Neural circuits for cognition

MIT 9.49/9.490/6.S076

Instructor: Professor Ila Fiete
TA: Gregg Heller
Senior Instruction Assistant: Adnan Rebei

Potential signatures and uses of E-I balanced/near-chaotic networks

- **Variance found:** solution to problem of explaining source of variance in large networks in balanced non-normal nets.
- **Mean subtraction/dynamic range extension** in balanced networks.
- **High temporal precision** responses to inputs.

TODAY
- **Fast amplification in sensory systems.** Murphy and Miller 2009; Hennequin, Vogels, Gerstner 2012
- Reservoir computing/Liquid State Machines: generating rich spatiotemporal dynamics for use as temporal basis functions for learning sequences for motor control, other tasks. Kirby 1991; Maass & Markram 2002; Sussillo and Abbott 2009
- Efficient coding by prediction. S. Deneve
- EI balance disfunction and human disease: hypothesized in autism, mental retardation, epilepsy, schizophrenia, Alzheimer's disease. Eichler & Meier 2008
- Hard to harness for memory/persistent states.

Fast amplification in non-normal networks

Murphy & Miller, 2009

What is a non-normal matrix?

- Matrices that are *not* normal.
- Normal matrix: same left and right eigenvector. Equivalently, a matrix A is normal if and only if there exists a diagonal matrix Λ and a unitary matrix Q such that $A = Q\Lambda Q^*$. (Q is the matrix of eigenvectors; when real matrices, then unitary → orthogonal. Q*=transpose conjugate.)
- Symmetric matrices and some others are normal:

Real	Complex
Diagonal	Diagonal
Symmetric	Hermitian
Skew-symmetric	Skew-Hermitian
Orthogonal	Unitary
Circulant	Circulant

- When left and right eigenvectors are not the same (equivalently, the matrix is not diagnonalizable by an orthogonal transformation), the matrix is non-normal.
- Typically (but not always), asymmetric matrices are non-normal: the left and right eigenvectors are usually not the same.
- Matrices can have “degrees” of non-normality that can be quantified: how much they deviate from being normal. (e.g. Elsner & Paardekooper 1987)

Diagonalization replaced by triangularization

Normal matrices are guaranteed to be *diagonalizable* by a unitary (orthogonal) matrix transformation.

For any normal square matrix A, there always exists a diagonal matrix Λ and a unitary matrix Q such that

$A = Q \Lambda Q^*$

Schur: *All matrices (and thus non-normal matrices too)* are guaranteed to be triangularizable by a unitary (orthogonal) matrix transformation.

For any square matrix A, there always exists an upper triangular matrix U and a unitary matrix Q such that

$A = QUQ^*$

$$U = \begin{bmatrix} u_{1,1} & u_{1,2} & u_{1,3} & \cdots & u_{1,n} \\ & u_{2,2} & u_{2,3} & \cdots & u_{2,n} \\ & & \ddots & \ddots & \vdots \\ & & & \ddots & u_{n-1,n} \\ 0 & & & & u_{n,n} \end{bmatrix}$$

Diagonalization replaced by triangularization

Normal matrices are guaranteed to be *diagonalizable* by a unitary (orthogonal) matrix transformation.

For any normal square matrix A, there always exists a diagonal matrix Λ and a unitary matrix Q such that

$A = Q \Lambda Q^*$

The diagonal form allowed us to replace one system with N coupled variables into N systems with one variable each, uncoupled

Schur: *All matrices (and thus non-normal matrices too)* are guaranteed to be triangularizable by a unitary (orthogonal) matrix transformation.

For any square matrix A, there always exists an upper triangular matrix U and a unitary matrix Q such that

$A = QUQ^*$

$$U = \begin{bmatrix} u_{1,1} & u_{1,2} & u_{1,3} & \cdots & u_{1,n} \\ & u_{2,2} & u_{2,3} & \cdots & u_{2,n} \\ & & \ddots & \ddots & \vdots \\ & & & \ddots & u_{n-1,n} \\ 0 & & & & u_{n,n} \end{bmatrix}$$

Diagonalization replaced by triangularization

Normal matrices are guaranteed to be *diagonalizable* by a unitary (orthogonal) matrix transformation.

For any normal square matrix A, there always exists a diagonal matrix Λ and a unitary matrix Q such that

$A = Q \Lambda Q^*$

The diagonal form allowed us to replace one system with N coupled variables into N systems with one variable each, only self-interactions

Schur: *All matrices (and thus non-normal matrices too)* are guaranteed to be triangularizable by a unitary (orthogonal) matrix transformation.

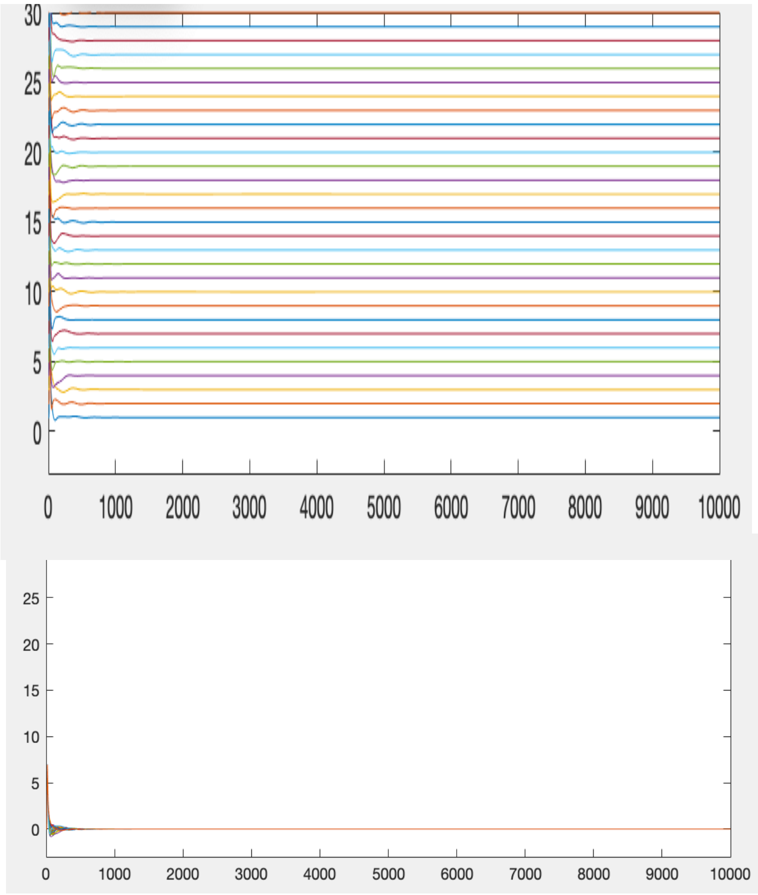
For any square matrix A, there always exists a upper triangular matrix U and a unitary matrix Q such that

$A = QUQ^*$

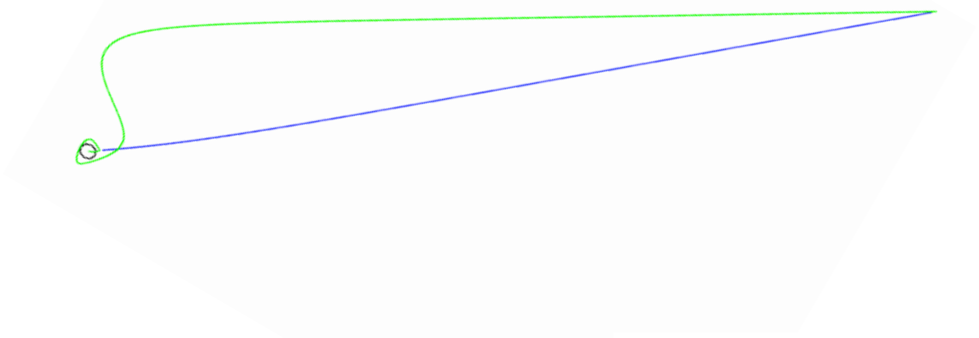
$$U = \begin{bmatrix} u_{1,1} & u_{1,2} & u_{1,3} & \cdots & u_{1,n} \\ & u_{2,2} & u_{2,3} & \cdots & u_{2,n} \\ & & \ddots & \ddots & \vdots \\ & & & \ddots & u_{n-1,n} \\ 0 & & & & u_{n,n} \end{bmatrix}$$

An upper-triangular coupling matrix reveals a feedforward system: Last element interacts only with itself; it is input into (n-1)th and all other elements; (n-1)th element takes this input, couples with itself, feeds into (n-2)th and all other elements....

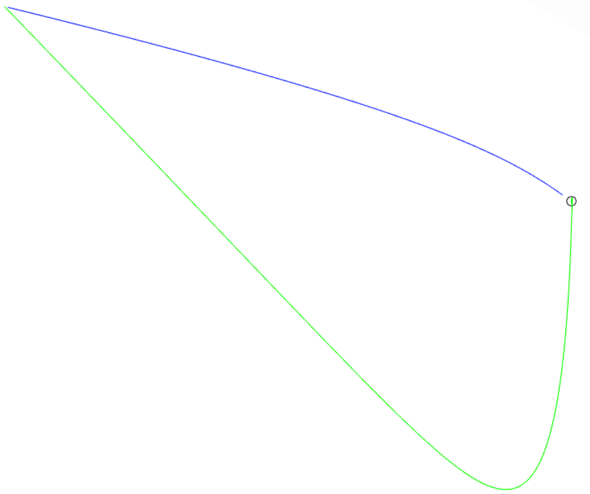
Synaptic scaling parameter g near 1



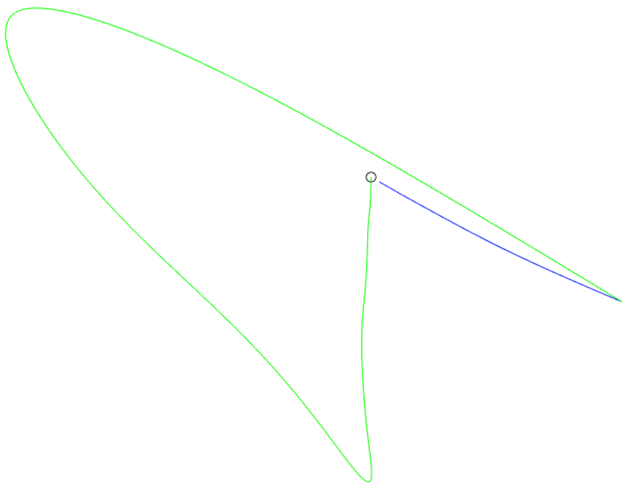
g = 0.98; n = 512



Random 2-D projection of N-D dynamics



PC1, PC2



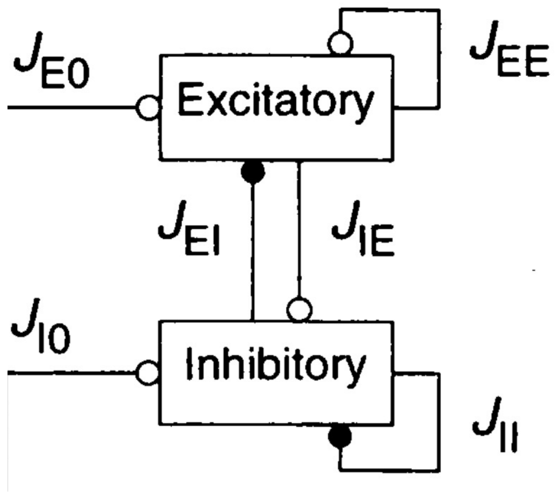
PC2, PC3

E-I balanced networks

$$\mathbf{W} = \begin{pmatrix} \mathbf{W}_{EE} & \mathbf{W}_{EI} \\ \mathbf{W}_{IE} & \mathbf{W}_{II} \end{pmatrix}$$

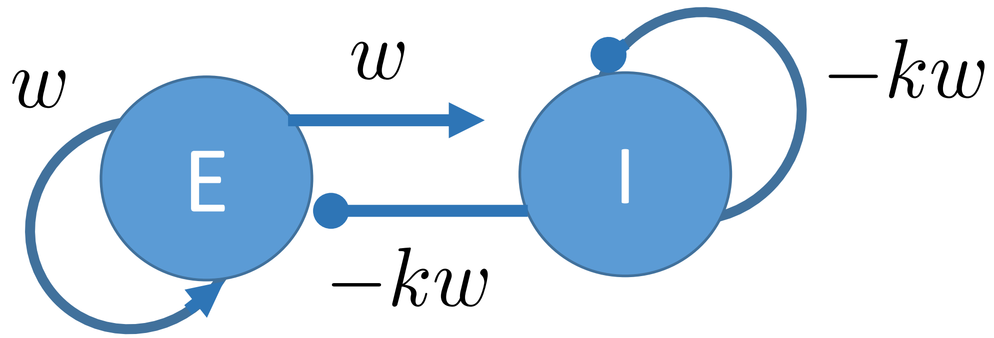
Non-negative Non-positive

→ non-normal



Simplest example

$$\tau \frac{d\delta \mathbf{s}}{dt} = -\delta \mathbf{s} + \mathbf{W}\delta \mathbf{s}$$



$$\mathbf{W} = \begin{pmatrix} w & -kw \\ w & -kw \end{pmatrix}$$

$$w, k > 0$$
$$k \geq 1$$

Inhibition balances (k=1) or dominates (k>1) over excitation

Eigenvalues

$$\mathbf{W} = \begin{pmatrix} w & -kw \\ w & -kw \end{pmatrix}$$

Eigenvalues: $\det(\mathbf{W} - \lambda \mathbb{I}) = 0$

$$(w - \lambda)(-kw - \lambda) + kw^2 = 0$$

$$\lambda = 0, \quad \lambda = w(1-k) \leq 0 \text{ since } k \geq 1$$

Both eigenvalues are <=0 (in addition to decay term) so system stable.
Also, not amplifying in conventional (symmetric matrix) sense.

(right) Eigenvectors

$$\mathbf{v} = \begin{pmatrix} 1 \\ 1/k \end{pmatrix} \qquad \lambda = 0,$$

$$\mathbf{v} = \begin{pmatrix} 1 \\ 1 \end{pmatrix} \qquad \lambda = w(1-k)$$

*Linearly independent but **not** orthogonal; nearly aligned as k→1*

Response to perturbations

Define $\delta \mathbf{s}^+ = \delta \begin{pmatrix} 1 \\ 1 \end{pmatrix}$

Common-mode perturbation, one of the eigenvectors

$$W\delta \mathbf{s}^+ = w(1-k)\delta \mathbf{s}^+ \leq 0$$

Zero or negative feedback; common-mode perturbation rapidly decays

Define $\delta \mathbf{s}^- = \delta \begin{pmatrix} 1 \\ -1 \end{pmatrix}$

Difference-mode perturbation

$$W\delta \mathbf{s}^- = w(1+k)\delta \mathbf{s}^+$$

Difference-mode perturbation can induce large change in common mode if k, w large

Small changes in difference between E, I can drive large changes in their sum.

$\delta \mathbf{s}^-$, $\delta \mathbf{s}^+$orthogonal (but $\delta \mathbf{s}^-$ not an eigenvector), can be used as a basis.

Decomposition into a feedforward system

$$\tau \frac{d\delta \mathbf{s}}{dt} = -\delta \mathbf{s} + \mathbf{W} \delta \mathbf{s}$$

Write any $\delta \mathbf{s} = \begin{pmatrix} \delta s_E \\ \delta s_I \end{pmatrix} = c_+ \delta \mathbf{s}^+ + c_- \delta \mathbf{s}^-$ where $c_+ = \frac{1}{2}(\delta s_E + \delta s_I), c_- = \frac{1}{2}(\delta s_E - \delta s_I)$

$$\delta \mathbf{s}^{-T} \tau \frac{d\delta \mathbf{s}}{dt} = \delta \mathbf{s}^{-T}(-\delta \mathbf{s} + W \delta \mathbf{s})$$

$$\tau \frac{dc_-}{dt} = -c_-$$

$$\delta \mathbf{s}^{+T} \tau \frac{d\delta \mathbf{s}}{dt} = \delta \mathbf{s}^{+T}(-\delta \mathbf{s} + W \delta \mathbf{s})$$

$$\tau \frac{dc_+}{dt} = -c_+ + w(1-k)c_+ + w(1+k)c_-$$

Interpretation: The – mode is simply decaying without any input from the + mode. However, the – mode feeds into the + mode, providing a feedforward drive to it. And the + model also feeds into itself. Effectively a feedforward circuit between modes, with some feedback within modes.

Decomposition into a feedforward system

$$\tau \frac{dc_-}{dt} = -c_-$$

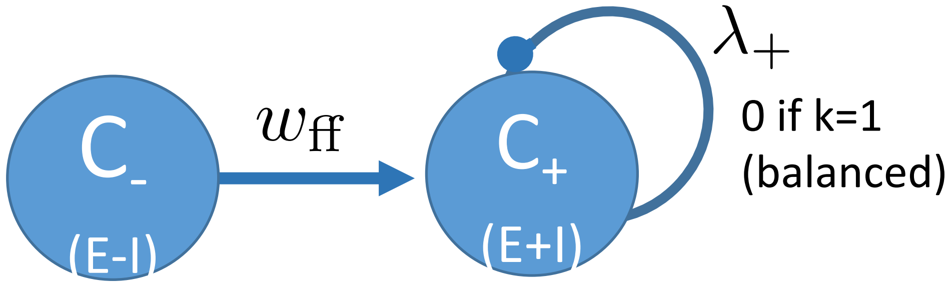
timescale τ

$$\tau \frac{dc_+}{dt} = -c_+ + \lambda_+ c_+ + w_{\text{ff}} c_-$$

timescale ≤ τ

$$\frac{\tau}{1-\lambda_+} = \frac{\tau}{1+2(k-1)} \leq \tau$$

$w(1-k) \leq 0$ $\quad$ $w(1+k) > 0$



Total network amplification of any input to differential mode: $$\frac{w_{\text{ff}}}{1-\lambda_+} = \frac{w(1+k)}{1-w(1-k)} \approx 2w$$ when k ≈ 1

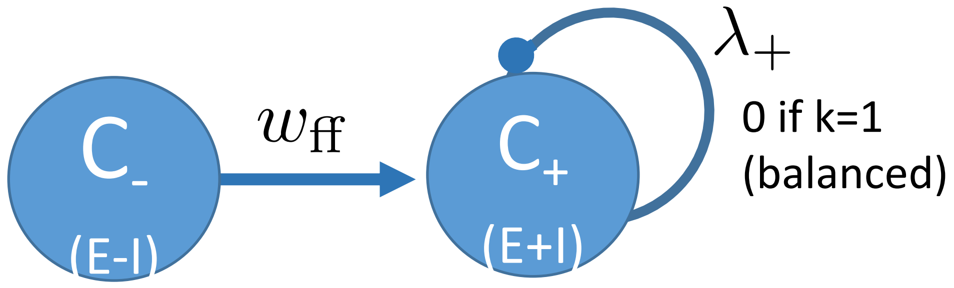
Amplification can be large if w large! But no slowdown in timescale.

Decomposition into a feedforward system

$$\tau \frac{dc_-}{dt} = -c_-$$

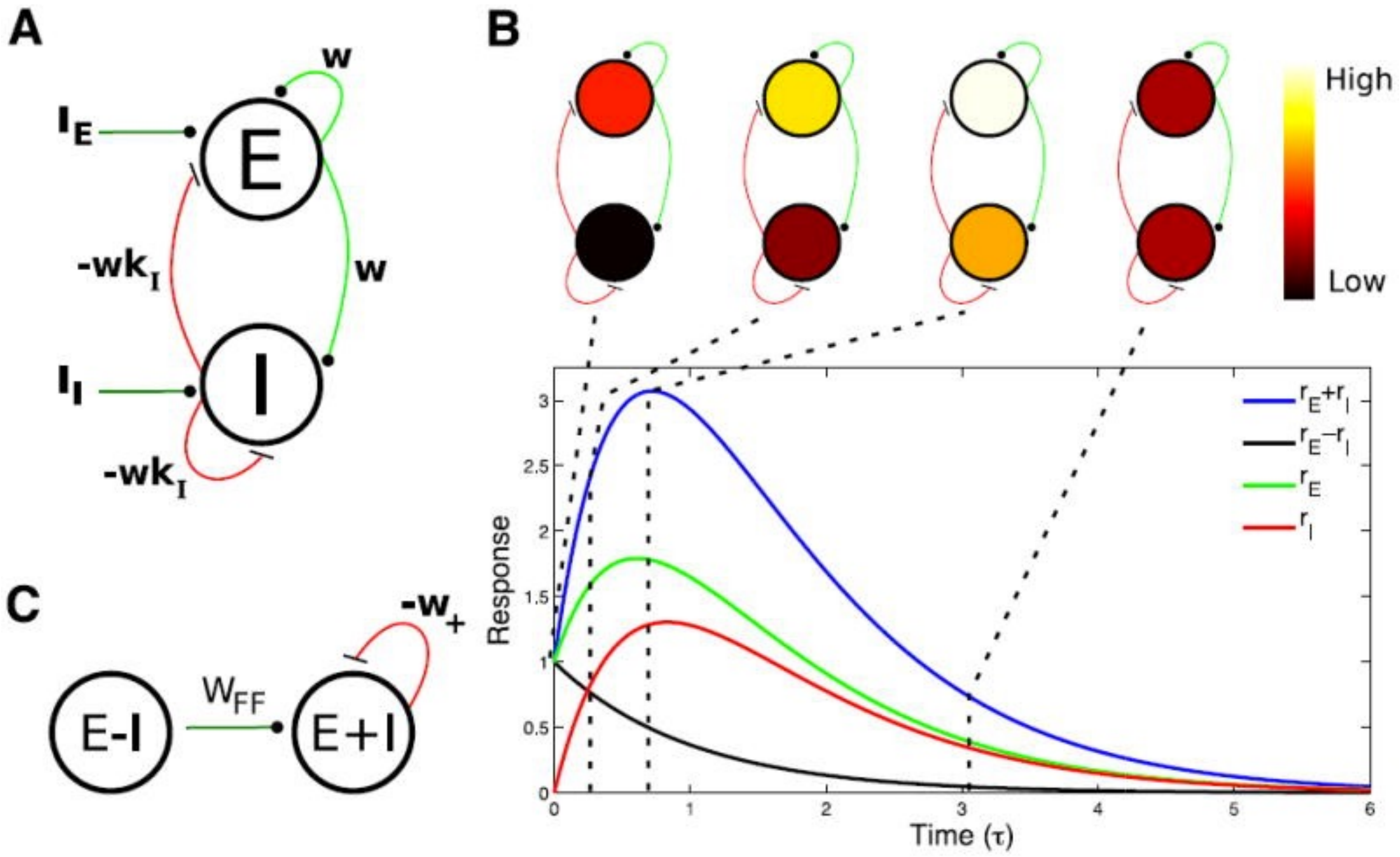
$$\tau \frac{dc_+}{dt} = -c_+ + \lambda_+ c_+ + w_{\mathrm{ff}} c_-$$

$w(1-k) \leq 0$ $\qquad$ $w(1+k) > 0$

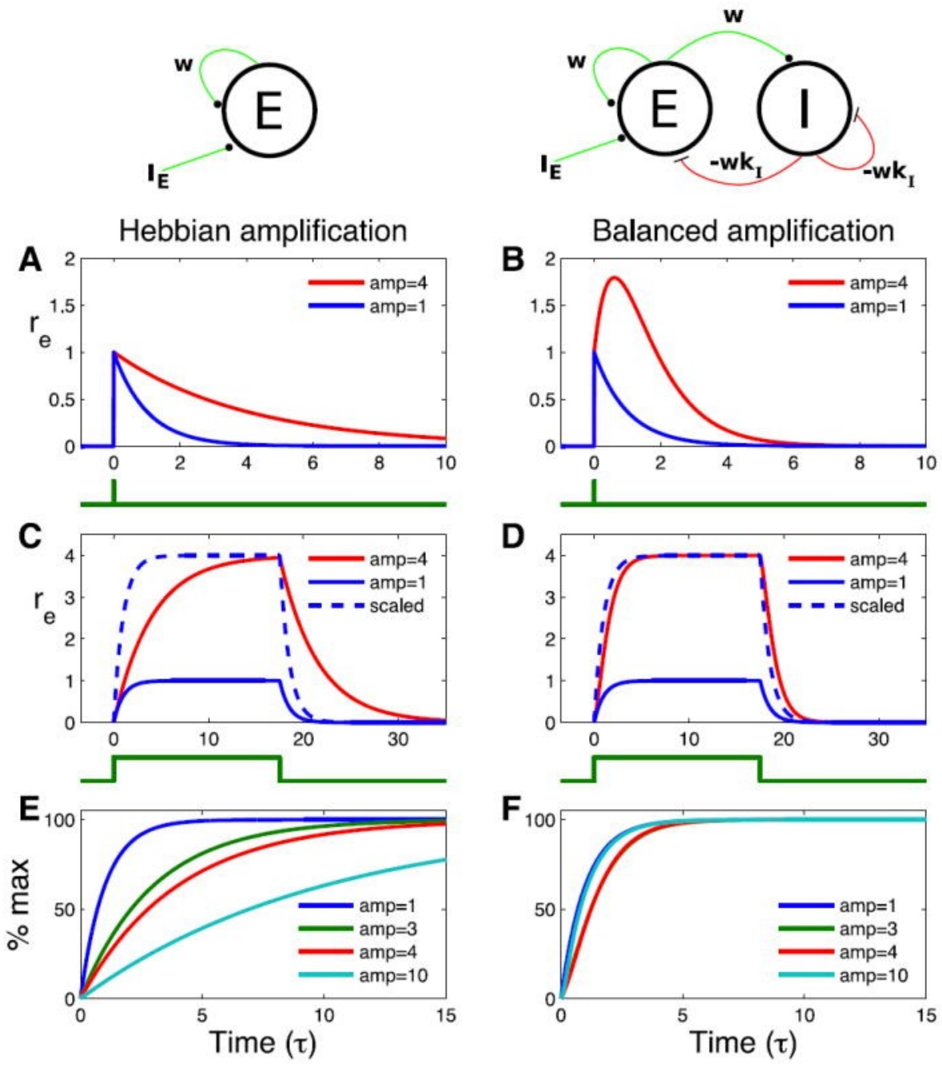


- Small change in c_ is fed into c_+ with strong amplification, driving large changes in c_+
- While c_+ gets large, c_ is decaying to rest and the drive to c_+ is decreasing
- In addition, negative feedback from c_+ to itself also restores c_+ to its resting state
- In all: large transient growth in c_+ followed by return to rest

Transient amplifying modes and activity in the 2-cell non-normal network



Comparison of response speed: normal vs non-normal amplification in linear network



Normal weights Non-normal weights

High amplification: when k is large (inhibition-dominated rather than balanced regime)

Schur decomposition of non-normal matrices

A (non-unique) orthonormal basis that converts any square non-normal matrix into diagonal and upper-triangular form.

$$A \in \mathbf{C}^{n \times n}$$

Arbitrary nxn complex-valued matrix

$$A = QUQ^{-1}$$

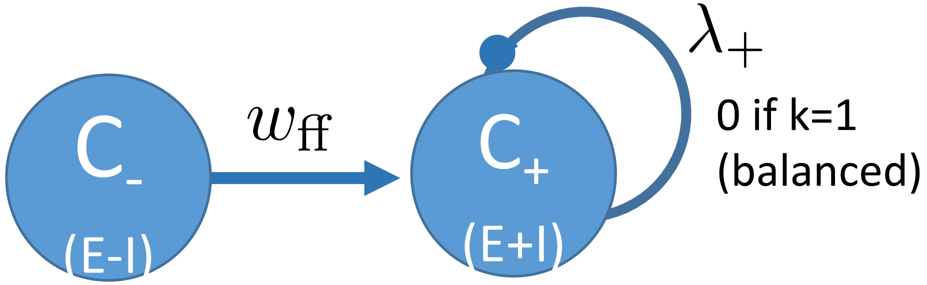
Factorization of A: Q is unitary ($Q^{-1} = Q^H$) and U is upper-triangular; diagonal of U consists of the eigenvalues of A.

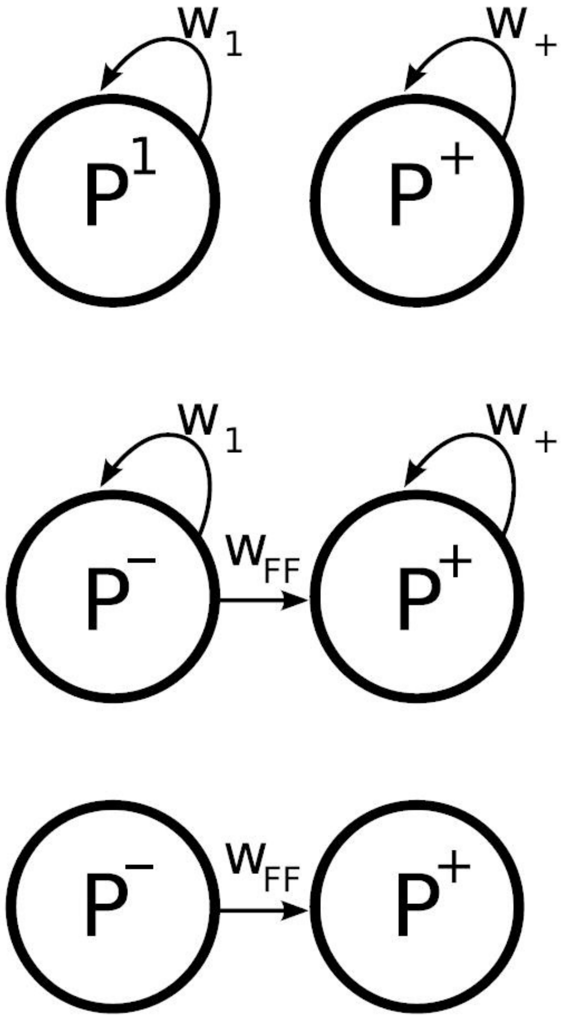
$$U = \begin{bmatrix} u_{1,1} & u_{1,2} & u_{1,3} & \cdots & u_{1,n} \\ & u_{2,2} & u_{2,3} & \cdots & u_{2,n} \\ & & \ddots & \ddots & \vdots \\ & & & \ddots & u_{n-1,n} \\ 0 & & & & u_{n,n} \end{bmatrix}$$

Interpretation: This upper-triangular matrix is a combination of a normal network with uncoupled self-feedback in each mode (diagonal entries), but with the different modes interacting in a purely feedforward way (i→j only if i<j).

$\delta\mathbf{s}^-, \delta\mathbf{s}^+$ are a Schur basis for W in our previous example (if properly normalized)

Decomposition of general network dynamics





Normal network, eigenvector basis: complete decoupling of modes (diagonalization of coupling matrix)

Non-normal network, Schur basis (diagonal entries = self-interaction of modes; upper-triangular entries = ff connections)

Balanced non-normal network (k=1): modes do not interact with themselves, decomposition into pure ff chain

Large amplifying transients also in non-normal systems without division into E/I

$$\frac{d\mathbf{x}}{dt} = \mathbf{A}\mathbf{x} \qquad \mathbf{A} = \begin{pmatrix} -1/2 & 500 \\ 0 & -5 \end{pmatrix} \qquad \mathbf{x}(0) = \begin{pmatrix} 1 \\ 0.1 \end{pmatrix}$$

Implications of highly non-normal dynamics

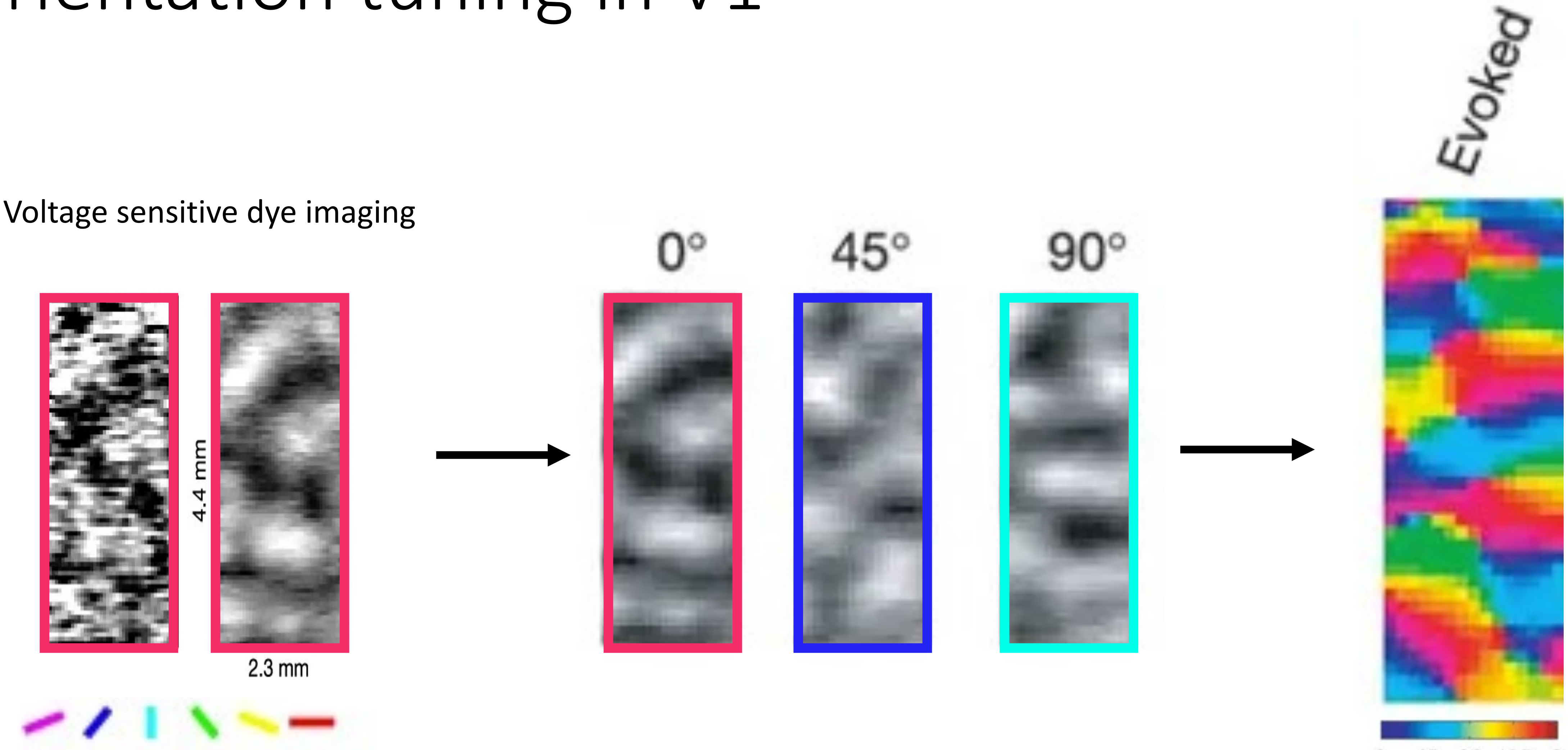
- Large excursions of state away from a stable fixed point.
- In linear systems with a single stable fixed point at 0, these excursions are transient and the system returns to fixed point after the transient has decayed.
- In nonlinear systems with a single stable fixed point at 0 in the linearized dynamics, even small perturbations can lead to large excursions and push the system out of the attracting neighborhood of 0 so it becomes trapped in the nonlinear dynamics away from the linearized stable fixed point at 0.
- Famous example: Onset of turbulence in fluid flows (Trefethen 1993).
- Might the non-existence of a fixed point at 0 in the sharply nonlinear EI networks be related to this?

Why relevant for neuroscience?

- Non-normal matrices are more generic than normal ones given the directionality of neural information processing.
- Separate E, I populations also make neural systems predisposed towards non-normality.
- Sensory systems, which depend on amplification and speed simultaneously might exploit nonnormal amplification (though jury's still out).

Orientation tuning in V1

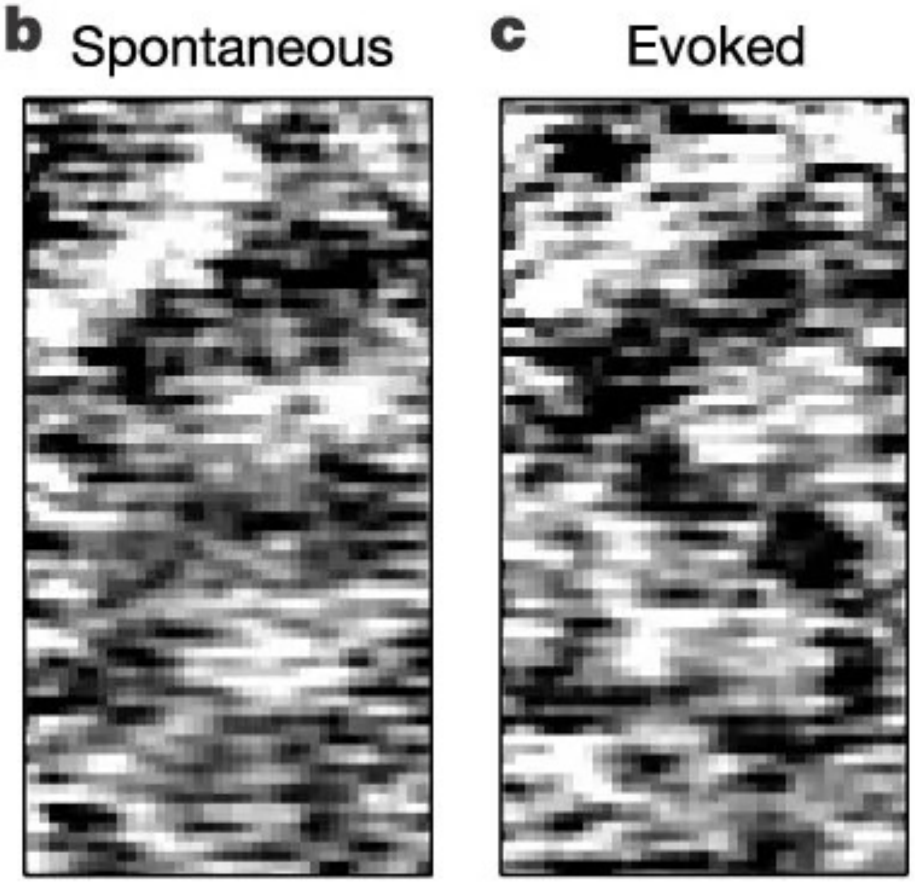
Voltage sensitive dye imaging



evoked

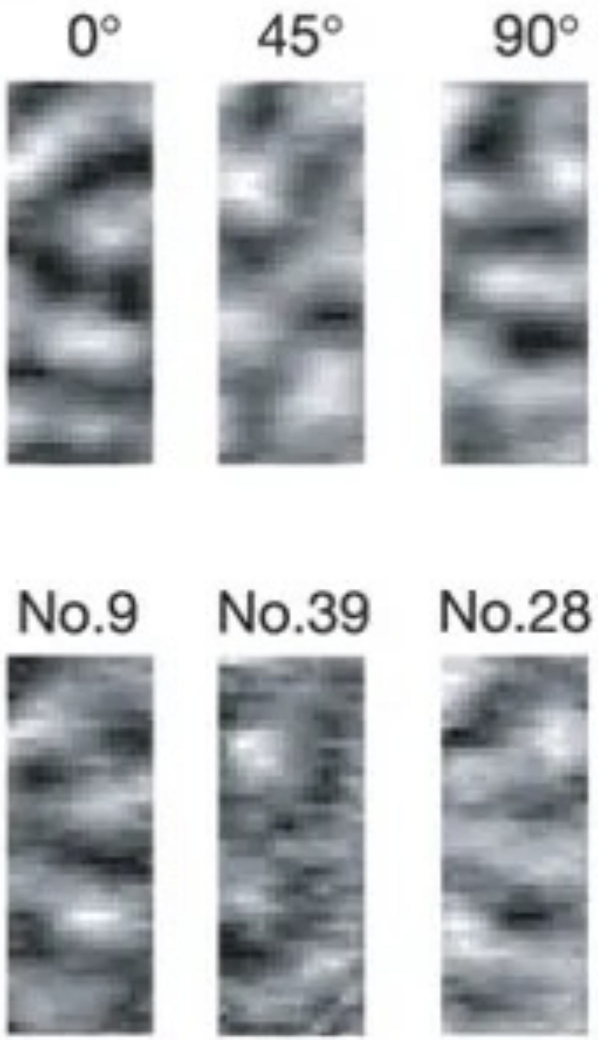
Spontaneously emerging cortical representations of visual attributes. Kenet, Bibitchkov, Tsodyks, Grinvald, Arieli

Spontaneous activity patterns in cortex (V1)



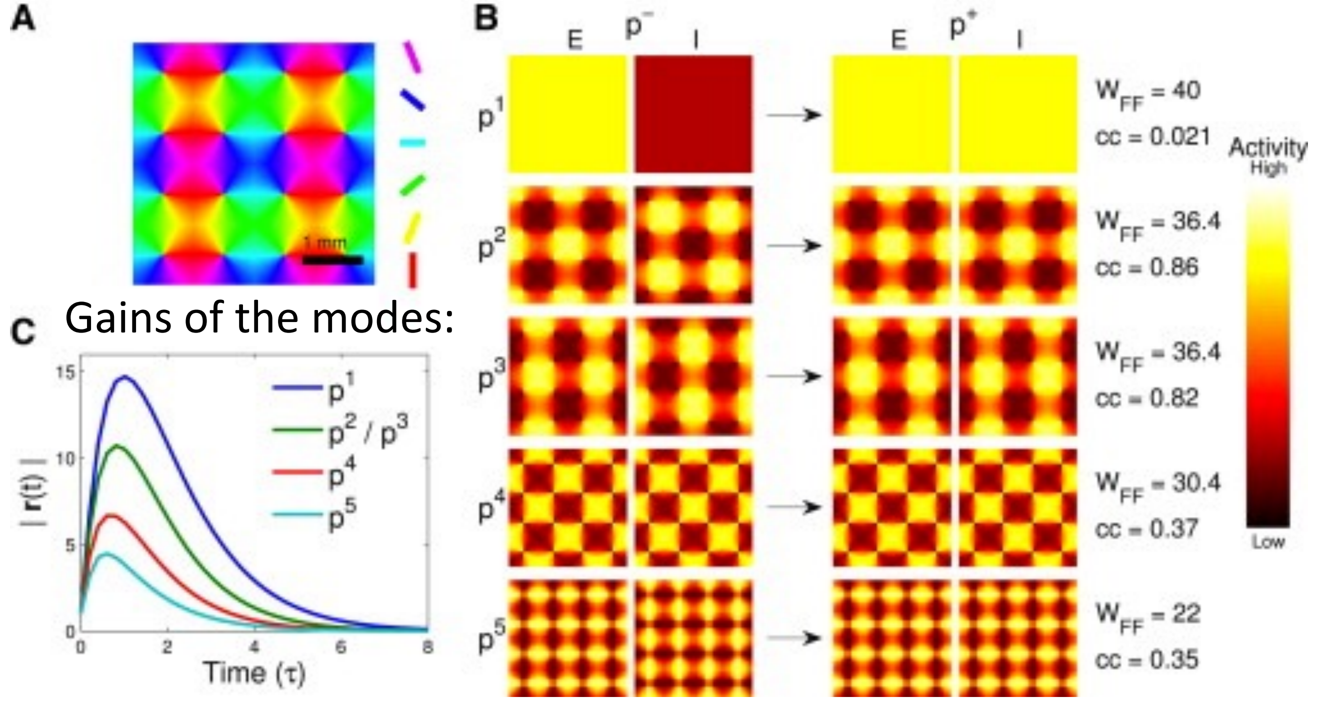
evoked

spontaneous



Spatially extended balanced amplification model

Orientation map (wts setup to produce this)



One difference mode per spatial frequency

One sum mode per spatial frequency

$$\mathbf{W} = \begin{pmatrix} \mathbf{W}_{EE} & \mathbf{W}_{EI} \\ \mathbf{W}_{IE} & \mathbf{W}_{II} \end{pmatrix}$$

If each submatrix in **W** is spatially structured and translation-invariant, then Fourier basis functions (an orthogonal set) simultaneously diagonalize each submatrix (we'll see this in a future class). Result: The network dynamics decomposes into N distinct spatial frequency networks, each with a difference mode projecting into a sum mode, both with the same spatial pattern frequency.

The N difference modes feedforward into the N sum modes

Interpretations of spontaneous activity

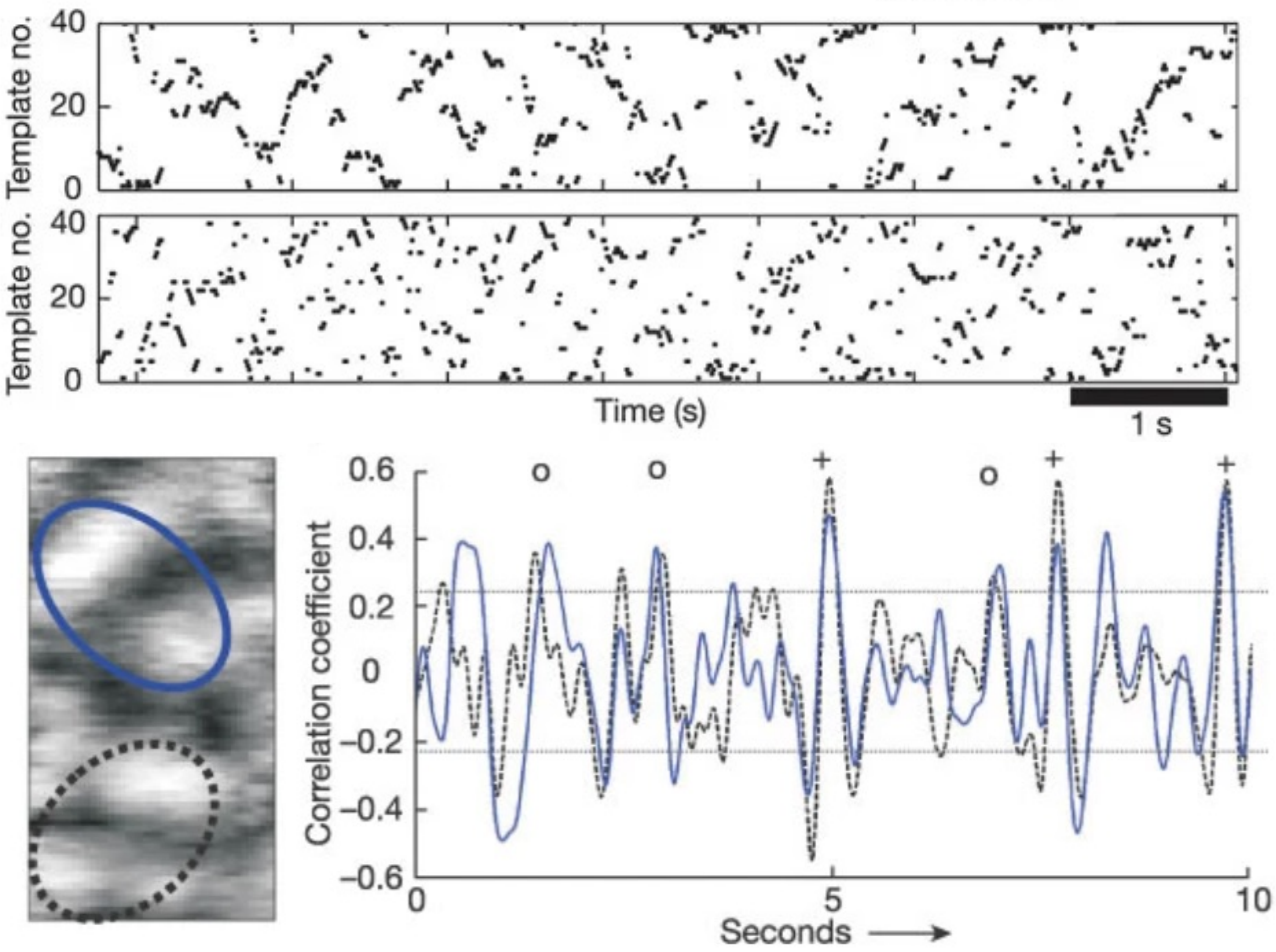
- States are stable fixed points, and the system moves or switches between them during spontaneous activity through some other temporal process. (Normal coupling models.) Ben Yishai, Bar-Or, Sompolinsky 1995

VERSUS

- States are the sub-critical (non-stable) eigenvectors of the system, with transient amplification of the dynamics leading to amplification of the state before decay. (Non-normal coupling models.) Murphy, Miller 2009

Temporal dynamics

spontaneous



The autocorrelation times of recorded spontaneous dynamics are ~1 s: not too long or too short, making it hard to cleanly distinguish between normal/non-normal hypotheses.

Summary

- Non-normal recurrent networks including E-I networks act like feedforward networks (mathematically understand through the Schur decomposition)
- E-I networks in the balanced or inhibition-dominated regime can transiently amplify their inputs.
- The response-time of the transient amplification is fast, in contrast to amplification slowing in normal networks.
- Plausible model of amplification in the brain: is this how sensory cortex amplified its inputs?
- Some experimental evidence consistent with balanced networks and E-I based non-normal amplification in the brain.