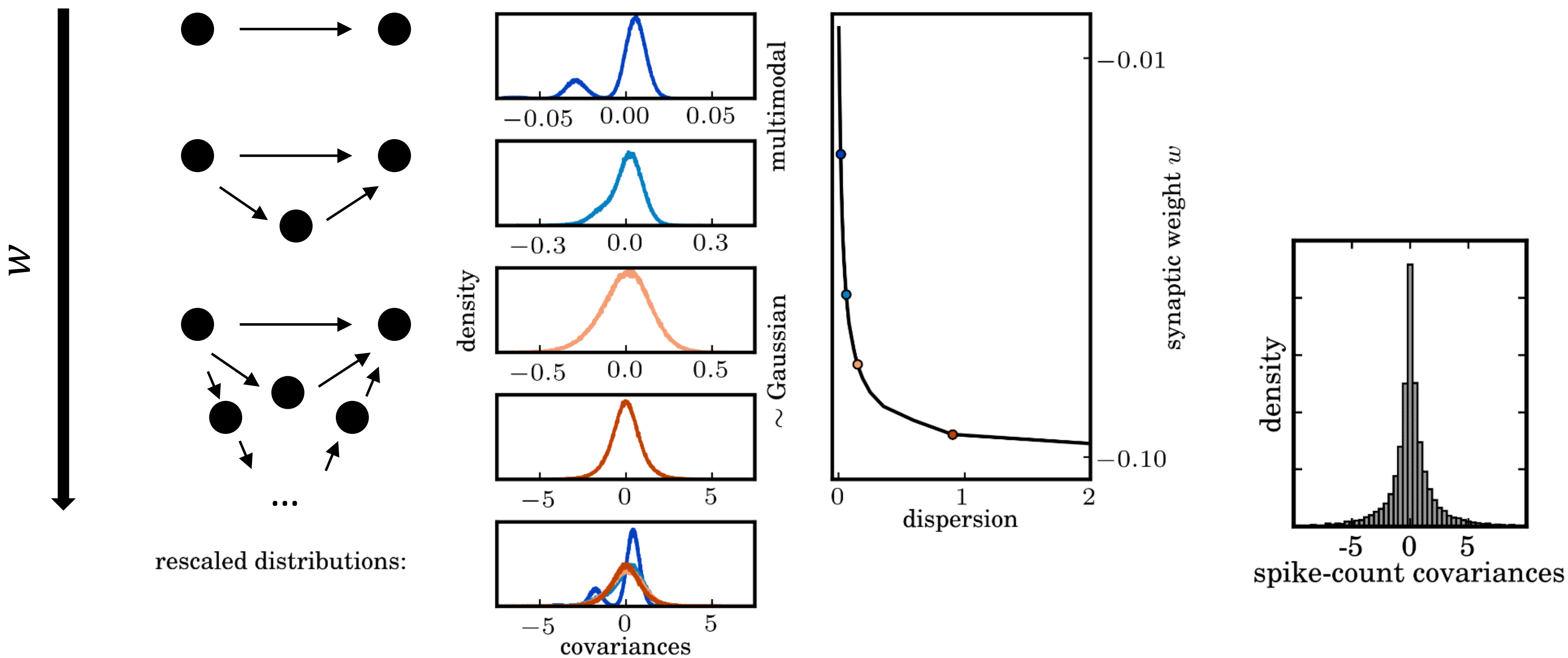
Distribution of covariances

- sparse random networks: spectral radius determined by variance of entries in **W**
- variance in W determined by synaptic weight *w*
- ➢ the larger the synaptic weight, the larger the spectral radius



- rescaled: not distinguishable by shape for intermediate to strong couplings
- distributions always centred around ≈ 0
- ➢ distinguish by <u>width of distribution</u>

Hypothesis



- effective connection strength/spectral radius close to critical value
  - activity propagates over several synapses
  - activity effectively distributed through the network via various parallel paths

Quantitative test

- need relation between statistics of correlations and statistics of connections
- calculate disorder-averaged generating function

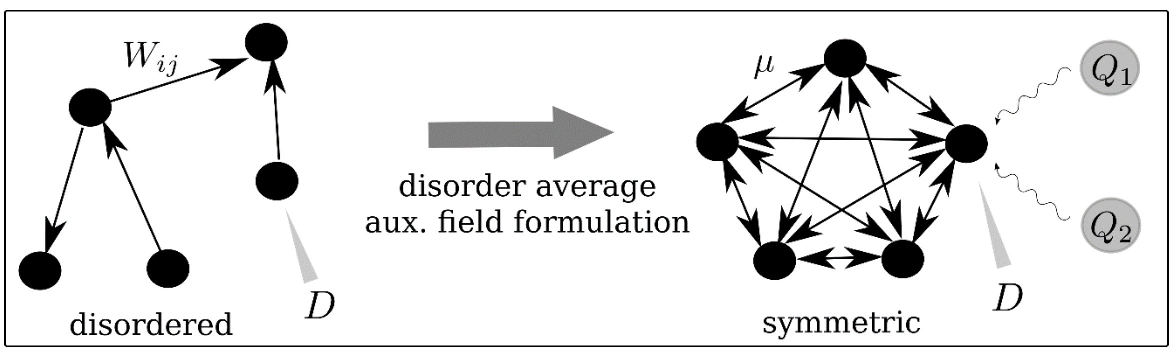
$$\langle Z[\mathbf{J}]\rangle \sim \int D\mathbf{X} \int D\tilde{\mathbf{X}}\, e^{S_0(\mathbf{X},\tilde{\mathbf{X}})+S_{\mathrm{int}}(\mathbf{X},\tilde{\mathbf{X}})+\mathbf{J}^T\mathbf{X}}$$

$$S_0(\mathbf{X},\tilde{\mathbf{X}}) = \tilde{\mathbf{X}}^T\left(-\mathbf{1}+\mu\{1\}\right)\mathbf{X} + \frac{D}{2}\tilde{\mathbf{X}}^T\tilde{\mathbf{X}}$$

$$S_{\mathrm{int}}(\mathbf{X},\tilde{\mathbf{X}}) = \frac{\sigma^2}{2N}\tilde{\mathbf{X}}^T\tilde{\mathbf{X}}\,\mathbf{X}^T\mathbf{X}.$$

- Hubbard-Stratonovich transformation: auxiliary field formulation

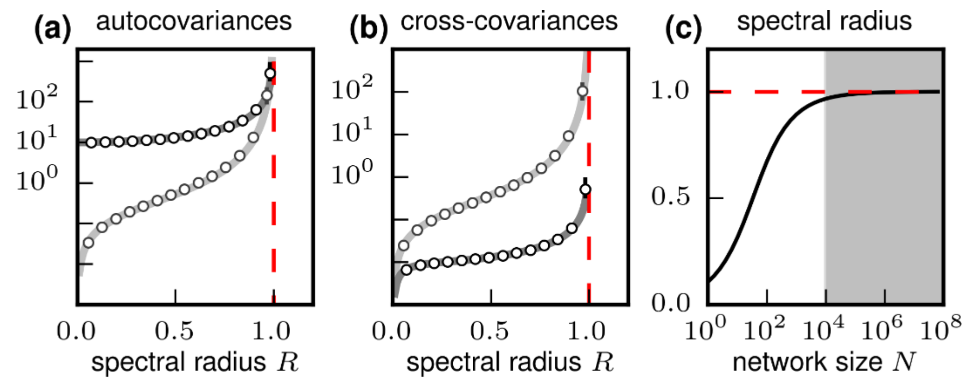
$$e^{S_{\mathrm{int}}(\mathbf{X},\tilde{\mathbf{X}})} \sim \int D\mathbf{Q}\; e^{-\frac{N}{\sigma^2}Q_2Q_1+\frac{1}{2}Q_1\tilde{\mathbf{X}}^T\tilde{\mathbf{X}}+Q_2\mathbf{X}^T\mathbf{X}}$$



Mean-field theory beyond self-averaging

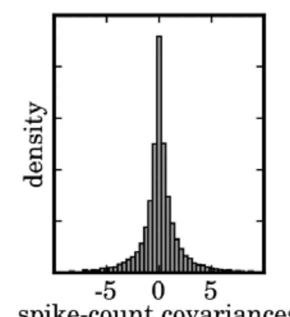
- moments of the distribution of covariances can be obtained from two- and four-point correlators of the disorder-averaged generating function

➢ extract distribution of covariances from auxiliary field fluctuations



- relation between the (normalized) width of the distribution of covariance and the spectral radius

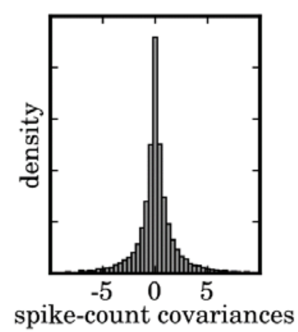
$$R^2 = 1 - \sqrt{\frac{1}{1 + N\frac{\overline{\delta c_{ij}^2}}{\overline{c_{ii}}^2}}}$$

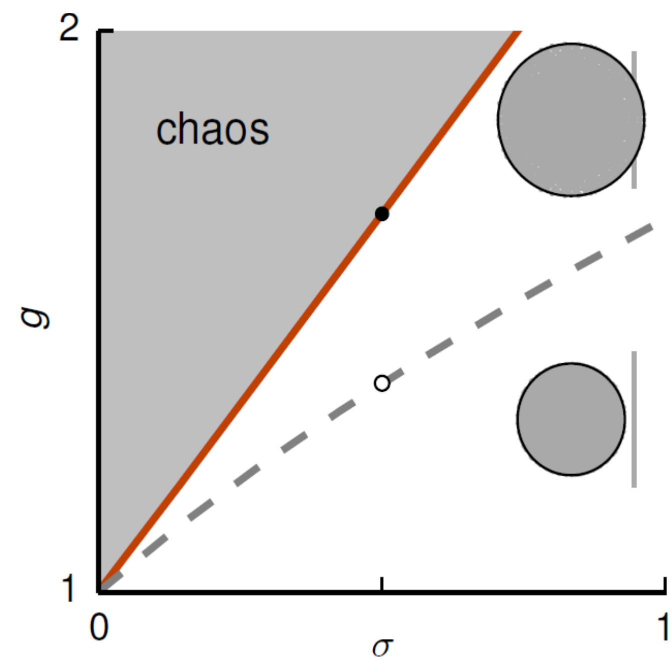


Cortex operates close to regime of optimal performance

- data from macaque motor cortex suggests operation close to breakdown of linear stability
- functional relevance: individual connections are strong enough to propagate information over multiple synaptic steps to allow complex processing, mixing and integration of information of various sources
- complex activity patterns are strengthened

$$R^2 = 1 - \sqrt{\frac{1}{1 + N\frac{\overline{\delta c_{ij}^2}}{\overline{c_{ii}}^2}}}$$





Contributors & Acknowledgements

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Summary

- mean-field theory of large random recurrent driven network
- emergence of new dynamic regime with:
  - local amplification
  - globally regular dynamics
  - optimal signal memory
  - wide distribution of correlations
- cortical data support operation close to critical point of optmial memory

Supplementary slides

Decoupling of 4-point interaction

- average generating functional

$$\bar{Z}[\mathbf{l}] := \langle Z[\mathbf{l}](\mathbf{J})\rangle_{\mathbf{J}} = \int \mathcal{D}\{\mathbf{x},\tilde{\mathbf{x}}\}\,\exp\Big(S_0[\mathbf{x},\tilde{\mathbf{x}}] + \mathbf{l}^{\mathrm{T}}\mathbf{x}\Big)$$

$$\times\,\frac{1}{2}\sum_i \int\int \tilde{x}_i(t)\tilde{x}_i(t')\,\underbrace{\left(\frac{g^2}{N}\sum_j \varphi(x_j(t))\varphi(x_j(t'))\right)}_{\equiv Q_1}\,dt\,dt'$$

- decouple 4-point coupling by Hubbard Stratonovich transform
- field theory in the auxiliary fields Q_1 and conjugate field Q_2

$$\bar{Z}[j,\tilde{j}] = \int \mathcal{D}\{Q_1,Q_2\}\,\exp\left(-\frac{N}{g^2}Q_1^{\mathrm{T}}Q_2 + N\,\ln\,Z[Q_1,Q_2] + j^{\mathrm{T}}Q_1 + \tilde{j}^{\mathrm{T}}Q_2\right)$$

$$Z[Q_1,Q_2] = \int \mathcal{D}\{\mathbf{x},\tilde{\mathbf{x}}\}\,\exp\left(S_0[x,\tilde{x}] + \frac{1}{2}\tilde{x}^{\mathrm{T}}Q_1\tilde{x} + \varphi(x)^{\mathrm{T}}Q_2\varphi(x)\right)$$

- single-neuron problem in fluctuating background field

Saddle-point approximation for auxiliary fields

- saddle-point approximation for auxiliary fields $0 = \frac{\delta S[Q_1,Q_2]}{\delta Q_{\{1,2\}}}$

$$Q_1^*(s,t) = g^2 \langle \varphi(x(s))\varphi(x(t))\rangle_{Q^*} =: g^2\langle\varphi\varphi\rangle(t,s) \qquad Q_2^*(s,t) = 0$$

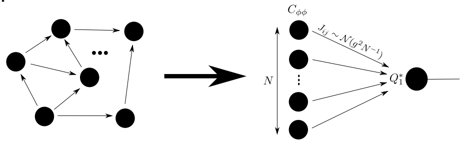
- Generating functional at saddle node solution

$$\bar{Z}^* \propto \int \mathcal{D}x \int \mathcal{D}\tilde{x} \, \exp\left(S_0[x,\tilde{x}] + \frac{g^2}{2}\tilde{x}^{\mathrm{T}}\langle\varphi\varphi\rangle\tilde{x}\right).$$

- Gaussian noise with correlation function $\langle\varphi\varphi\rangle(t,s)$
- corresponds to off effective equation

$$\frac{dx}{dt} = -x + \eta(t) + \xi(t).$$

$$\langle\eta(t)\eta(s)\rangle = g^2\langle\varphi\varphi\rangle(t,s)$$



Saddle-point approximation for auxiliary fields

- vertex function

$$\Gamma(q_1, q_2) := \sup_{j,\tilde{j}} \, j^{\mathrm{T}} q_1 + \tilde{j}^{\mathrm{T}} q_2 - \ln \bar{Z}[j, \tilde{j}]$$

- equation of state for lowest order mean-field $\Gamma[q_1, q_2] \simeq -S[q_1, q_2]$,

$$0 = \frac{\delta S[Q_1, Q_2]}{\delta Q_{\{1,2\}}}$$

- saddle-point solution for auxiliary fields

$$Q_1^*(s,t) = g^2 \, \langle \varphi(x(s)) \varphi(x(t)) \rangle_{Q^*} =: g^2 C_{\varphi(x)\varphi(x)}(s,t)$$
$$Q_2^*(s,t) = 0$$

- Generating functional at saddle node solution

$$\bar{Z}^* \propto \int \mathcal{D}x \int \mathcal{D}\tilde{x} \, \exp\left(S_0[x, \tilde{x}] + \frac{g^2}{2} \tilde{x}^{\mathrm{T}} C_{\varphi(x)\varphi(x)} \tilde{x} \right).$$

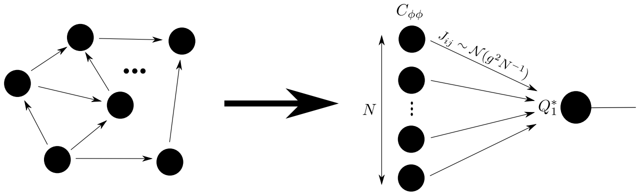
Effective dynamical mean-field equation

- generating functional with saddle node solutions

$$\bar{Z}^* \propto \int \mathcal{D}x \int \mathcal{D}\tilde{x} \, \exp\left(S_0[x,\tilde{x}] + \frac{g^2}{2}\tilde{x}^{\mathrm{T}} C_{\varphi(x)\varphi(x)} \tilde{x}\right).$$

- Gaussian noise with correlation function $C_{\varphi(x)\varphi(x)}(s,t)$
- read off effective equation

$$\frac{dx}{dt} = -x + \eta(t) + \xi(t).$$
$$\langle \eta(t)\eta(s) \rangle = g^2 C_{\varphi(x)\varphi(x)}(t,s)$$



Memory capacity

- capacity to reconstruct past input from the current network state

$$M(\tau) = \frac{1}{c_0 \langle z^2(t) \rangle} \sum_{i=1}^{N} \langle x_i(t)\, z(t-\tau) \rangle^2$$

- consider pair of system with independent noise and common input

$$Z[\{\mathbf{l}^\alpha\}_{\alpha\in\{1,2\}}](\mathbf{J}) = \Pi_{\alpha=1}^{2} \Big\{ \int \mathcal{D}\mathbf{x}^\alpha \int \mathcal{D}\tilde{\mathbf{x}}^\alpha \, \exp\left(S_0[\mathbf{x}^\alpha, \tilde{\mathbf{x}}^\alpha] - \tilde{\mathbf{x}}^{\alpha\mathrm{T}} \mathbf{J} \varphi\left(\mathbf{x}^\alpha\right) + \mathbf{l}^{\alpha\mathrm{T}} \mathbf{x}^\alpha \right)$$

$$\times \exp\left(\sum_{k,l} \int \varepsilon(t)\, \tilde{x}_k^1(t)\, \tilde{x}_l^2(t)\, dt \right)$$

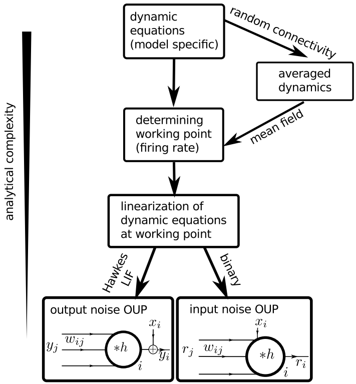
- idea: $\langle x_i(t)\, z(t-\tau) \rangle^2$ related to cross-correlation c^{12} between pair of systems, which obeys

$$(\partial_t + 1)\, (\partial_s + 1)\; c^{12}(t,s) - g^2 \langle \varphi'(x) \rangle^2\, c^{12}(t,s) = \delta(t)\, \delta(s),$$

- explicit solution for memory curve

$$M(\tau) = \frac{1}{c_0} e^{-2\tau} I_0(2g\langle \varphi' \rangle \tau)\,.$$

Two step reduction of recurrent (LIF) networks



Grytskyy D, Tetzlaff T, Diesmann M and Helias M (2013)
A unified view on weakly correlated recurrent networks.
Front. Comput. Neurosci. 7:131.

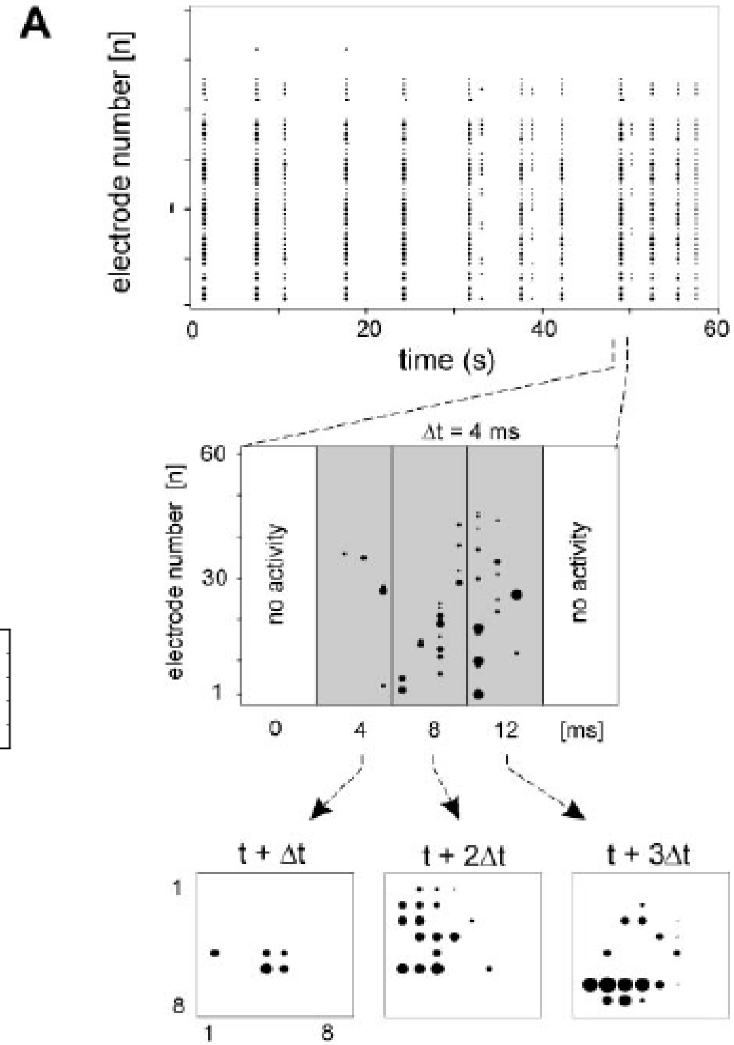
- step 1: mean firing rates
  $\langle s \rangle = \nu = \varphi(\nu)$
- step 2: fluctuations
  $y_i(t) = s_i(t) - \nu_i$

$$y_i(t) = \sum_k [h_{ik} * y_k](t) + \xi_i(t)$$

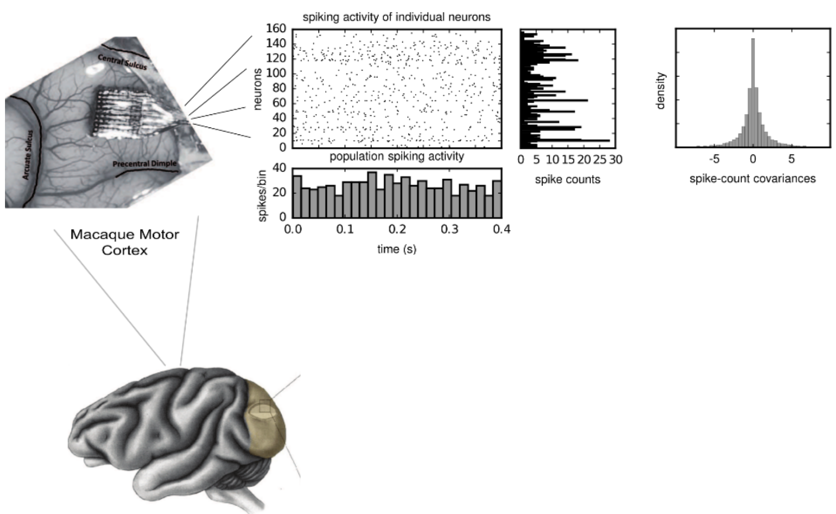
- equivalent covariances for:
  - linear approx. of influence
  - Dirac-δ autocorrelation
- holds for several model classes
- differ in location of noise

Criticality in neuroscience

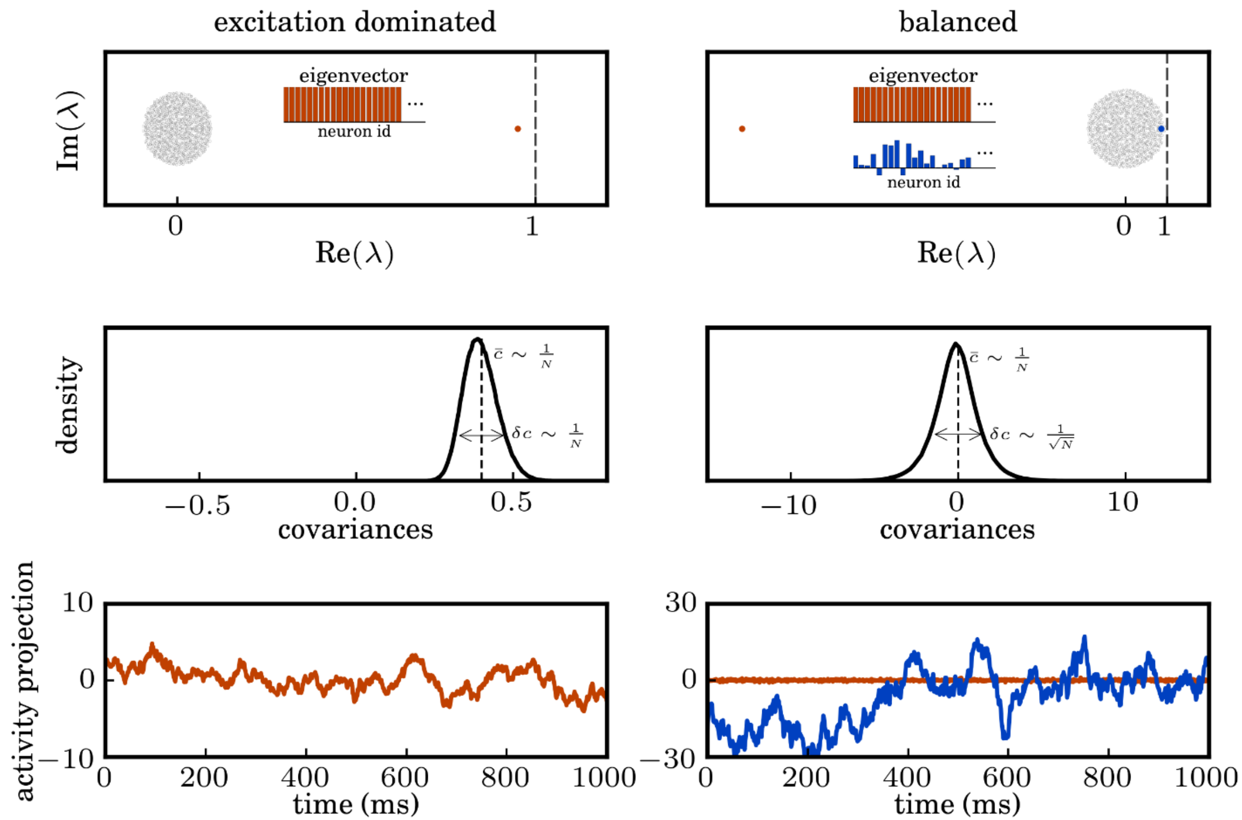
- criticality has been observed in experimental data with different dynamics:
  - “neural avalanches”
- this type of dynamics arises in excitation-dominated networks
- however, motor cortex data suggest balanced between excitation and inhibition



Beggs and Plenz (2003)



Two types of criticality



- so far studied criticality: visible on population level, because population mode unstable
  - large, global fluctuations
- criticality found in the data:
  - complex combination of activations of neurons