Associative memory in realistic neuronal networks

Peter E. Latham

University of California, Los Angeles

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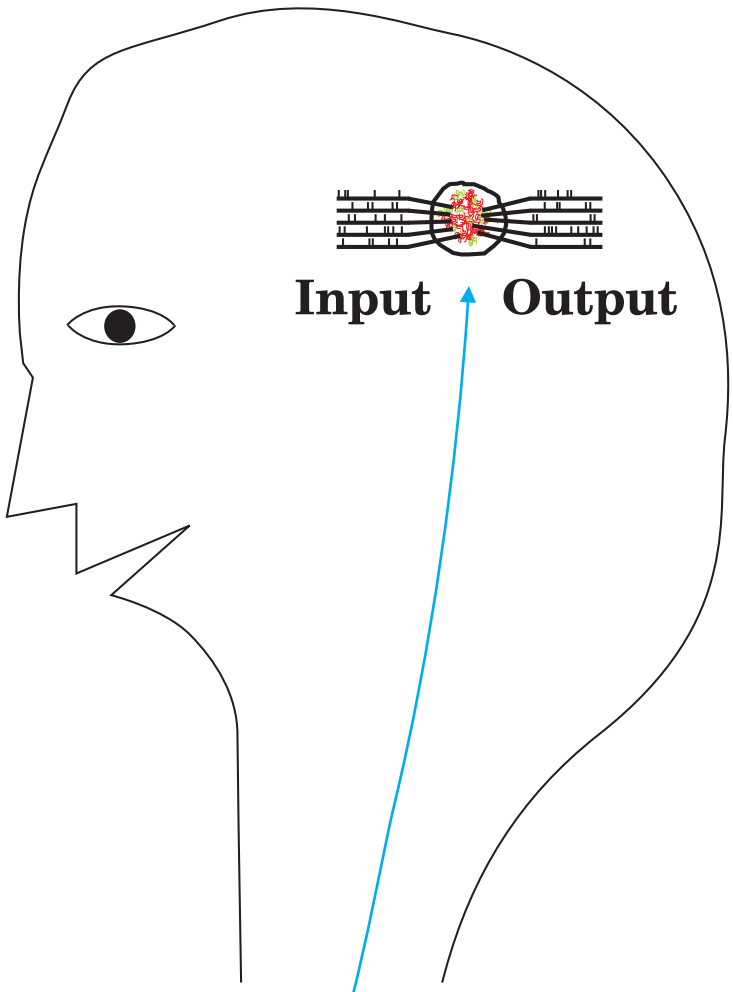
How the brain works:



- We need to understand computation in highly recurrent neuronal networks.

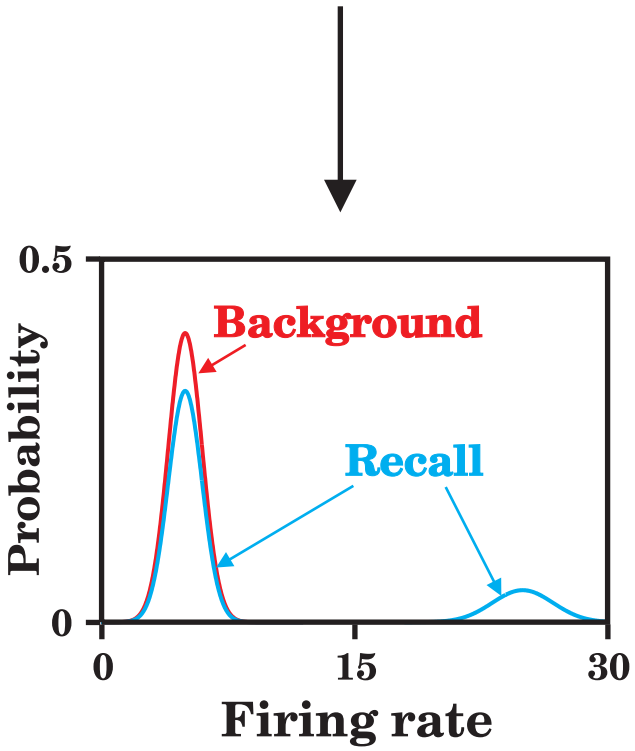
- One of the simplest non-trivial computations are those performed by attractor networks.

Can realistic neuronal networks support attractors?

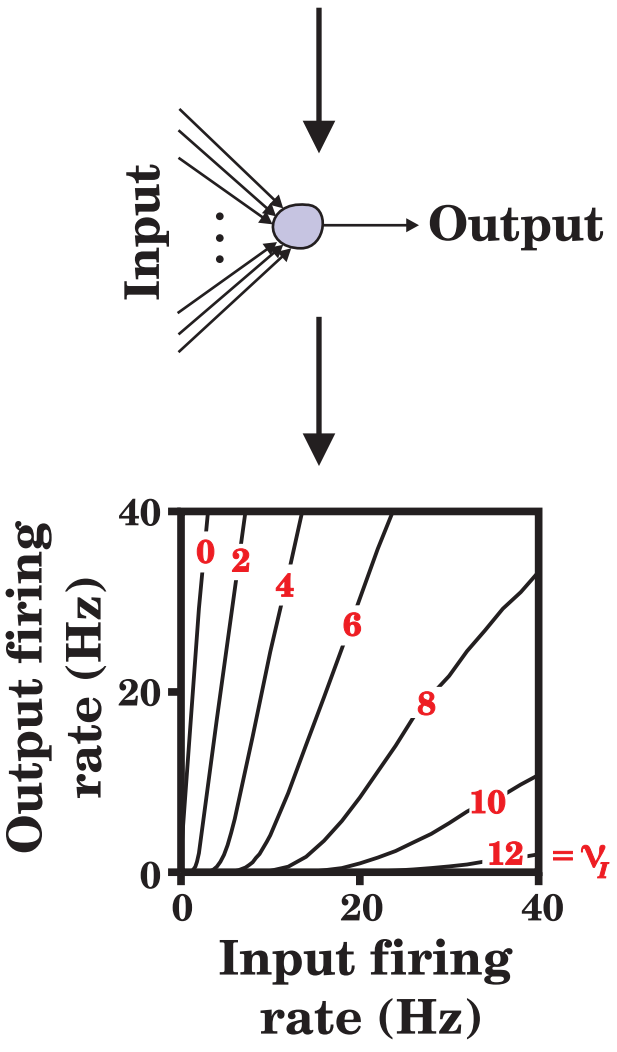
realistic:

1. Low firing rate background state

2. Low firing rate during recall



3. Realistic gain functions.



Why is this a hard problem?

First observation: neuronal networks are high gain.

- **Small amount of bicuculine;**
  Small amount of kindling;
  Bad luck:

  $\Rightarrow$ **Epilepsy**

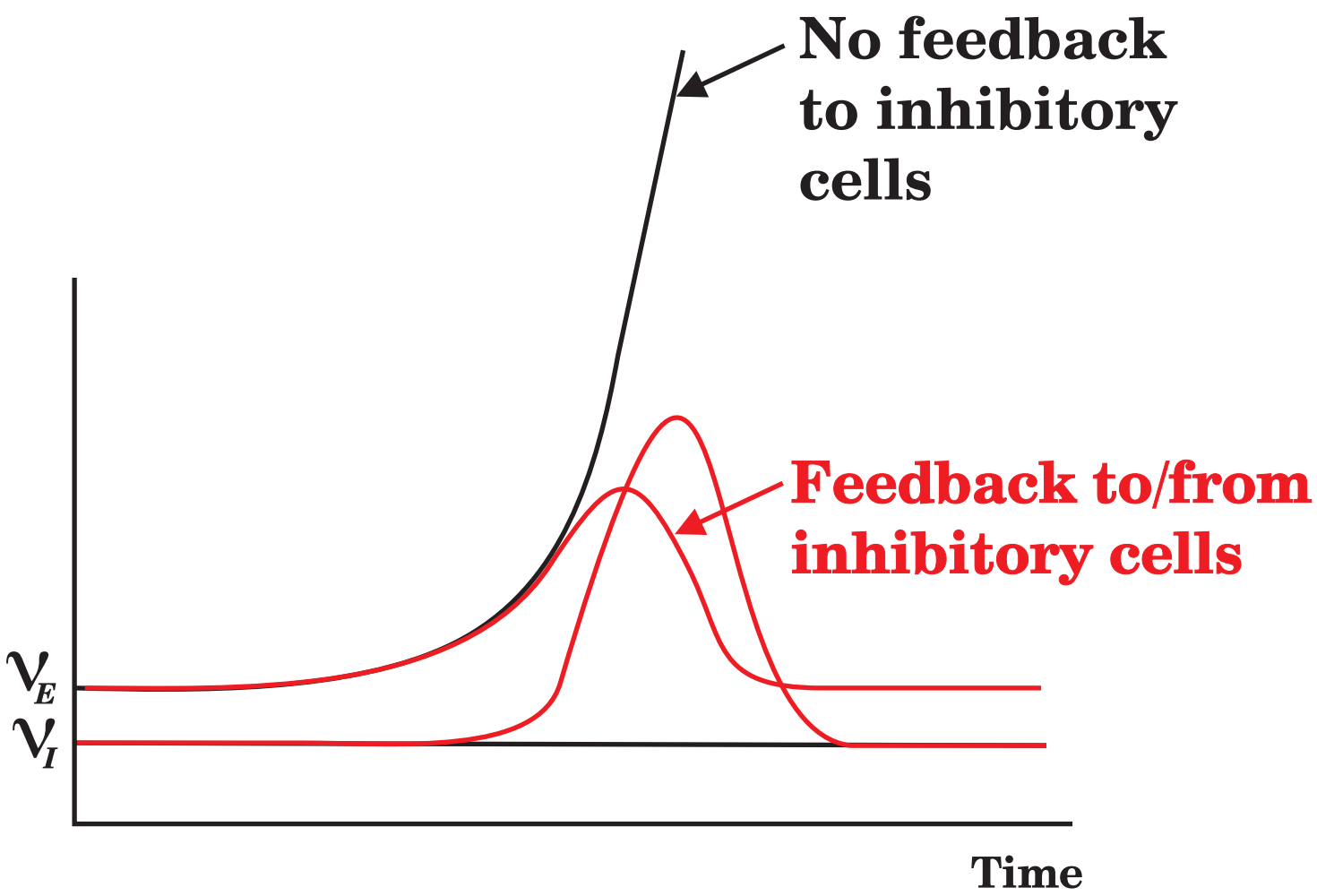
- **Back-of-the envelope:**

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

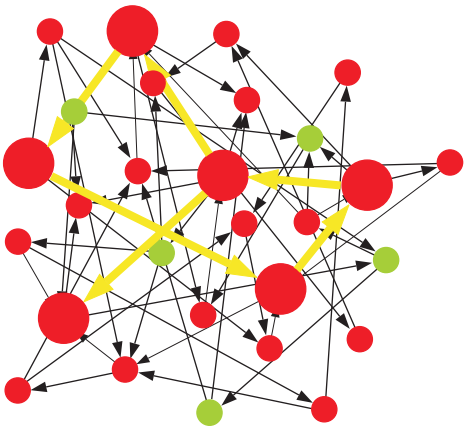
$\Rightarrow$ **EPSC=.02 pA**
x5000=.1 nA

$\Rightarrow$ **each excitatory spike causes 25 other spikes!**

Consequences

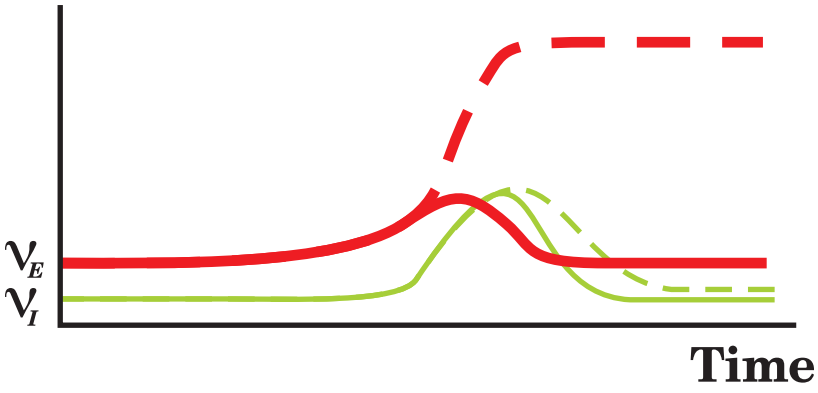


Attractor Network

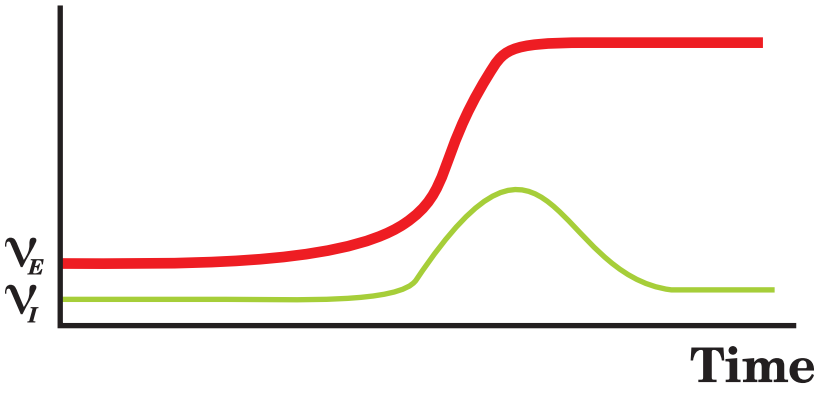


Excitatory
Inhibitory

What we want:



What we are likely to get:



Toy model

$$\nu_{Ei} = \Phi_E\left(J^{EE}\nu_E - J^{EI}\nu_I + \theta_{Ei} + \hat{\beta}\sum_j \xi_i \xi_j \nu_{Ej}\right)$$

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

$$\hat{\beta} = \frac{\beta}{N_E f(1-f)}$$

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

ν_E = Average excitatory firing rate

ν_I = Average inhibitory firing rate

A little algebra

1. **Inhibitory equation: average over threshold:**

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

$$\Rightarrow \nu_I = g(\nu_E)$$

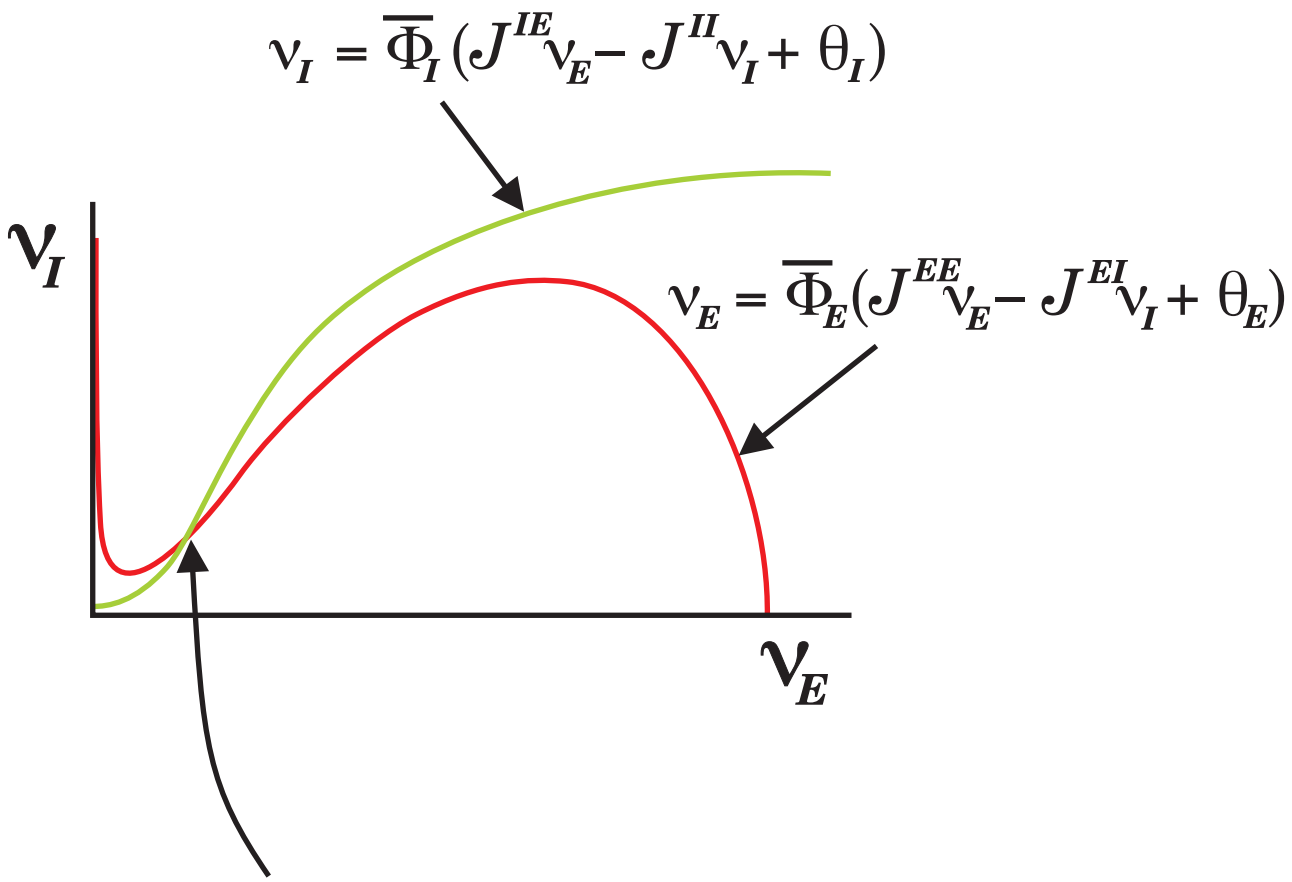
2. • **Replace ν_I by $g(\nu_E)$ in ν_E equation.**
   • **Drop "*E*" sub- and super-scripts.**
   • **Define:**

$$m \equiv \frac{1}{N_E f(1-f)} \sum_j \xi_j \nu_j$$

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

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

Why -$J\nu$ (rather than +$J\nu$)?



Balanced excitation and inhibition

- **van Vreeswijk and Sompolinsky (1996, 1998)**
- **Latham et al. (2000)**

Average over θ and ξ:

overbar indicates average over distribution of θ

$$\nu = f\overline{\Phi}\left(\theta - J\nu + (1-f)\beta m\right) + (1-f)\overline{\Phi}\left(\theta - J\nu - f\beta m\right)$$

$$m = \overline{\Phi}\left(\theta - J\nu + (1-f)\beta m\right) - \overline{\Phi}\left(\theta - J\nu - f\beta m\right)$$

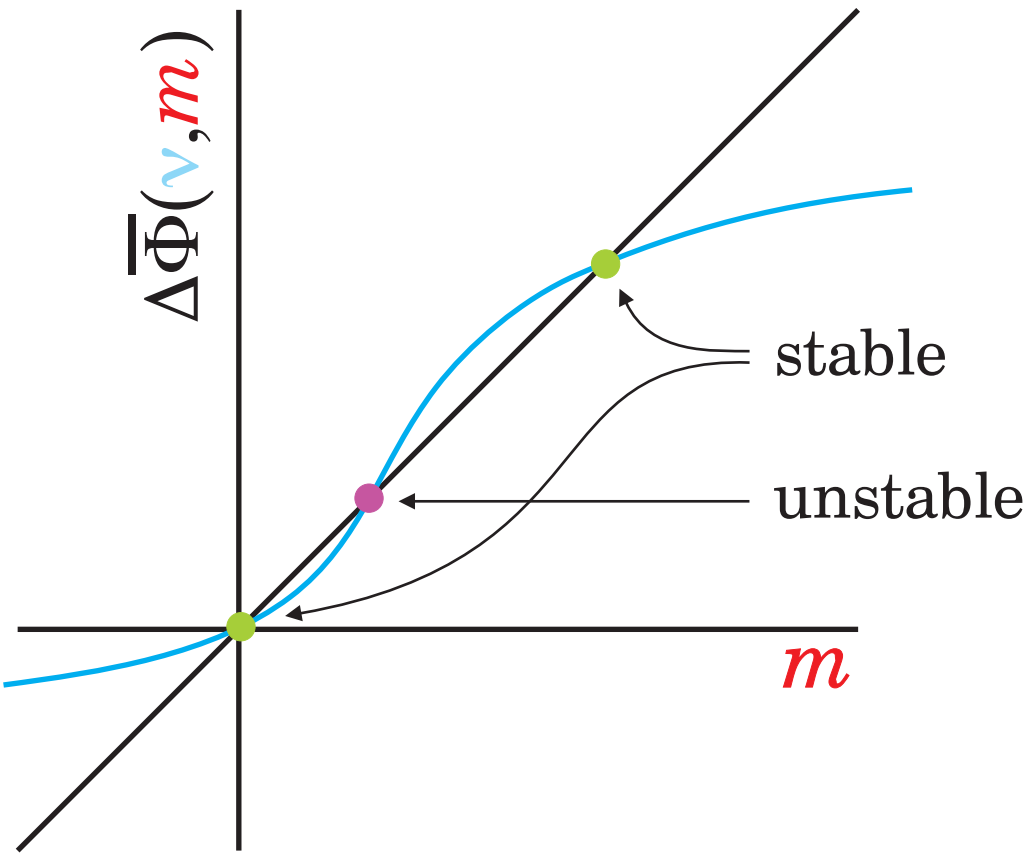
Or:

$$\nu = \overline{\Phi}\left(\theta - J\nu - f\beta m\right) + f\Delta\Phi(\nu, m)$$

$$m = \Delta\overline{\Phi}(\nu, m)$$

in the sparse coding limit ($f \to 0$), ν is independent of m

Graphical approach

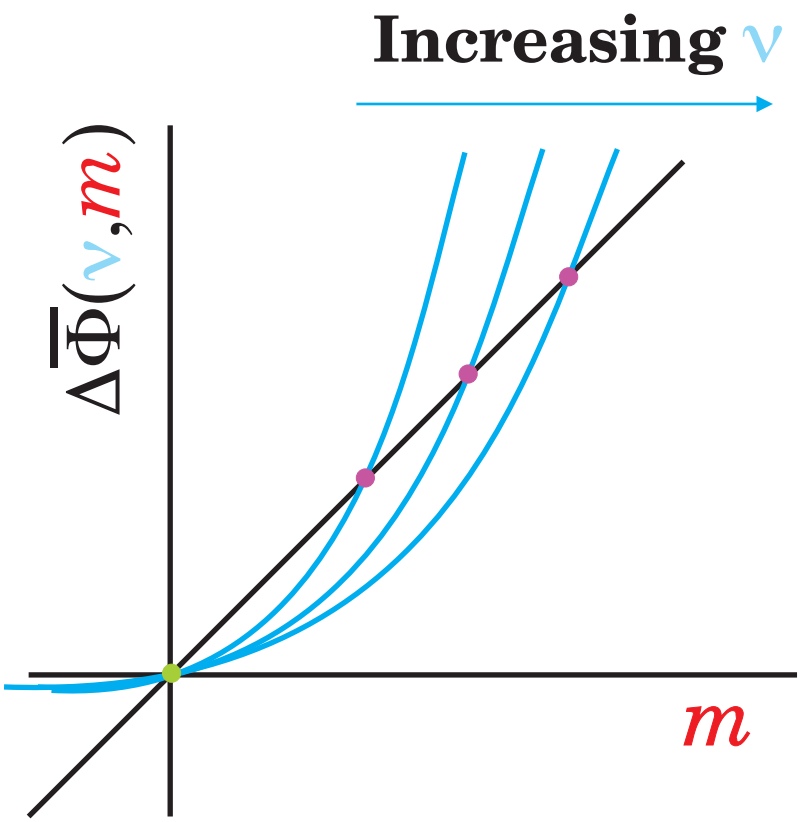


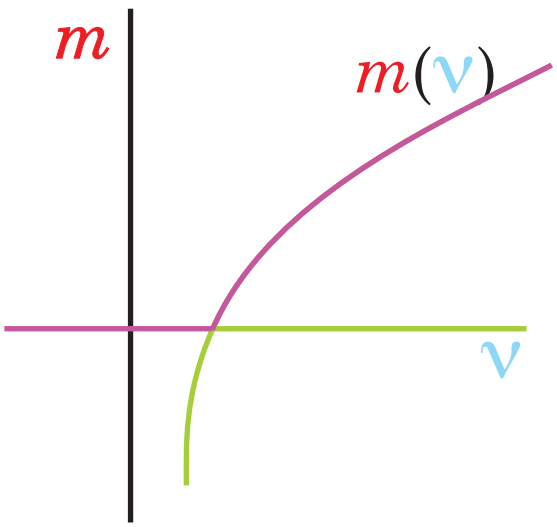
Bistability (a.k.a. attractors) exist, but parameter regime is narrow.

Not robust!!

- **Brunel (2000)**
- **Latham et al. (1999)**

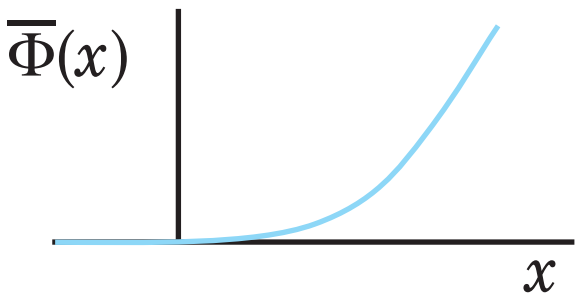
$m(\nu)$

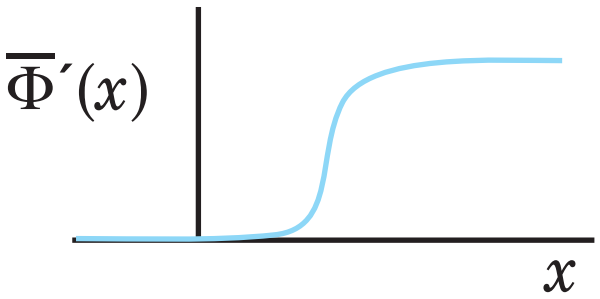


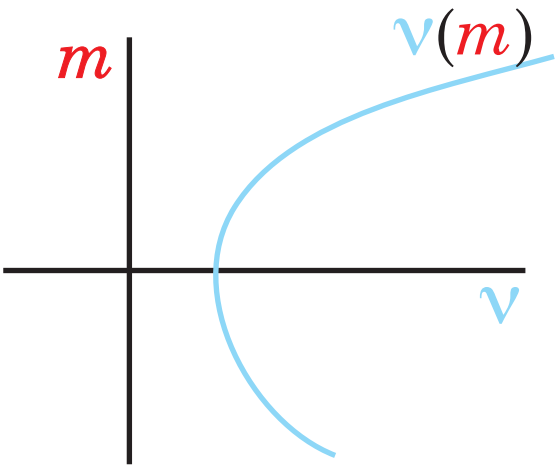


$\nu(m)$

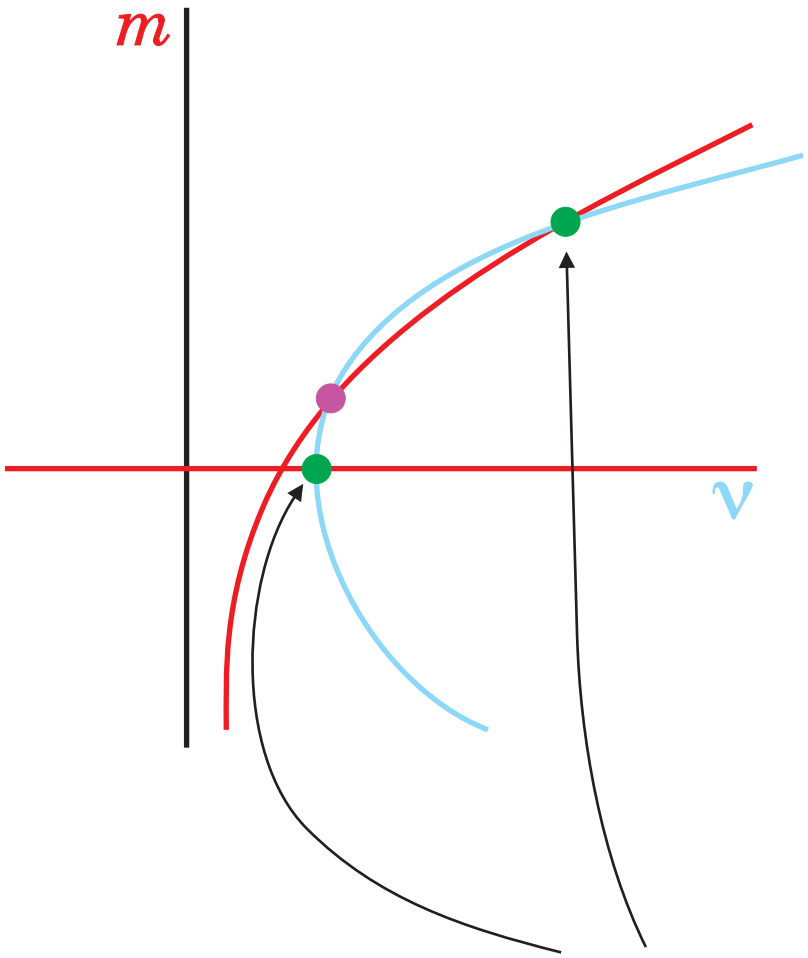
$$d\nu/dm = \beta f(1-f)\left[\overline{\Phi}'\left(\theta - J\nu + (1-f)\beta m\right) - \overline{\Phi}'\left(\theta - J\nu - f\beta m\right)\right]$$







ν–m phase space



Bistable and robust!

More realistic model

$$\nu_i = \beta p^{1/2} \Phi\left(\hat{\theta}_i - (a+1)\nu + (\bar{g}N)^{-1} \sum_j C_{ij}\, g(W_{ij} + J_{ij})\nu_j\right)$$

number of attractors

Gaussian distribution

sparseness (0's and 1's)

clipping function:

random connectivity

$$\varepsilon p^{-1/2} \sum_\mu \xi_i^\mu \xi_j^\mu$$

Mean field analysis:

$$\nu = (\ldots)\left[\overline{\Phi}\left(\theta - J\nu - f\beta m\right) + f\Delta\Phi(\nu, m, \theta)\right]$$

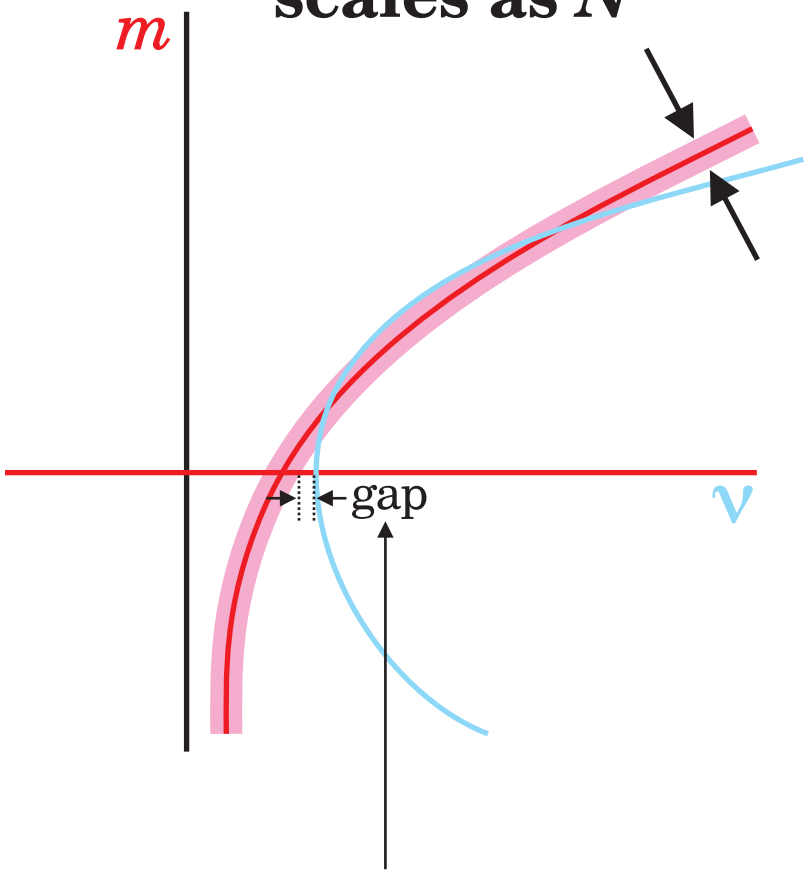
$$m = (\ldots)\Delta\overline{\Phi}(\nu, m)$$

$$\mathrm{Var}[\theta] = G(\nu, m)$$

Relatively unimportant factors associated with multiple attractors

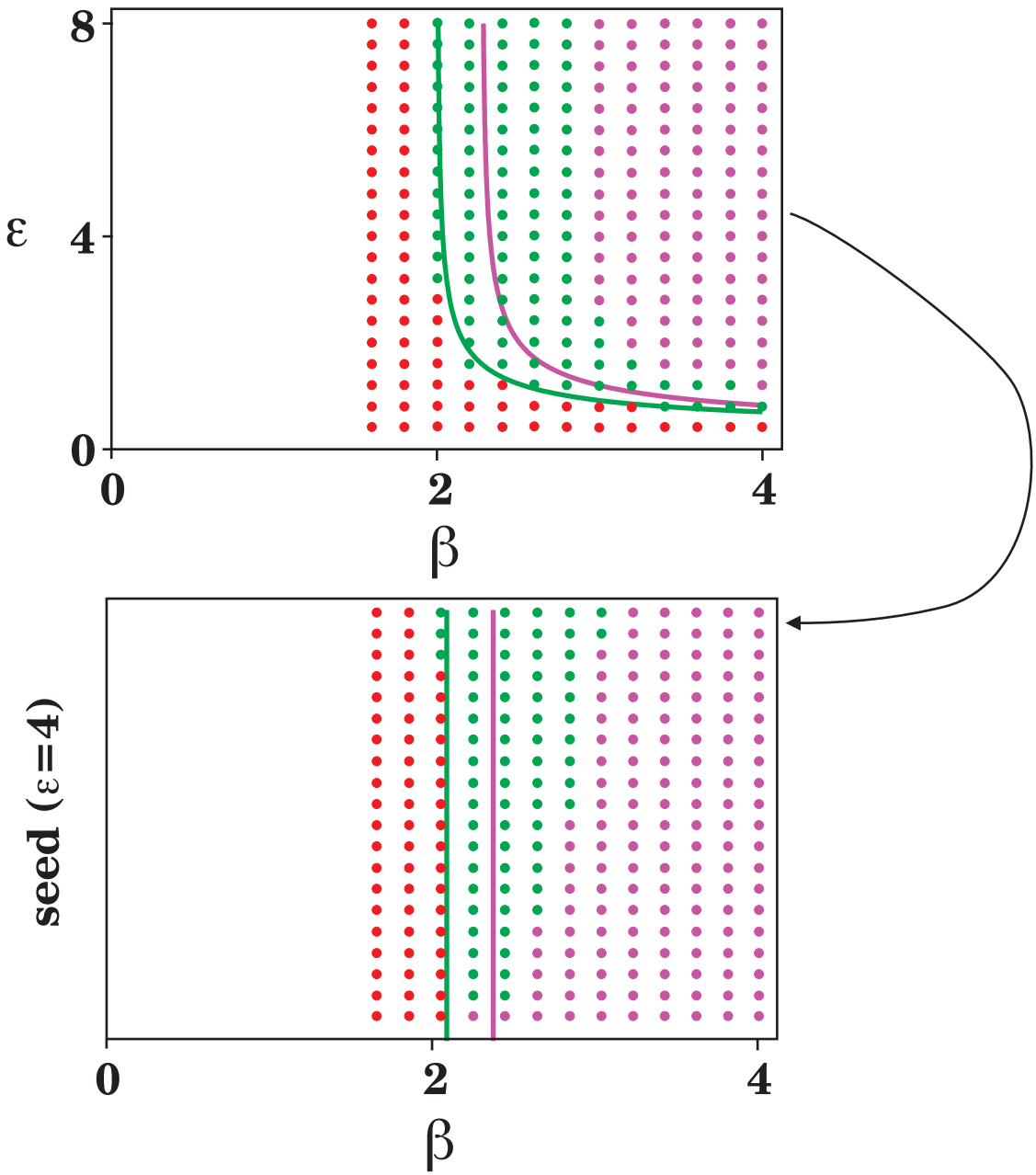
ν–m phase space

Additional thickness due to multiple attractors; scales as $N^{-1/2}$



Background unstable when gap vanishes

Simulations



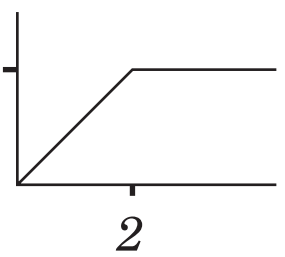
- No attractors embedded
- Attractors embedded; background stable
- Background unstable
- Boundaries, from mean field theory

Simulation details

$$\dot{\nu}_i = \beta p^{1/2} \Phi\left(\hat{\theta}_i - (a+1)\nu + (\bar{g}N)^{-1} \sum_j C_{ij}\, g(W_{ij} + J_{ij})\nu_j\right) - \nu_i$$

N	$=8000$
p	$=200$
f	$=0.1$
a	$=0.5$
Mean$[\hat{\theta}]$	$=1.5$
Var$[\hat{\theta}]$	$= 6.0/p$
P_{connect}	$= 0.3$
Mean$[W]$	$= 1$
Var$[W]$	$= 0.09$
$\Phi(x)$	$= \max(x, 0)$

g $=$



Summary

- **By avoiding sparse-coding limit, it becomes possible to robustly embed attractors in realistic neuronal networks.**

Future directions:

- **Simulations with spiking neurons.**
- **Scaling -- implications for cortical networks.**