Attractor networks in systems with underlying random connectivity.

P.E. Latham
and
S. Nirenberg

University of California at Los Angeles

898.14
SFN 1999

Introduction

Most treatments of Hopfield networks (PNAS 1982) assume a weight matrix of the form

$$J_{ij} \propto \sum_{\mu} \epsilon_{\mu} \eta_i^{\mu} \eta_j^{\mu}$$

where ϵ_{μ} represents the strength of the μth memory and η^{μ} is a vector of 0s and 1s. Here we consider the more realistic case in which the weight matrix has additional components:

$$J_{ij} = W_{ij} + c_{ij} \sum_{\mu} N_{\mu}^{-1} \epsilon_{\mu} \eta_i^{\mu} (\eta_j^{\mu} - f_{\mu})$$

where W_{ij} is a random matrix that corresponds to the (sparse) connectivity in the absence of stored memories, c_{ij} is 1 if neuron j is connected to neuron i and 0 otherwise, a fraction f_{μ} of the components of η^{μ} are equal to 1, and N_{μ} neurons participate in the μth memory.

Randomly connected networks of excitatory and inhibitory neurons with no memories (all the ϵ_{μ} equal to zero) exhibit, over a broad range of parameters, a single stable state at low firing rate. We investigate, using both mean field analysis and simulations with spiking model neurons, the conditions for the formation of additional fixed points — new memories — as the ϵ_{μ} grow.

The problem

It is well known that idealized neurons can form attractor (Hopfield) networks:
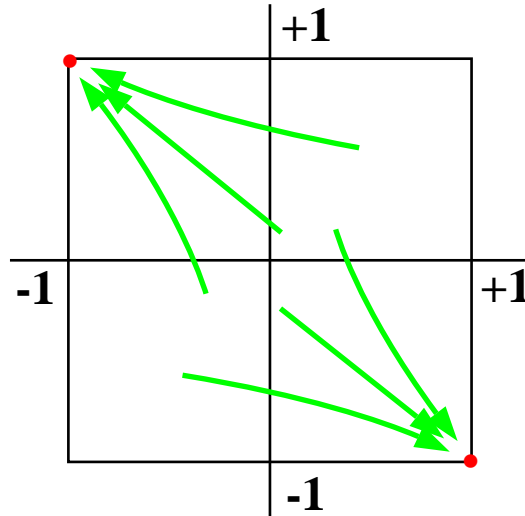
**2-neuron Hopfield network with fixed points
at (+1, -1) and (-1, +1).**

<u>A beautiful model, but simplifications have been made:</u>
- **Symmetric**
- **Units are +1 or -1**
- **All-all coupling**
- **Neurons are simple: no voltage gated channels ...**
- **Coupling is simple: no synapses or dendrites ...**
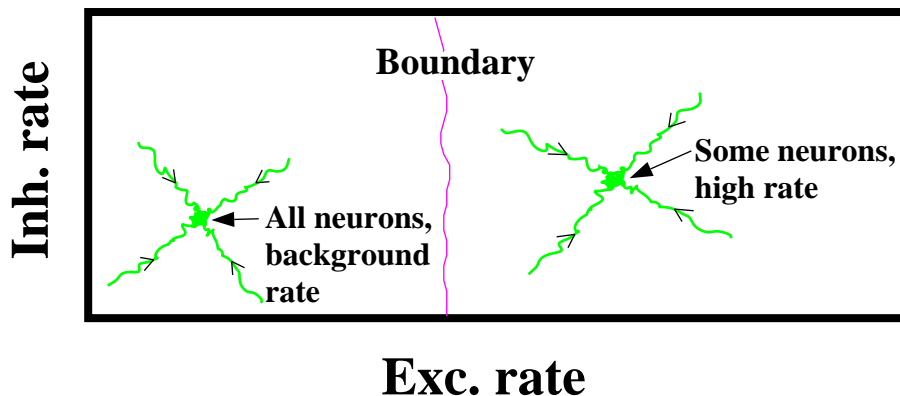
What about real, <u>spiking</u>, <u>excitatory</u> and <u>inhibitory</u> neurons with <u>synaptic</u>, <u>non-symmetric</u> coupling and <u>sparse</u> connectivity?

The Issues

Randomly connected excitatory and inhibitory neurons (often) have a globally attacting fixed point at low firing rate
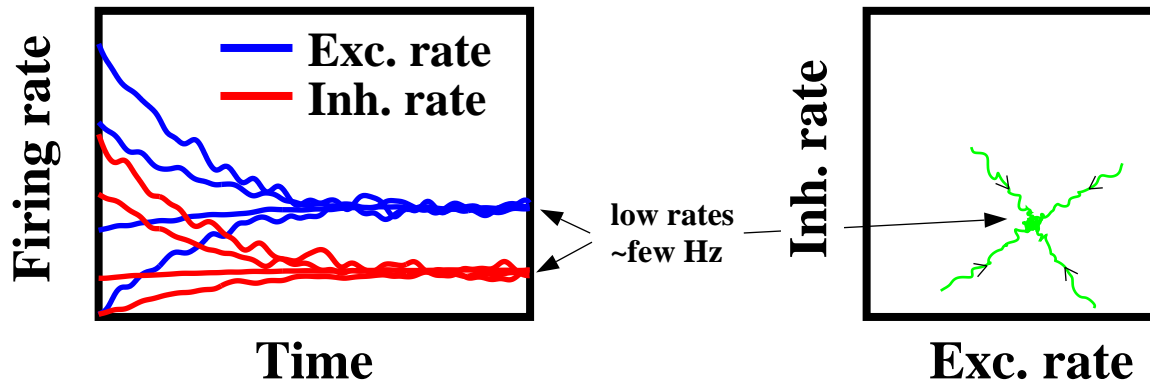
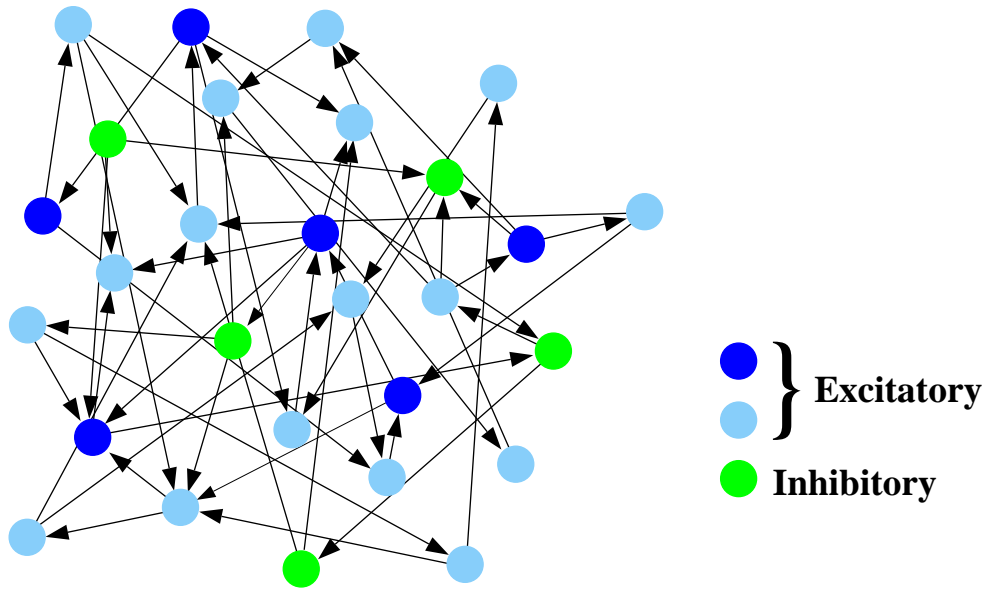**Structured connectivity can embed memories**

Constraints:

1. If no memories are active, network fires at background rate.
2. At most, one memory can be active at a time.

$\Big\}$ Important

i. Non-symmetric connectivity.
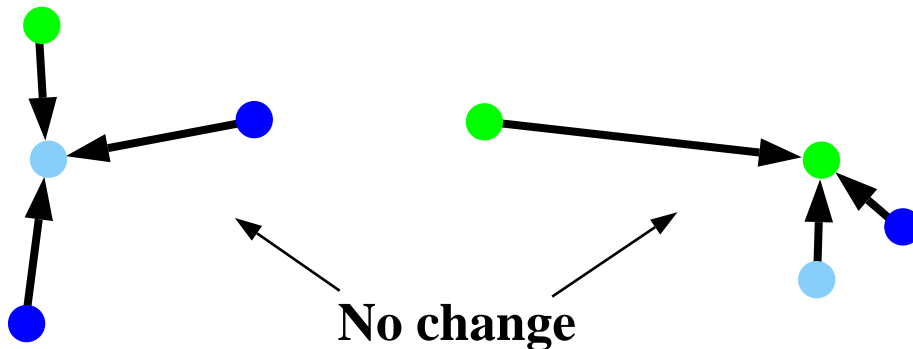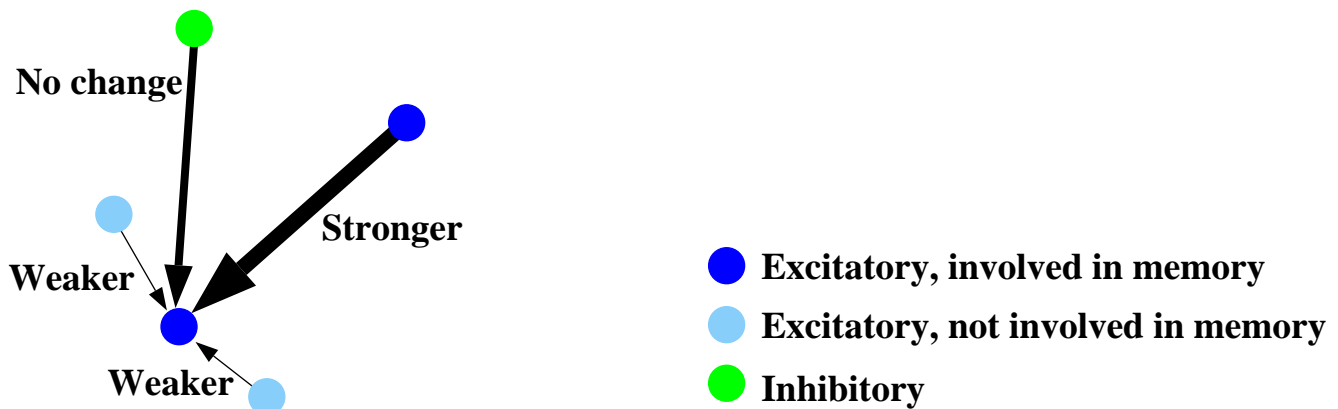ii. Sparse connectivity.

$\Big\}$ Not so important

Can these constraints be satisfied?

The Prescription

Start with a randomly connected network:

} **Excitatory**

Inhibitory

Embed memories:

No change

Stronger

Weaker

Weaker

Excitatory, involved in memory

Excitatory, not involved in memory
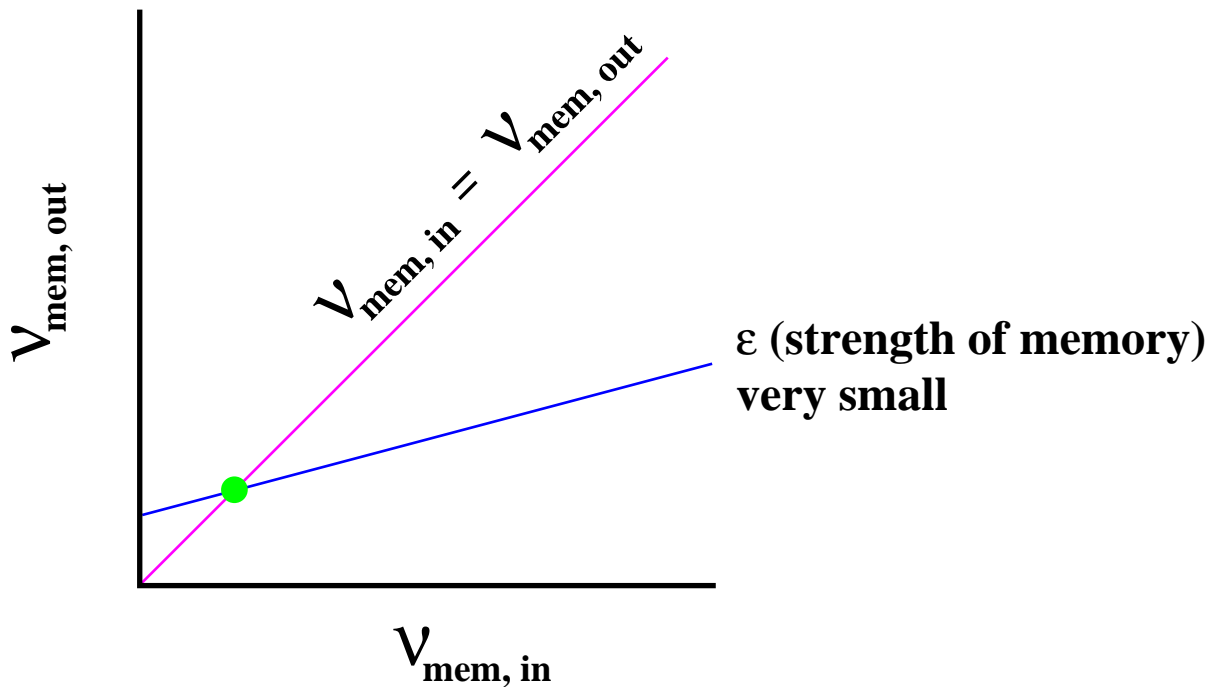
Inhibitory

No change

Analysis

Take the limit f (fraction of neurons in a memory) $\rightarrow 0$.

- **Each memory is all-excitatory network;**
- **Since $f \rightarrow 0$, background firing rate is independent of firing rate of memory neurons.**

Can use (relatively) standard graphical techniques:
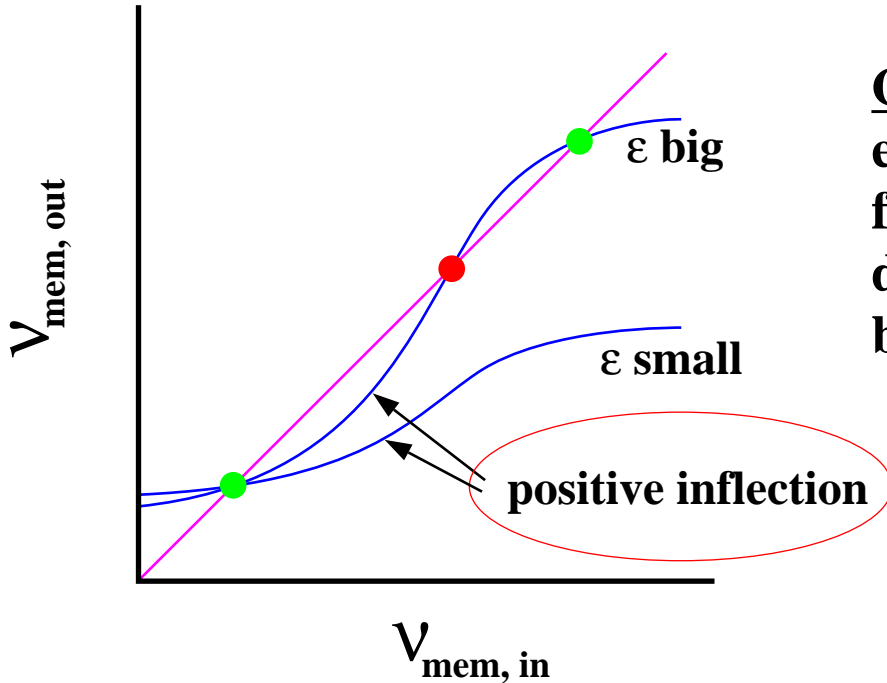

When **strength of memory** (i.e., the increase in connection strength among some subpopulation of neurons) is **small**, there is only one equilibrium and **no memory is embedded**.

- ● Stable equilibrium at background firing rate.

- — Gain functions: output firing rate of memory neurons as a function of input rate.
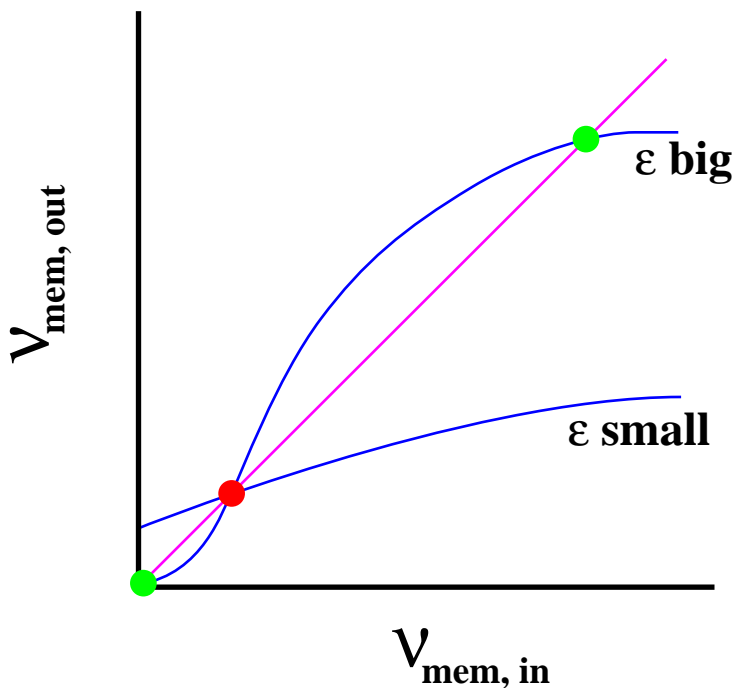
Two possibilities as ε increases:

Good: Memory is embedded at high firing rate without disturbing the background.

Bad:

1. Fluctuations typically destabilize new background.
2. Threshold is low -- this is a problem if you only want one memory to be active at a time.
2a. It's also a problem if you want to avoid epilepsy ...

● Stable equilibrium.
● Unstable equilibrium.
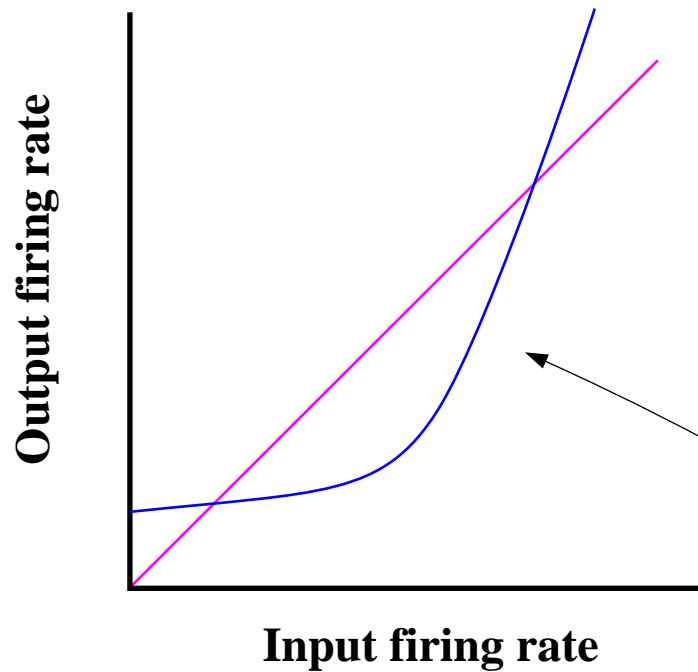— Gain functions: outuput firing rate of memory neurons as a function of input rate.

Gain curve from simulation with 10,000 θ-neurons
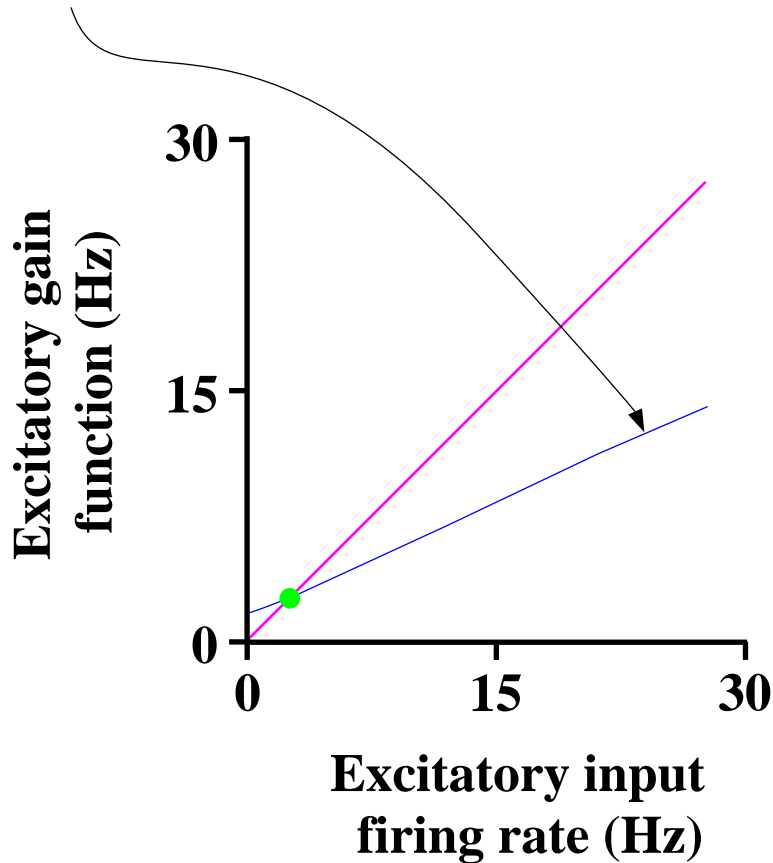
At equilibrium, <u>no</u> positive inflection

For details see: Latham et al, "Intrinsic dynamics in neuronal networks. I. Theory." Available at
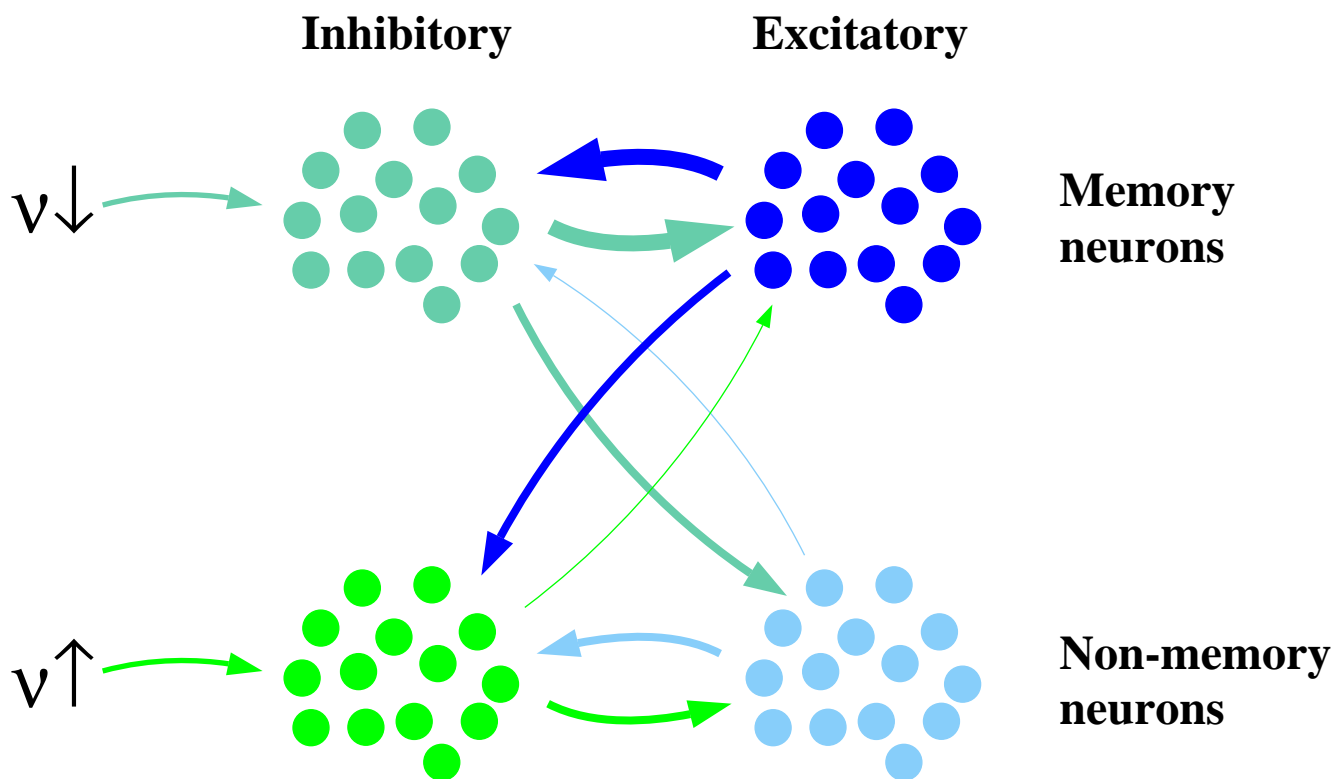
http://culture.neurobio.ucla.edu/~pel/

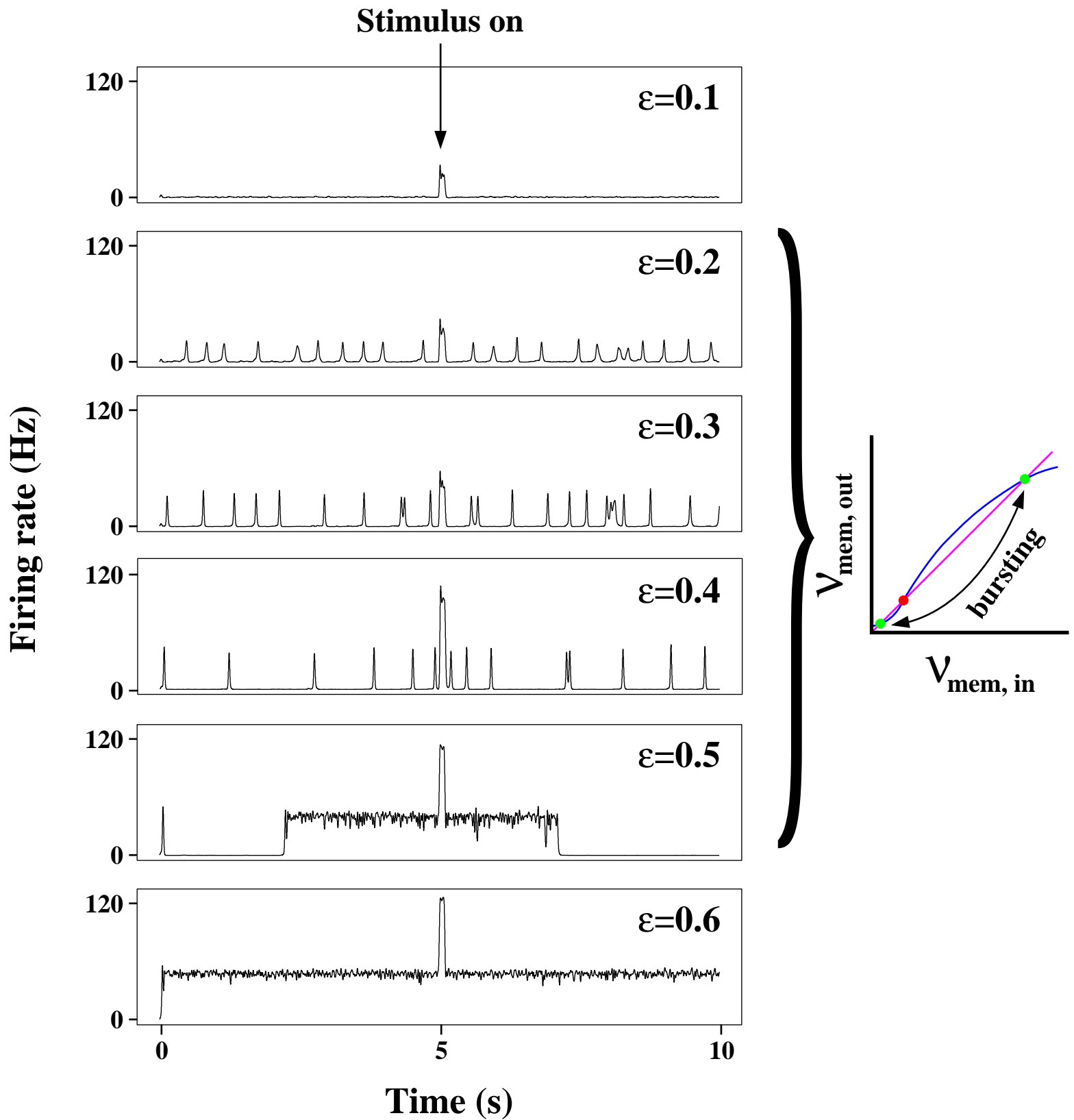**Possible mechanisms for a positive inflection:**

- **NMDA receptors,**
- **Paired-pulse facilitation.**

To enhance this effect, adjust connectivity so that the pool of inhibitory neurons that is firing at a relatively lower rate preferentially connects to the memory neurons:

Simulations

10,000 spiking θ-neurons -- no NMDA channels

10,000 spiking θ-neurons with pseudo-NMDA receptors

Connection strength

Spikes
...

Time (s)

τ=100 ms

~10% jump

One of 64 memories activated

memory 1

memories 2-11

Excitatory firing rate (hz)

Two memories activated

memory 1

memory 2

memories 3-11

Time (s)
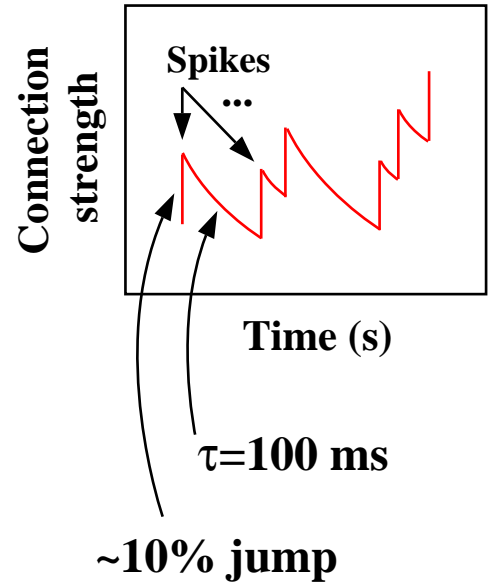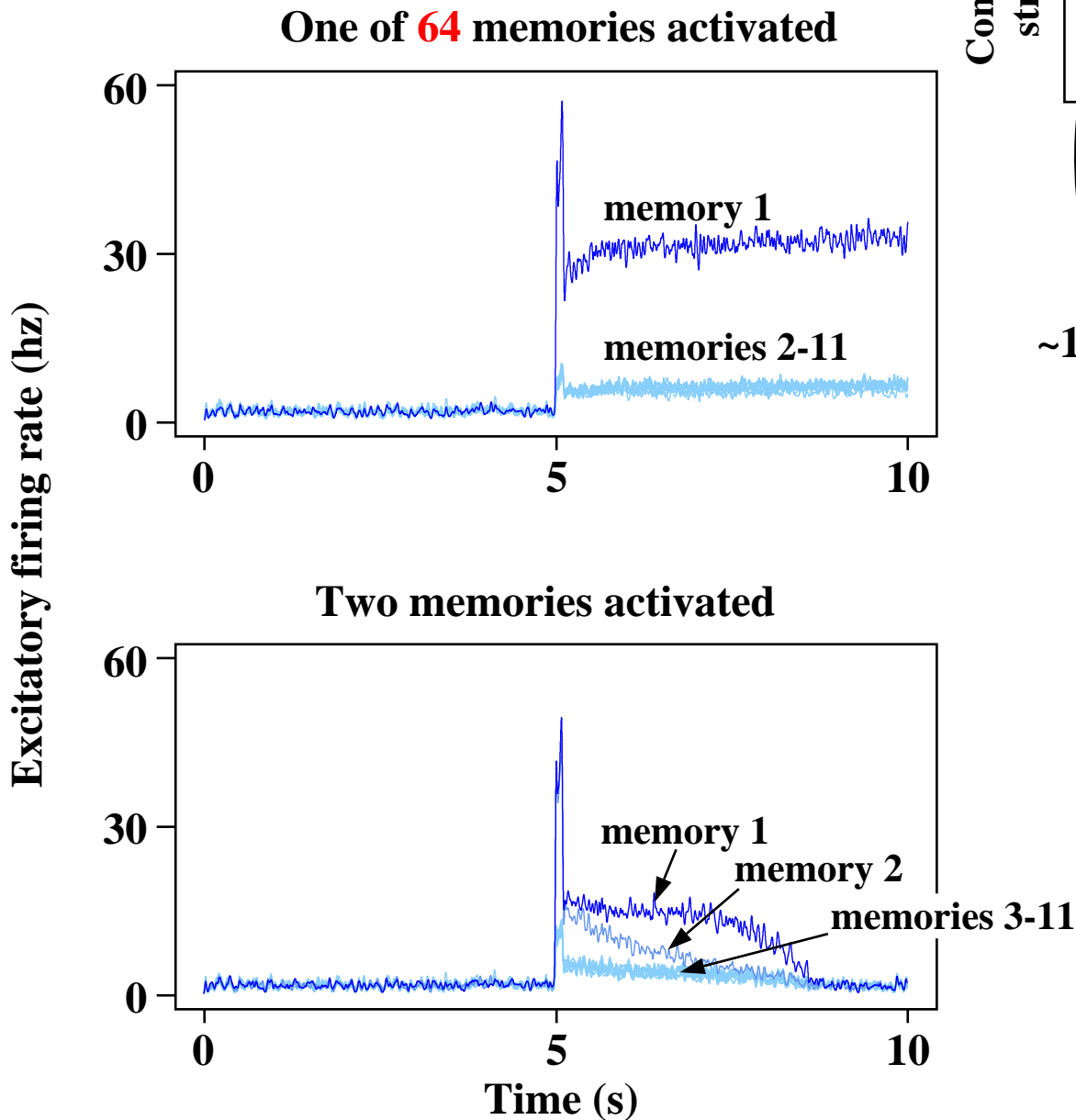
For these parameters, network is sensitive to degredation of input. For a memory to last indefinitely:

> 90% of the memory neurons must be activated
< 15% of non-memory neurons can be activated

Summary

- **Can embed memories <u>if</u> the gain curve (input firing rate versus output firing rate) has a positive inflection at the backgound firing rate.**

- **This will require something like NMDA channels or paired-pulse facilitation, for which the effective connection strength increases with post-synaptic voltage.**
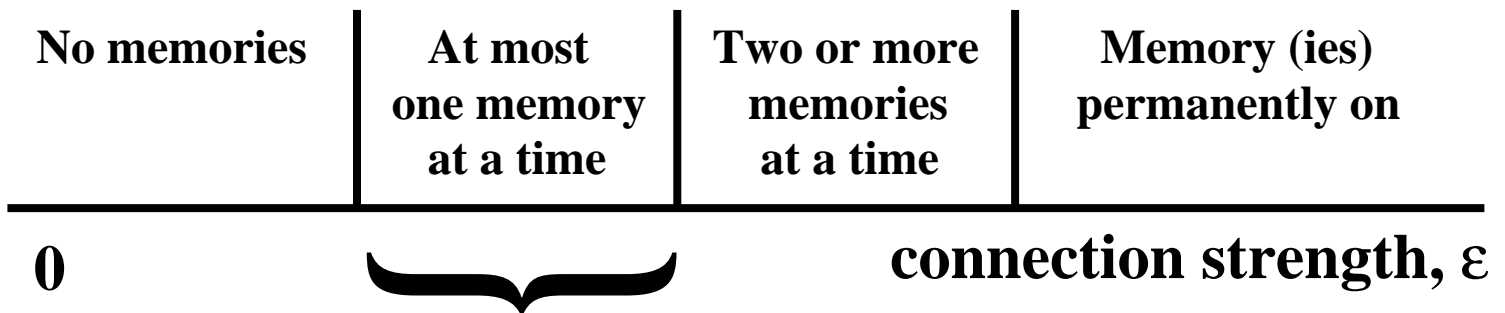
The picture:

No memories	At most one memory at a time	Two or more memories at a time	Memory (ies) permanently on

0   **connection strength, ε**

Desired regime.
In our simulations, this regime was small

Simulations with more realistic neurons are necessary!!

Mean Field Analysis

Equilibrium firing rate equations:

$$\nu_i = \Phi_i \left(\sum_j J_{ij} \nu_j \right)$$

Connectivity:

$$J_{ij} = W_{ij} + c_{ij} \sum_\mu N_\mu^{-1} \varepsilon_\mu \eta_i^\mu (\eta_j^\mu - f_\mu)$$

Sparse, random connectivity matrix

Sparse, random matrix of 0s and 1s.

Number of neurons in memory μ

Strength of memory

Determines which neurons are active during memory μ (vector of 1s and 0s)

Fraction of neurons in memory μ; post-synaptic normalization

Sources of randomness:

1. **W** and **c** -- random connectivity.
2. Non-active memories (see Chapter 10 of Hertz, Krogh and Palmer).

Define overlaps:

$$m^\mu = N_\mu^{-1} \sum_i \eta_i^\mu \nu_i$$

Perform suitable averaging, arrive at mean-field equations when 1 neuron is active:

$$m^\mu = \overline{\Phi}\left(C_0 \overline{\nu} + C_\mu m^\mu\right)$$

Mean firing rate (which has its own equilibrium equation)

Average is over random connectivity and non-active memories

Warning: the existence of excitatory neurons adds considerable algebra, but not much new conceptually.

Firing-rate-model simulations -- no memories

All excitatory network

Mean firing rate (Hz)

- — Mean field prediction
- × Simulations
- ⊨ SEM (n=100)

Variance of J•v

Standard deviation of elements of connectivity matrix (J)

Excitatory and inhibitory network

Mean inhibitory firing rate (Hz)

Increasing variance in connectivity matrix

- + Mean field prediction
- · Simulations

Mean excitatory firing rate (Hz)