Computation and memory in recurrent networks

Peter E. Latham

University of California at Los Angeles

152.17
SFN2002

Background

- **The cortex is high gain, in the sense that fluctuations in excitatory firing rate would grow without *active* feedback from inhibitory neurons. In other words, one *extra* excitatory spike causes *more than one* excitatory spike somewhere else in the network.**

- **This makes the cortex prone to instabilities (e.g., kindling and epilepsy).**

- **How is it that cortical networks are robust to instabilities?**

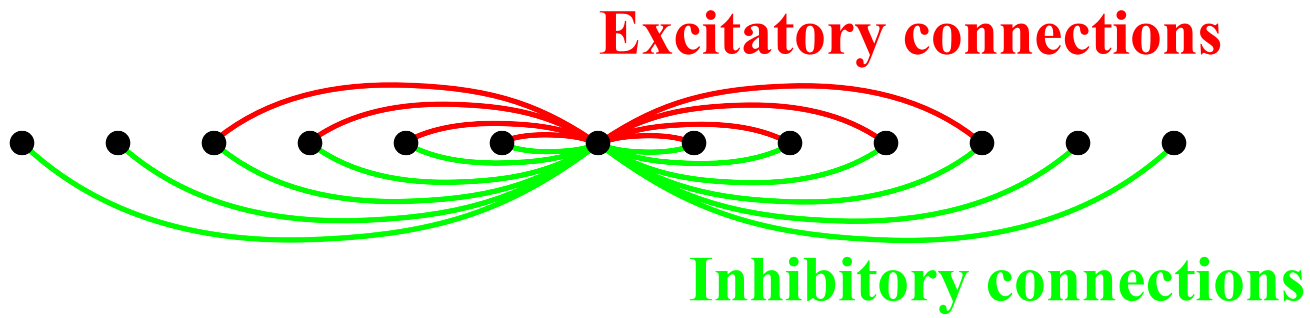
- **We address this question in the context of attractor networks, for which the stability problem is especially severe. If we can understand how to build stable attractor networks, we can gain a general understanding of how to build stable recurrent networks that do other kinds of computations.**

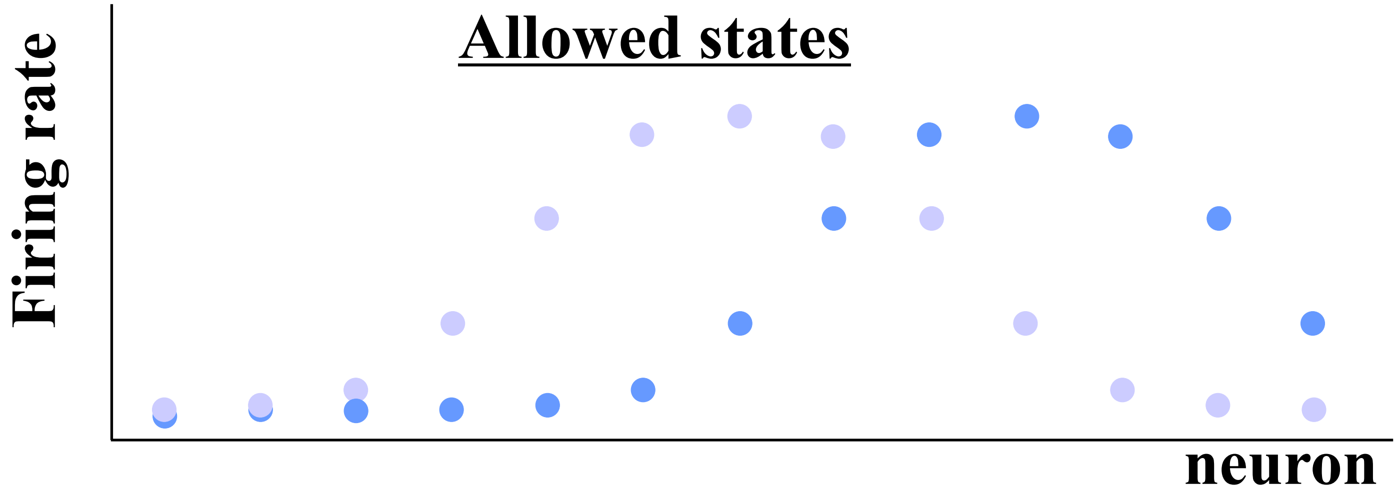
Supported by NIMH grant #MH62447

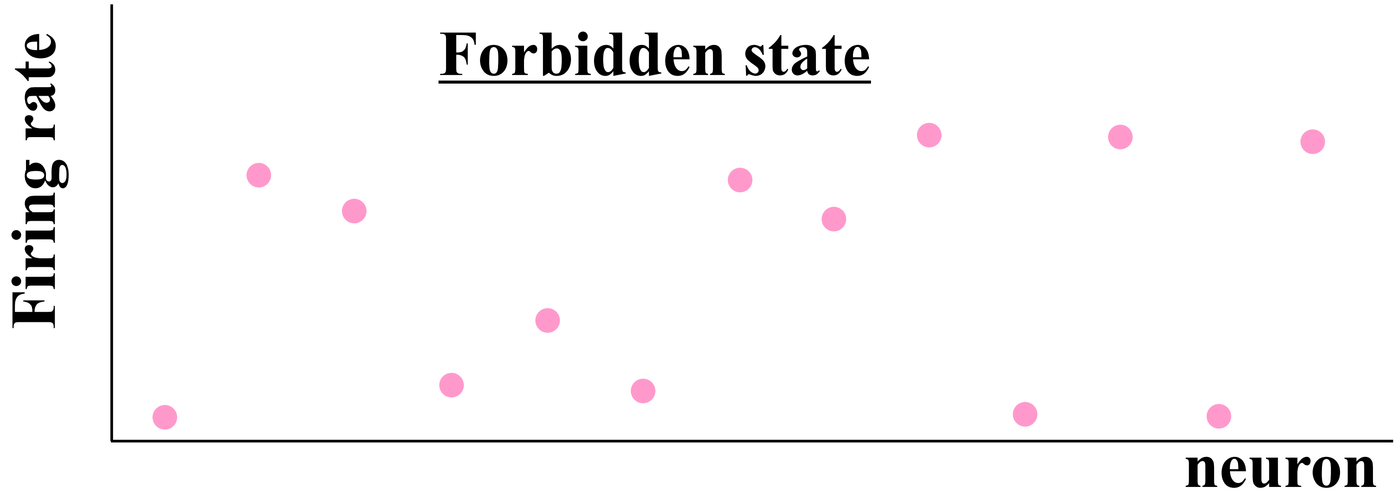
Observation: the cortex is dominated by recurrent connectivity?

Claim: its main purpose is to restrict space of input/output transformations.

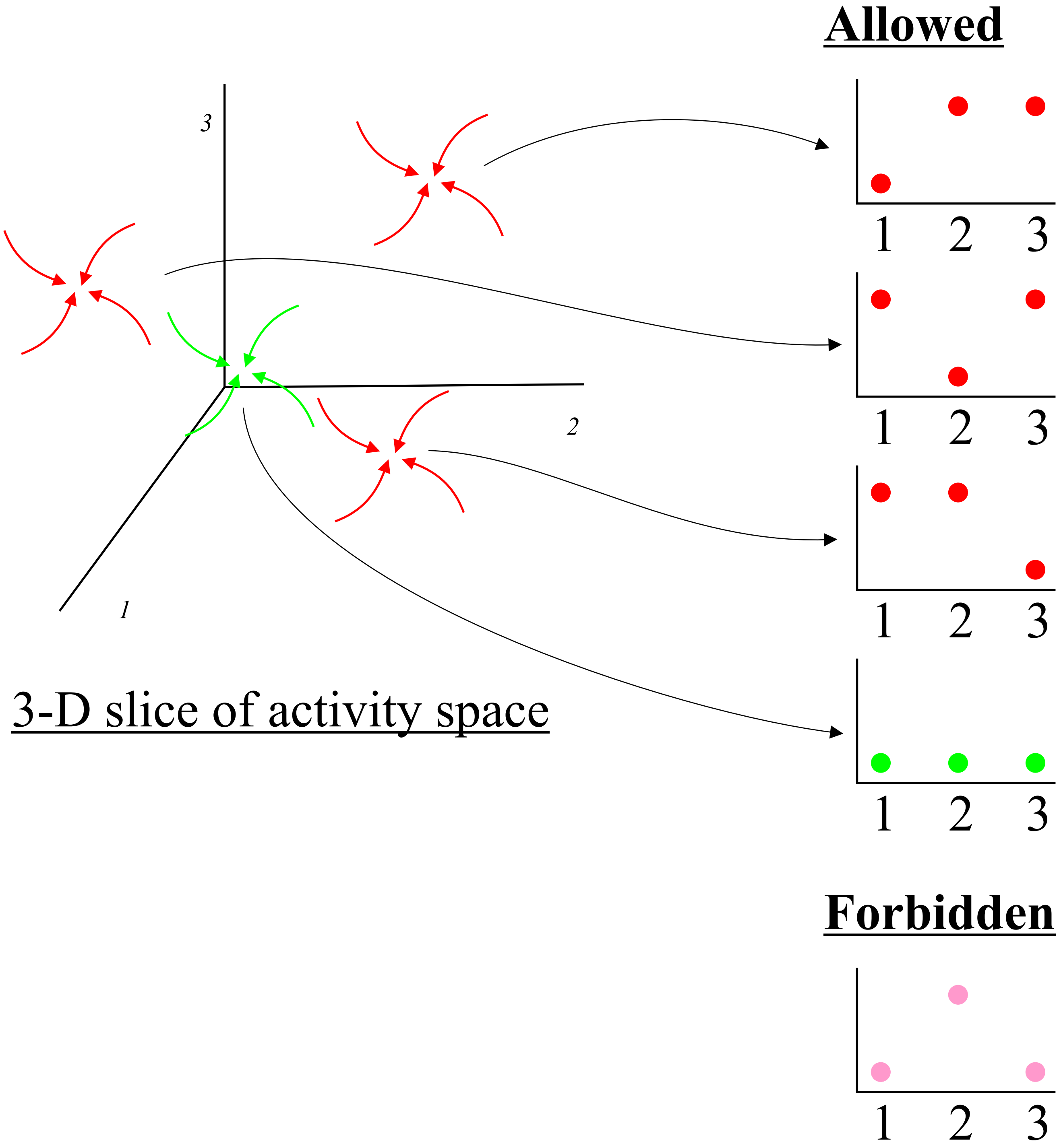
Example: orientation selectivity.




Allowed states


Forbidden state

Another example: attractor aetworks.



Allowed

3-D slice of activity space

Forbidden

Question:

Can we understand how to build biologically plausible recurrent networks with restricted input/output transformations?

Why are we even asking this question?

Because neuronal networks are high gain.

- **Back of the envelope calculation:**

PSP: 0.1 mV
R: 50 MΩ
τ: 10 ms
rate: 1 Hz

$$\left.\begin{array}{ll} \text{PSP:} & 0.1\ \text{mV} \\ R\text{:} & 50\ \text{M}\Omega \\ \tau\text{:} & 10\ \text{ms} \\ \text{rate:} & 1\ \text{Hz} \end{array}\right\} \Rightarrow$$

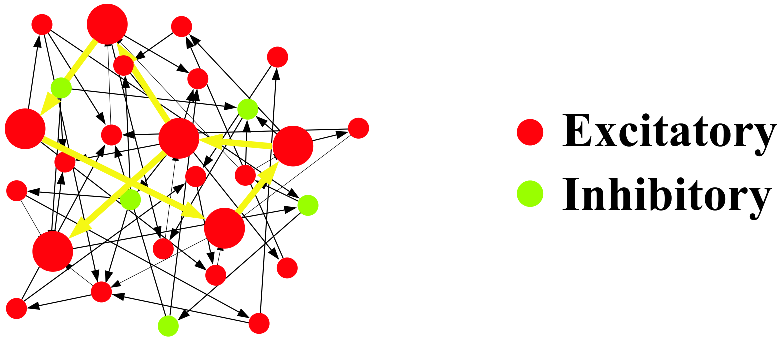
EPSC=.02 pA
×5000=.1 nA

⇒ **each excitatory spike causes 25 other spikes!**

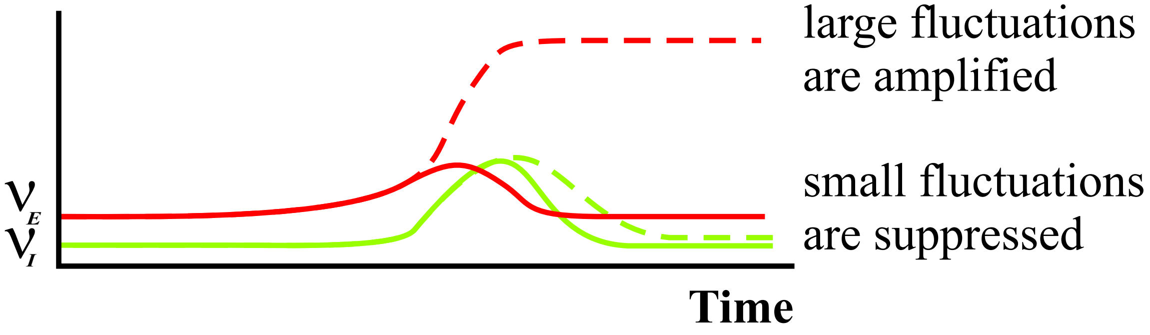
- **Small amount of kindling leads to seizures.**
- **1 in 200 people have epilepsy.**

- **High gain ⇒ networks live on the edge of stability.**
- **Strengthening connections to build a network with restricted input/output relation in such a high gain system is a recipe for disaster.**

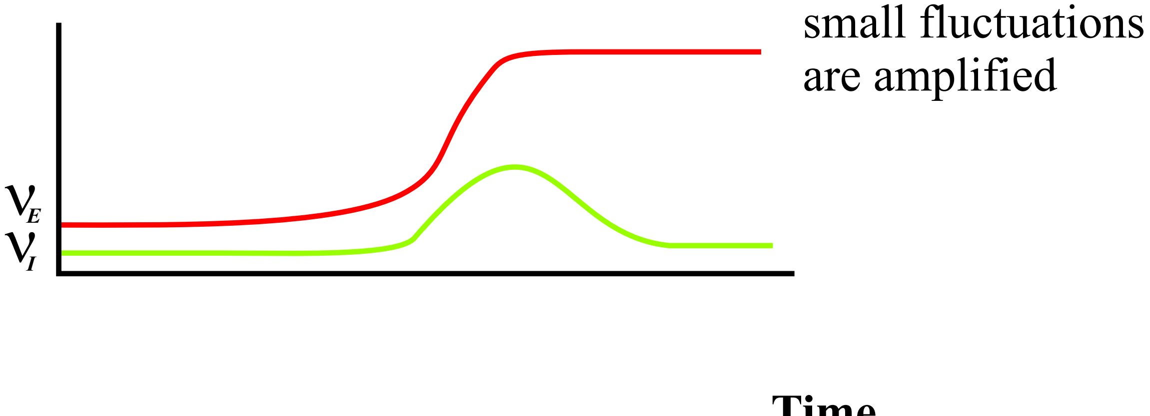
Attractor network



What we want:



What we're likely to get:



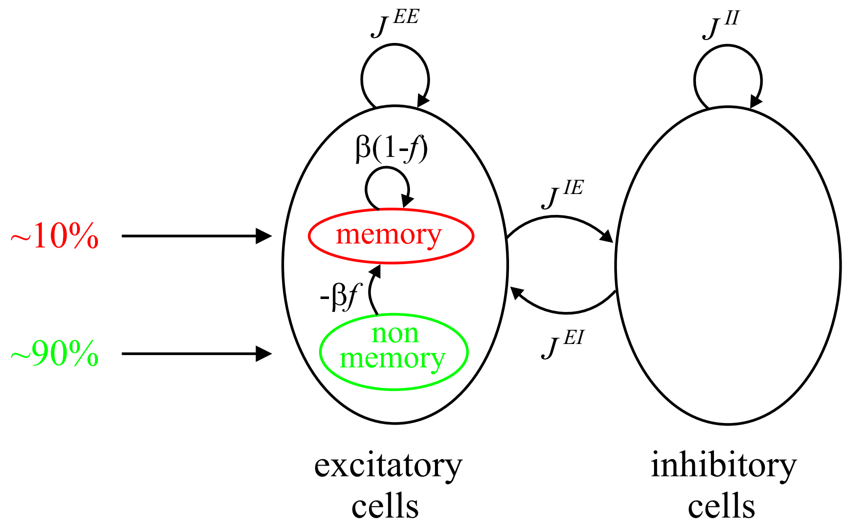
Our goal:

- **Understand how to build a network in the high gain regime that is resistant to instabilities.**

- **As an example, consider attractor networks.**

- **Take into account an additional experimental constraint: firing rates on attractor must be relatively low, ~10-20 Hz.**

Toy model with one memory



Equilibrium equations:

$$\nu_{Ei} = \Phi_E\left(J^{EE}\nu_E - J^{EI}\nu_I + \beta\xi_i \underbrace{[N_E\, f(1-f)]^{-1}\sum_j (\xi_j - f)\ \nu_{Ej}}_{\text{memory, } m}\right)$$

$$\nu_I = \Phi_I\left(J^{IE}\nu_E - J^{II}\nu_I\right)$$

firing rates. *i* labels cell;
ν_E and ν_I are average rates;
***E*=excitatory, *I*=ihibitory.**

$$\xi = \begin{cases} \mathbf{1} & \text{prob} = f \\ \mathbf{0} & \text{prob} = 1-f \end{cases}$$

f~0.1

A little algebra

1. **Solve for ν_I as a function of ν_E:**

$$\nu_I = \Phi_I\left(J^{IE}\nu_E - J^{II}\nu_I\right) \;\Rightarrow\; \nu_I = g(\nu_E)$$

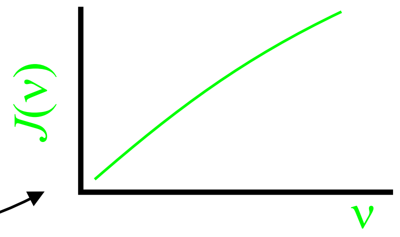
2. **• Replace ν_I by $g(\nu_E)$ in excitatory equation.**
   • Drop "*E*" sub- and super-scripts.
   • Define:

$$m \equiv \frac{1}{1-f}\left[\frac{1}{Nf}\sum_j \xi_j \nu_j - \frac{1}{N}\sum_j \nu_j\right]$$

3. ***N* equations for the excitatory cells:**

$$\nu_i = \Phi\left(J^{EE}\nu - J^{EI}g(\nu) + \beta\xi\, m_i\right)$$

$$\boxed{\nu_i = \Phi\left(-J(\nu) + \beta\xi_i m\right)}$$



Average over ξ:

$$\nu = f\,\Phi\left(-J(\nu) + \beta m\right) + (1-f)\,\Phi\left(-J(\nu)\right)$$

$$m = \underbrace{\Phi\left(-J(\nu) + \beta m\right) - \Phi\left(-J(\nu)\right)}_{\Delta\Phi(\nu,\, m)}$$

Or:

$$\nu = \Phi\left(-J(\nu)\right) + f\Delta\Phi(\nu, m)$$

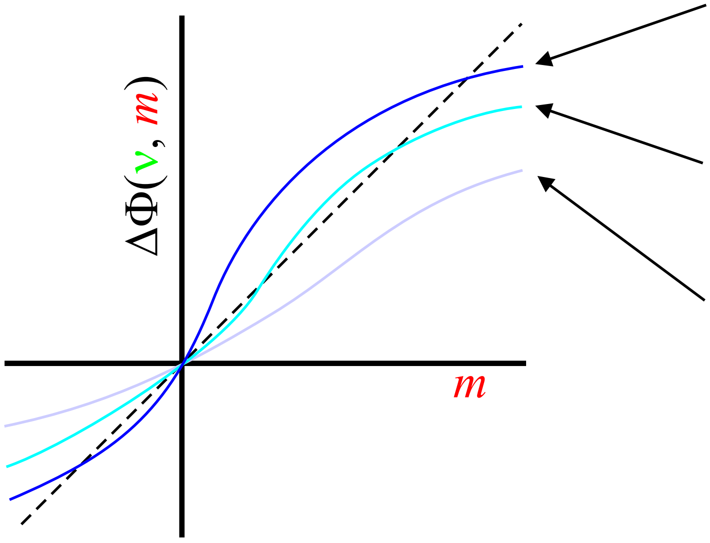
$$m = \Delta\Phi(\nu, m)$$

Dynamics:

$$\tau\, d\nu/dt = \Phi\left(-J(\nu)\right) + f\Delta\Phi(\nu, m) - \nu$$

$$\tau\, dm/dt = \Delta\Phi(\nu, m) - m$$

For a memory to exist, this equation must have two sable solutions



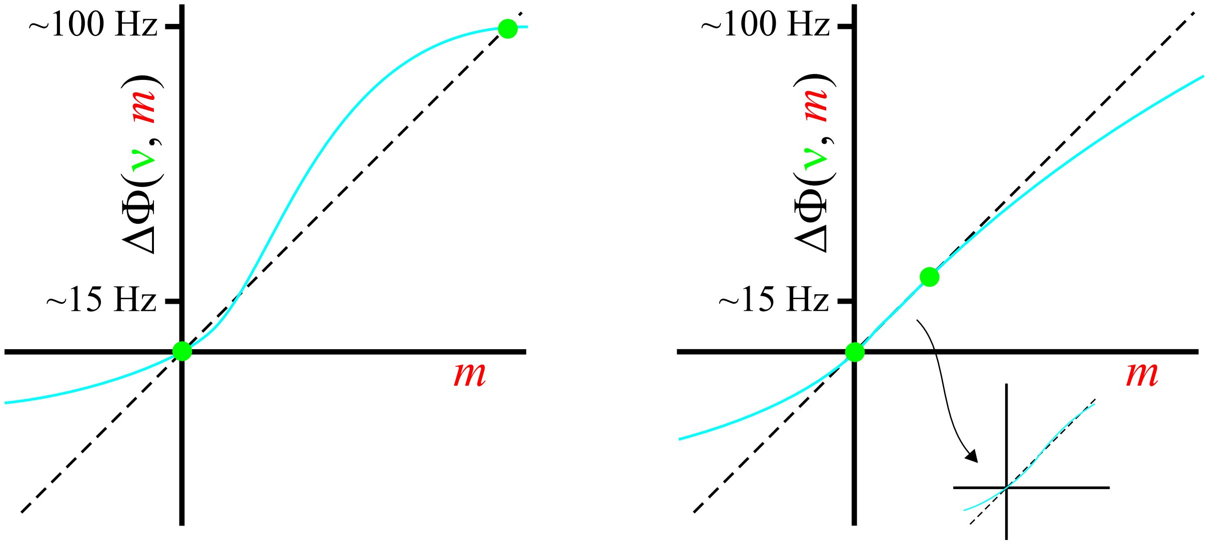
large β, background unstable

medium β, memory and background stable

small β, no memory

Sparse coding limit ($f \rightarrow 0$)

- ν is independent of m: $\nu=\Phi\big(-J(\nu)\big)$
- Equations for ν and m decouple
- Only have to worry about the m-equation

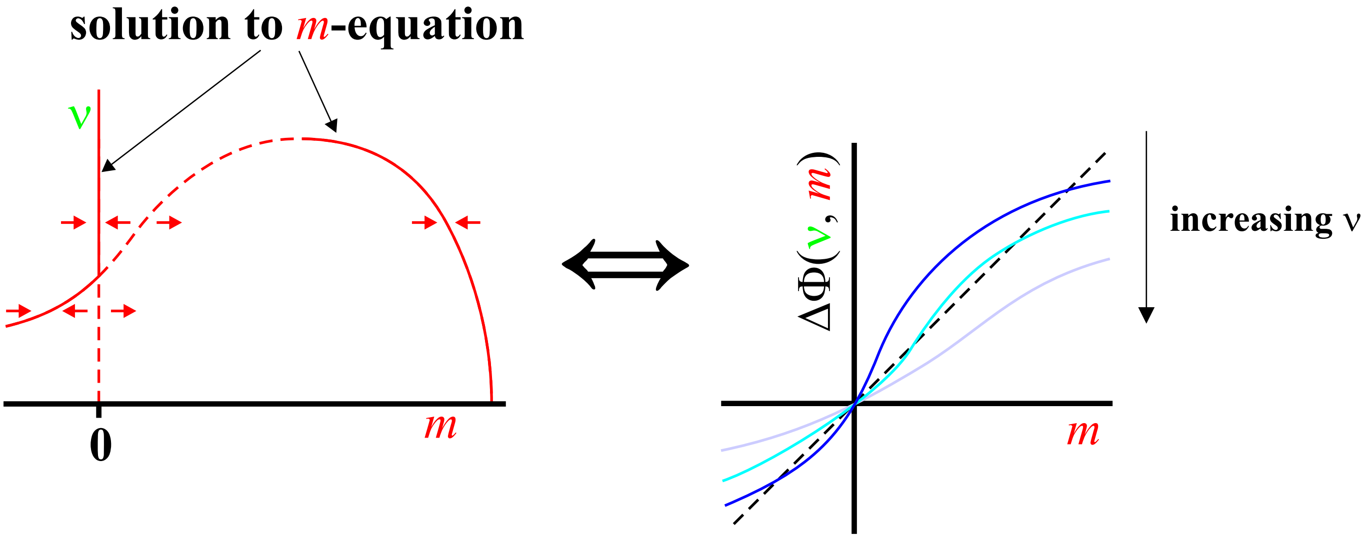


Bistability (memories) can exist, but ...

there is a firing rate/stability problem.

Beyond the sparse coding limit ($f > 0$)

- **Equations for ν and *m* no longer decouple**
- **Have to worry about both *m*- and ν-equations**
- **Therefore, have to consider 2-D equilibrium space**

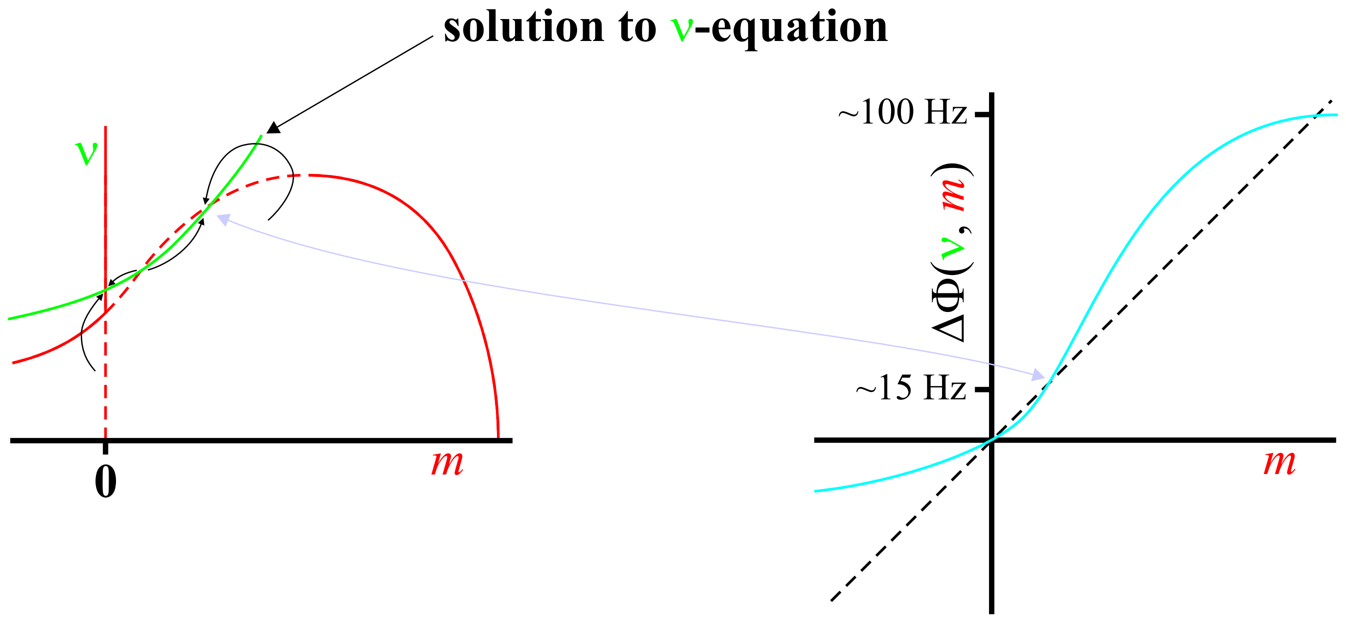


Why does ΔΦ(ν, *m*) drop as ν increases?

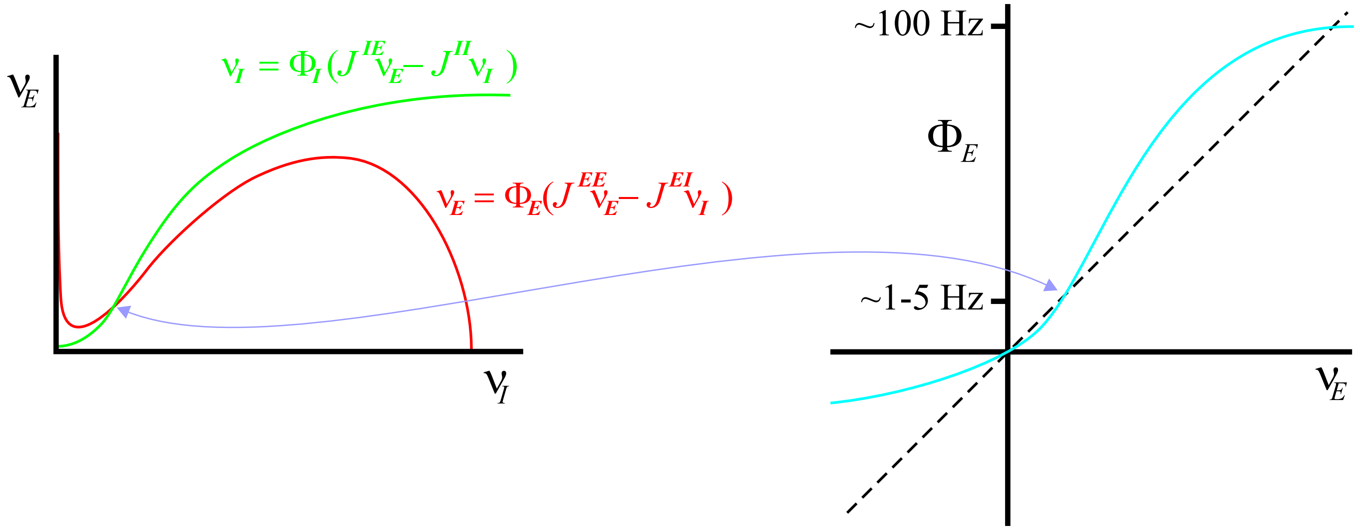
Because inhibition dominates, which leads to -*J*(ν) coupling:

$$\Delta\Phi(\nu, m) = \Phi\left(-J(\nu) + \beta m\right) - \Phi\left(-J(\nu)\right)$$

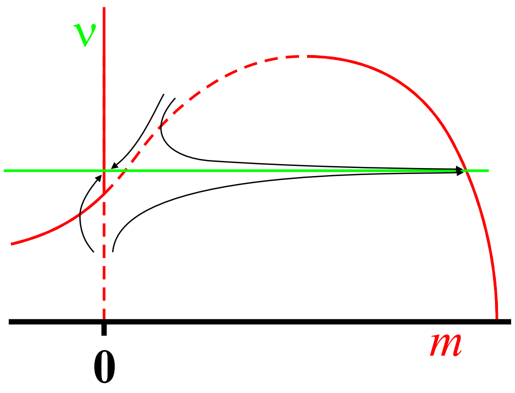
Potentially robust bistability; memory at low rates:



Analogous to low firing rate background state:



For comparison, the sparse coding ($f \to 0$) limit:



Simulations

- **Quadratic integrate-and-fire.**
- **Synaptic coupling: $g(t-t_j) \times (V-V_{\text{reverse}})$**

- **8000 excitatory neurons**
- **2000 inhibitory neurons**
- **Membrane time constant: 10 ms**
- **Synaptic time constants: 3 ms**
- **Fraction of neurons involved in a memory, *f*: 0.1**

- **Connectivity pattern:**

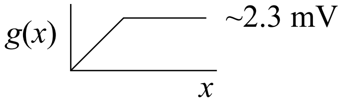
$$J_{ij} = g\Big(c_{ij}\,\big(W_{ij} + [N_E\, f(1\text{-}f)]^{-1}\,\beta \sum_{\mu=1}^{p} \xi_i^p(\xi_j^p - f)\big)\Big)$$

multiple (*p*) memories

random background

sparseness: 1 with probability 0.25; 0 otherwise

clipping function:

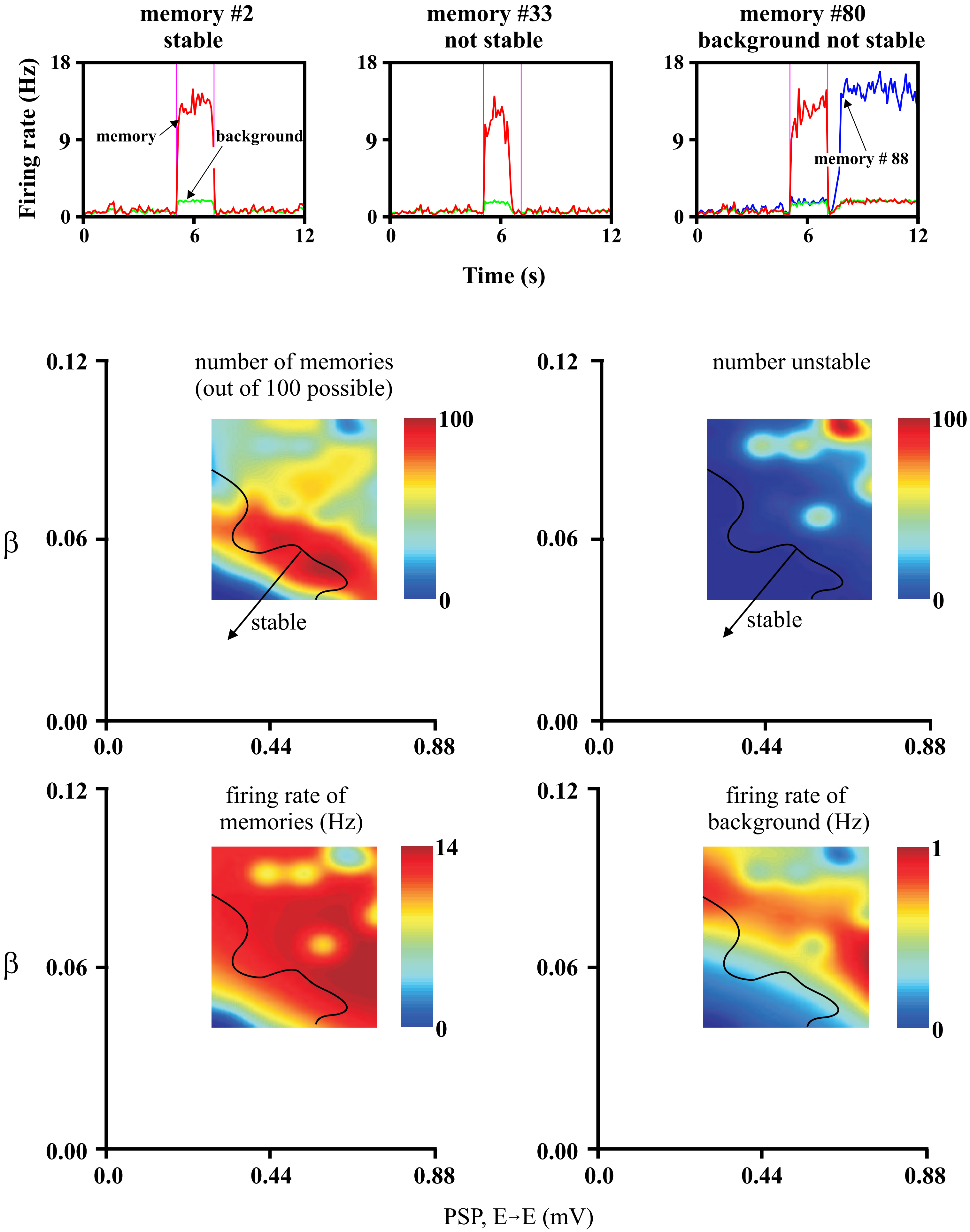


- **Current nonlinearity:**

$$I_{\text{syn}} \to I_{\text{syn}}\left[1 + \frac{1}{1 + \exp[-(I_{\text{syn}} - \hat{I})/\Delta I\,]}\right]$$

$\hat{I}$ ~ 24 PSPs above rest

ΔI ~ 8 PSPs


memory #2
stable
memory #33
not stable
memory #80
background not stable
Firing rate (Hz)
18
9
0
memory
background
memory # 88
0
6
12
Time (s)
number of memories
(out of 100 possible)
number unstable
100
0
stable
β
0.12
0.06
0.00
0.0
0.44
0.88
firing rate of
memories (Hz)
14
firing rate of
background (Hz)
1
PSP, E→E (mV)

Conclusions

- In most models of attractor networks, firing rates limited by saturation.

- We took advantage of dynamic stabilization to operate on unstable, non-saturating branch.

- This led to robust, low rates on attractor, and protected the network against instabilities.

- In future work we will investigate whether other types of computations – ones that do not rely on attractors – also operate in the dynamically stabilized regime.