Attractor networks in systems with underlying random connectivity.

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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 μ^{th} 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:

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

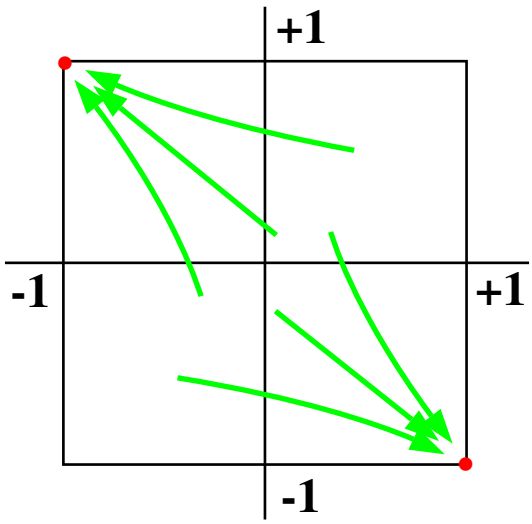
where W_{ij} is a random matrix that corresponds to the (sparse) connectivity in the absence of stored memories, c_{ij} is 1 if neuron j is connected to neuron i and 0 otherwise, a fraction f_μ of the components of η^μ are equal to 1, and N_μ neurons participate in the μ^{th} memory.

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.

Supported by the Klingenstein foundation.

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).

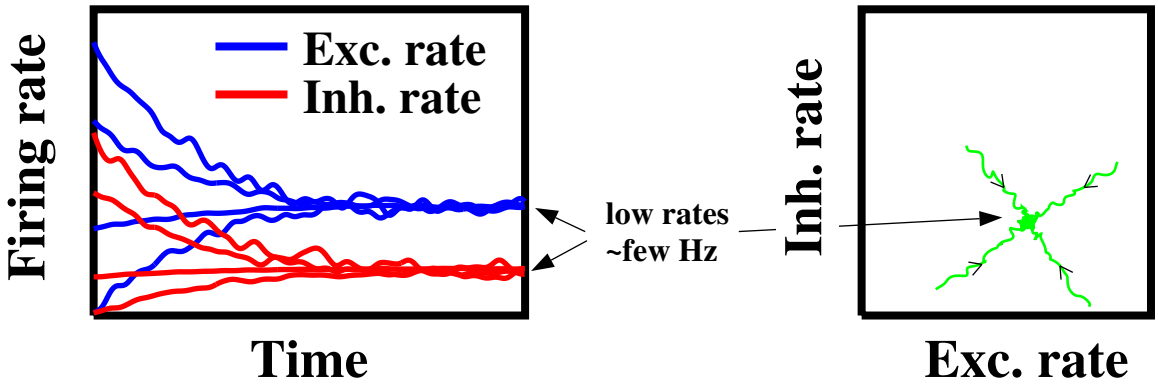
A beautiful model, but simplifications have been made:

- **Symmetric**
- **Units are +1 or -1**
- **All-all coupling**
- **Neurons are simple: no voltage gated channels ...**
- **Coupling is simple: no synapses or dendrites ...**

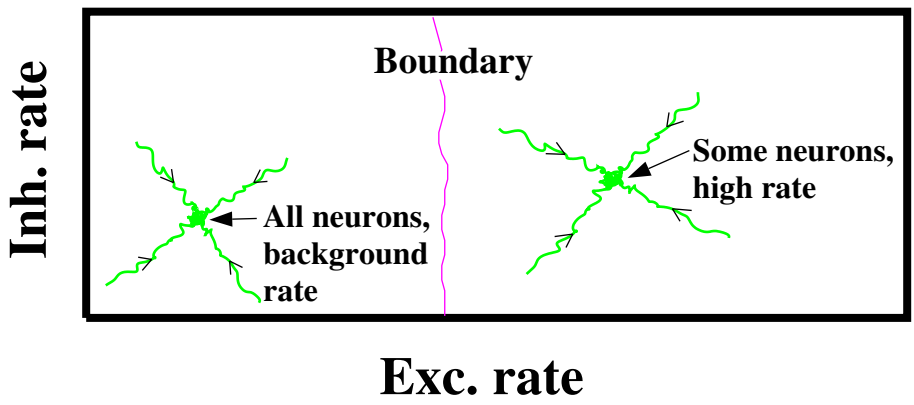
What about real, spiking, excitatory and inhibitory neurons with synaptic, non-symmetric coupling and sparse connectivity?

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.

} Important

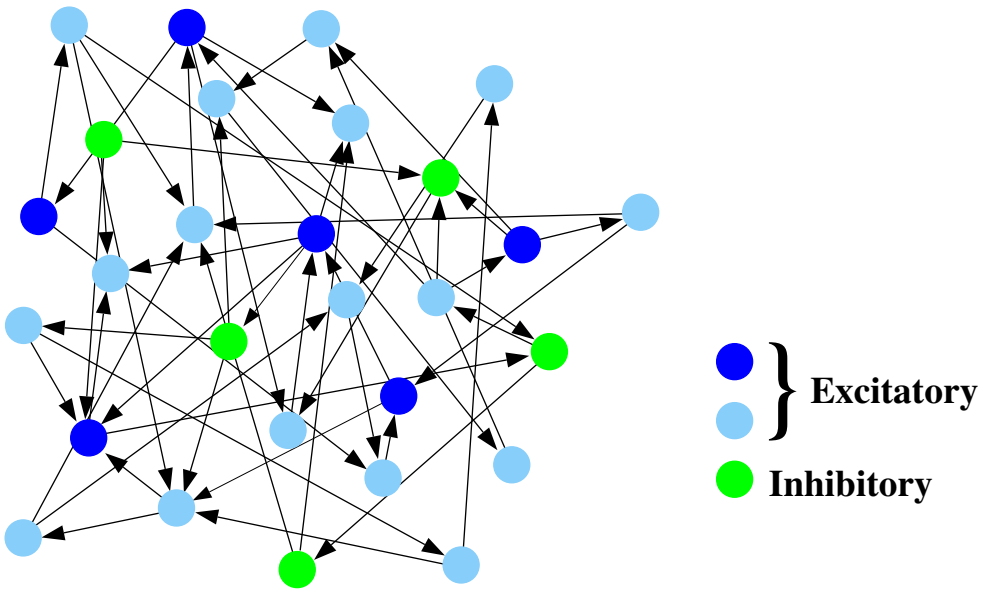
i. Non-symmetric connectivity.
ii. Sparse connectivity.

} Not so important

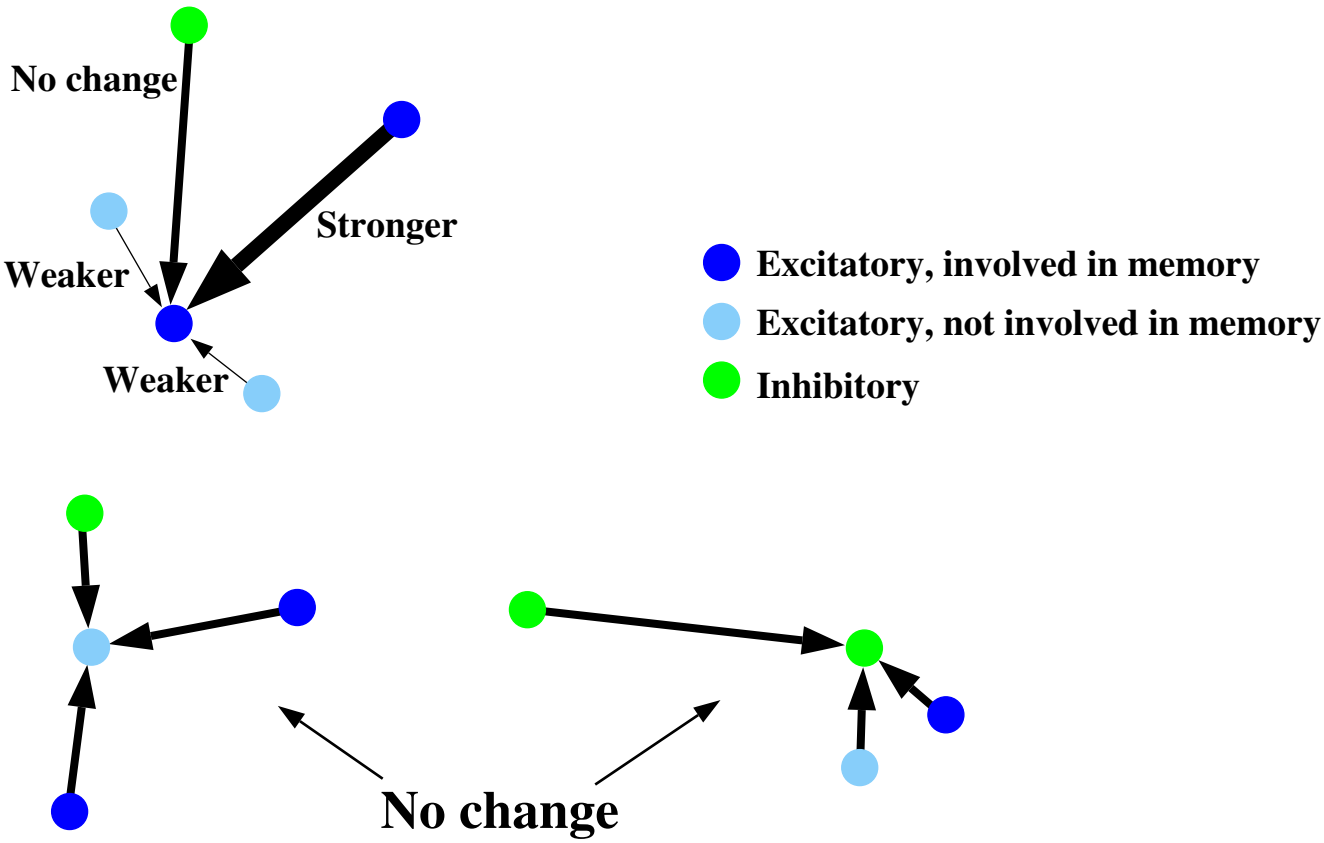
Can these constraints be satisfied?

The Prescription

Start with a randomly connected network:



Embed memories:

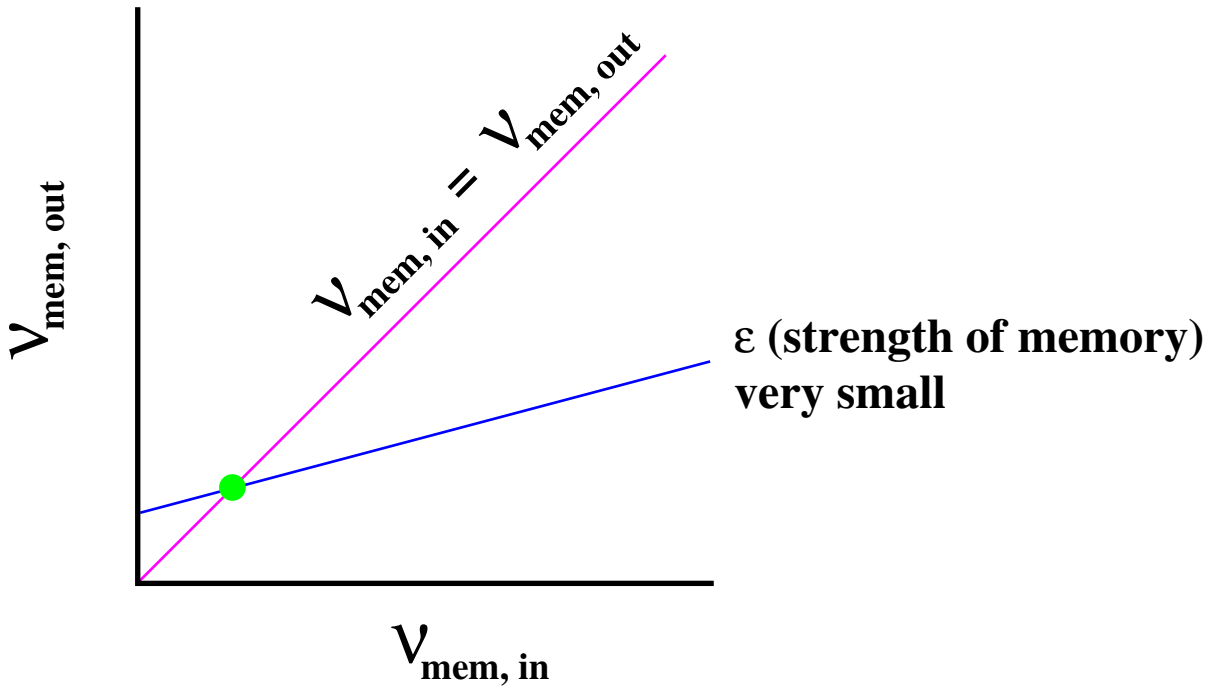


Analysis

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.**

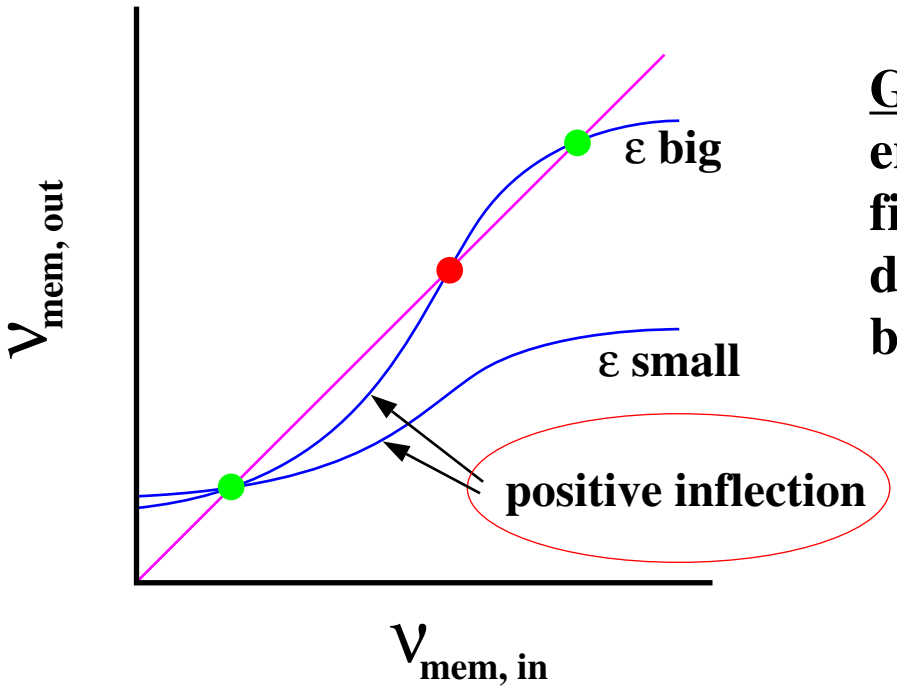
Can use (relatively) standard graphical techniques:



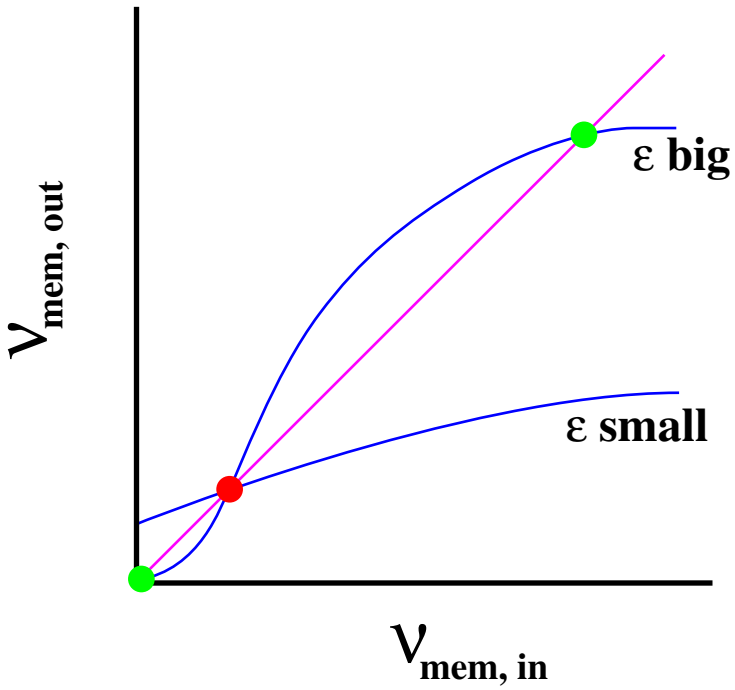
When strength of memory (i.e., the increase in connection strength among some subpopulation of neurons) is small, there is only one equilibrium and no memory is embedded.

- ● **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:



<u>Good:</u> Memory is embedded at high firing rate without disturbing the background.



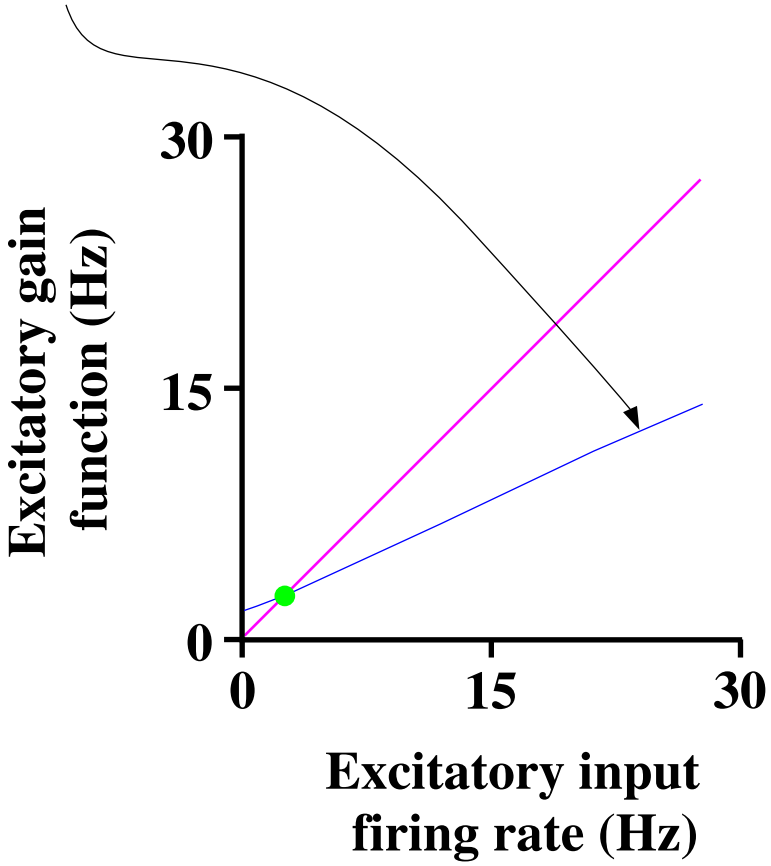
<u>Bad:</u>

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: outupt firing rate of memory neurons as a function of input rate.**

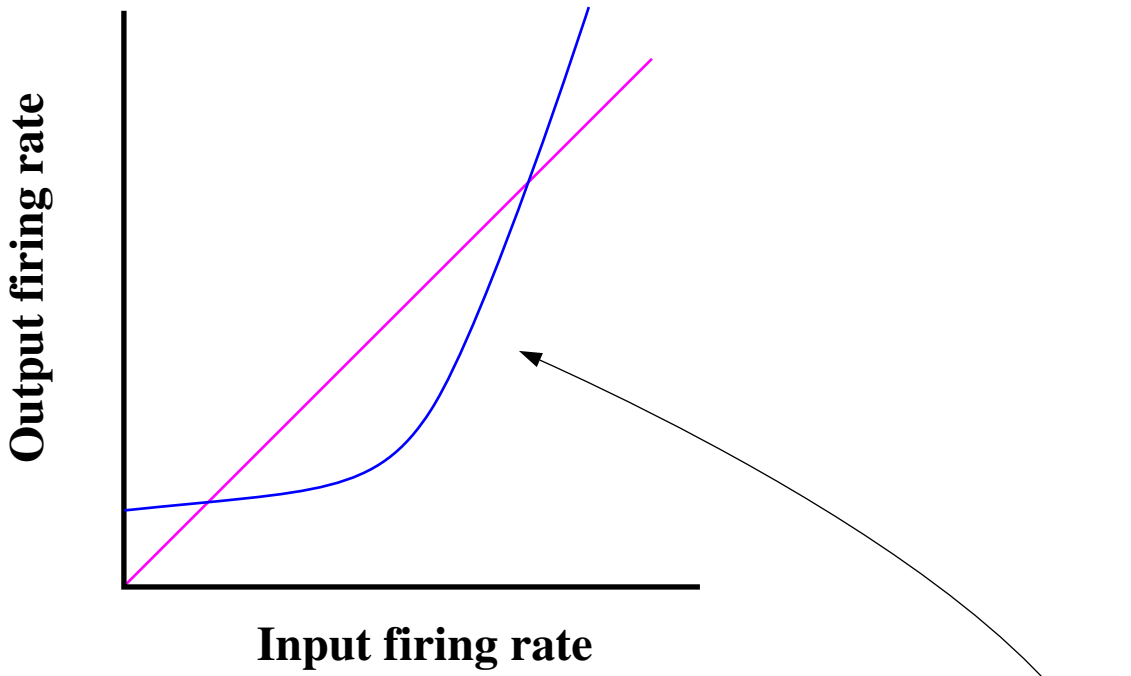
Gain curve from simulation with 10,000 θ-neurons



At equilibrium, no positive inflection

For details see: Latham et al, "Intrinsic dynamics in neuronal networks. I. Theory." Available at

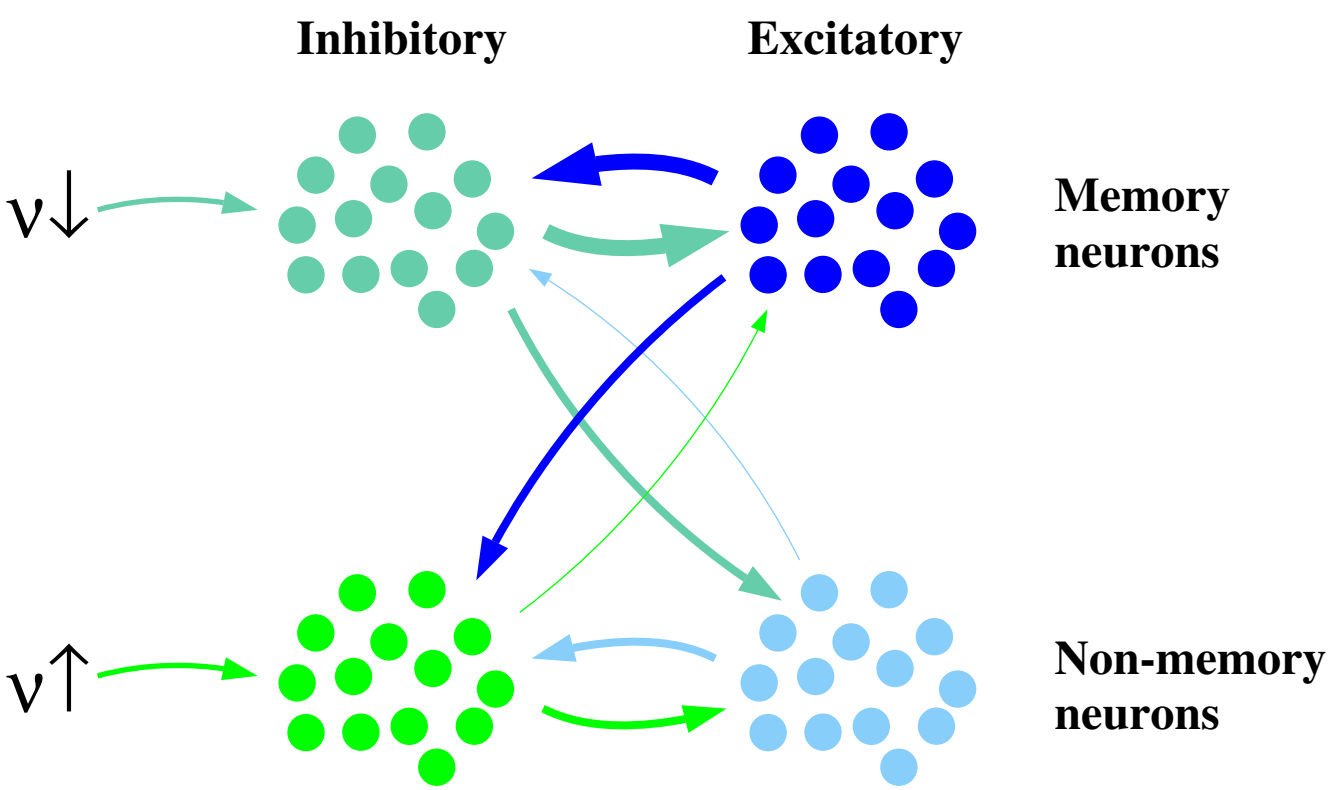
http://culture.neurobio.ucla.edu/~pel/



Possible mechanisms for a positive inflection:

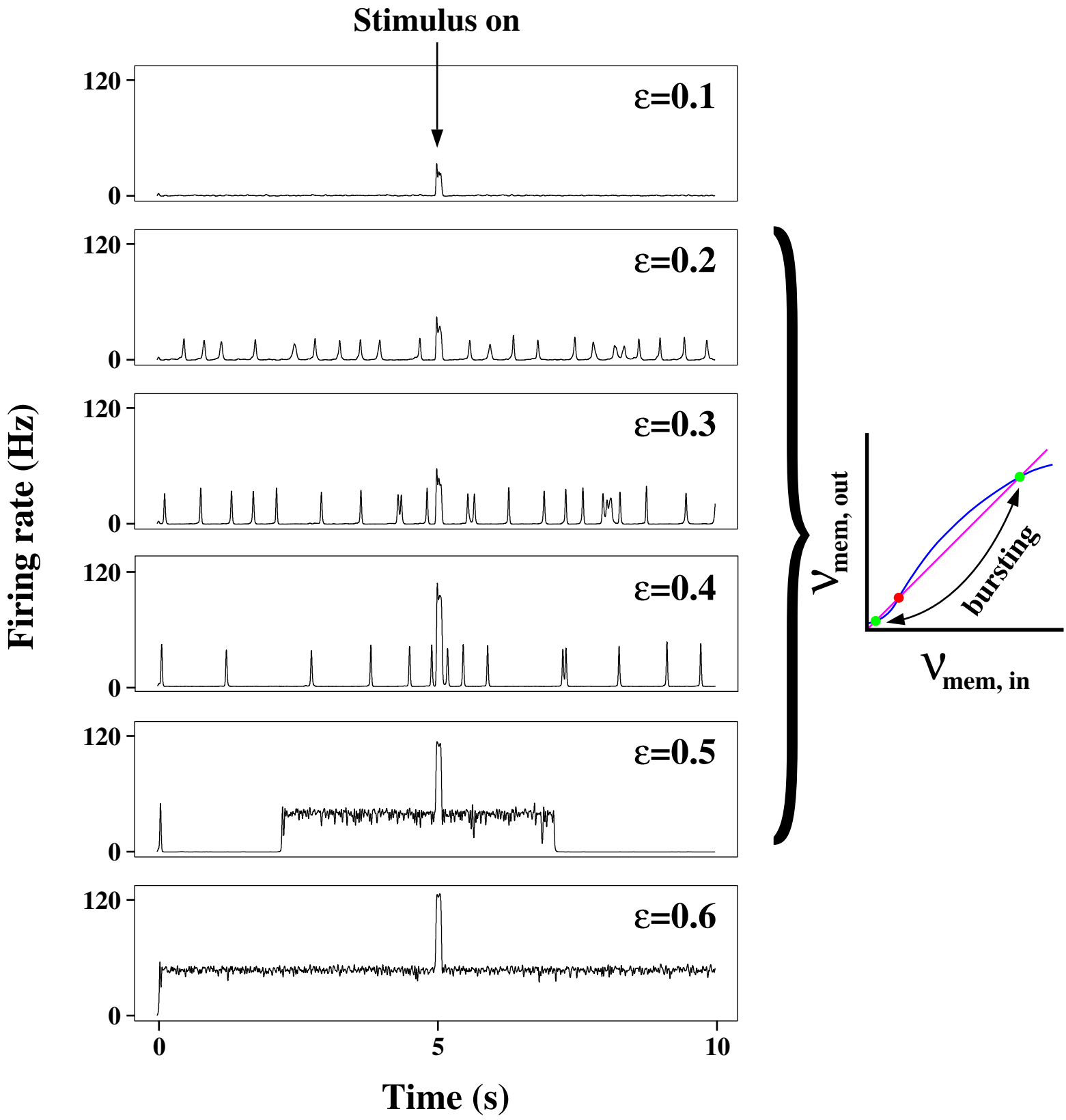
- **NMDA receptors,**
- **Paired-pulse facilitation.**

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:

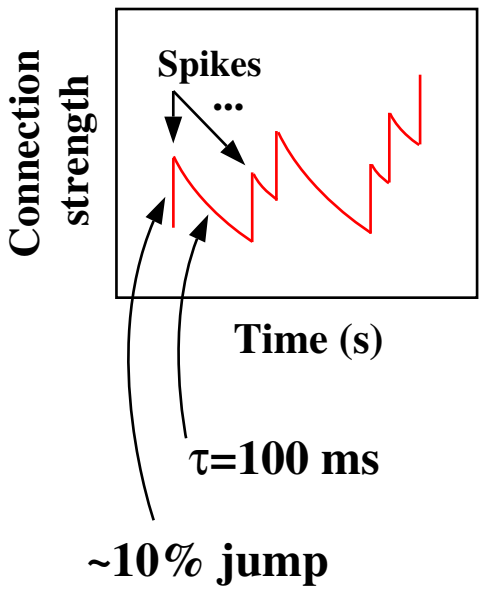


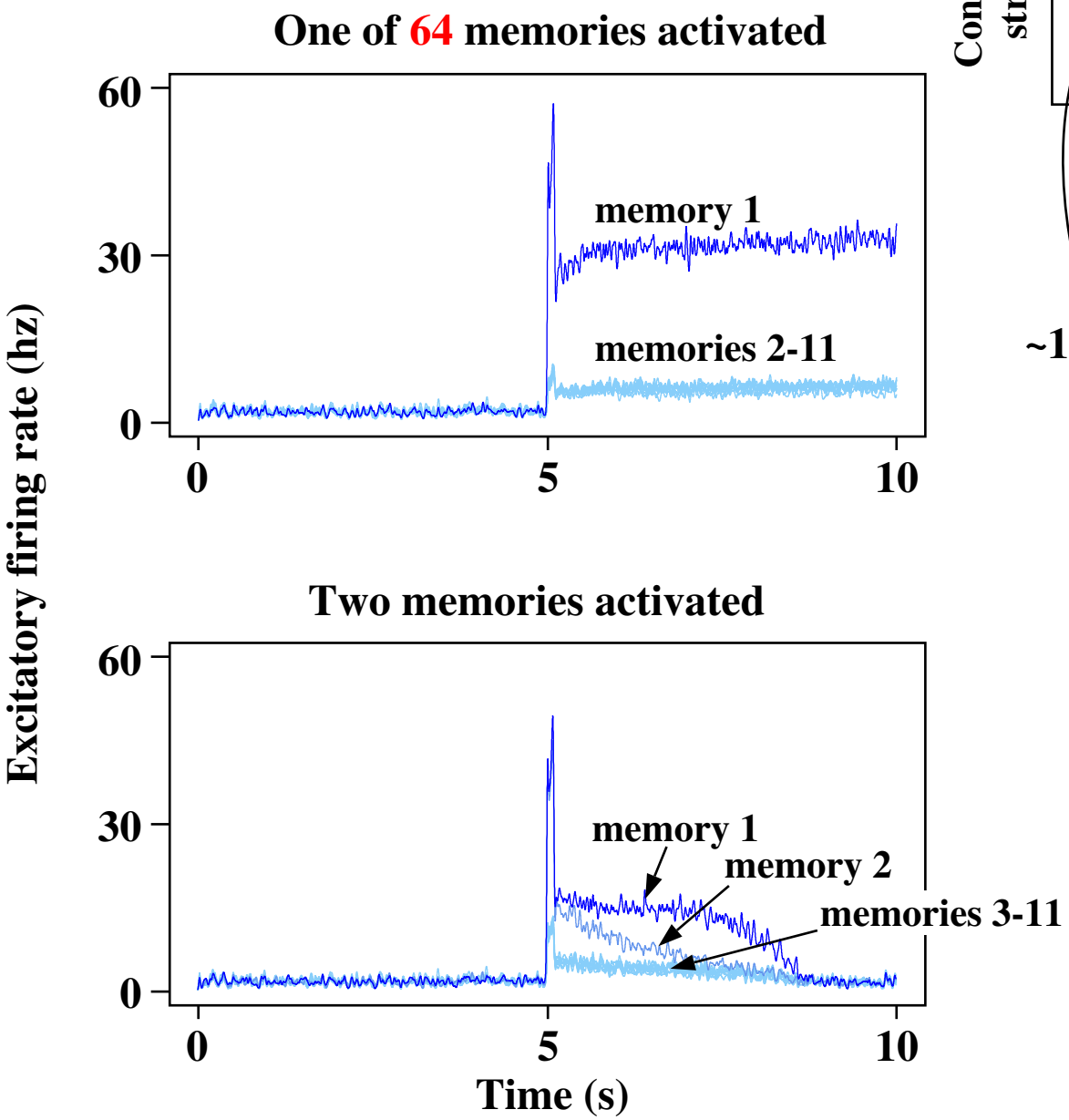
Simulations

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



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





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

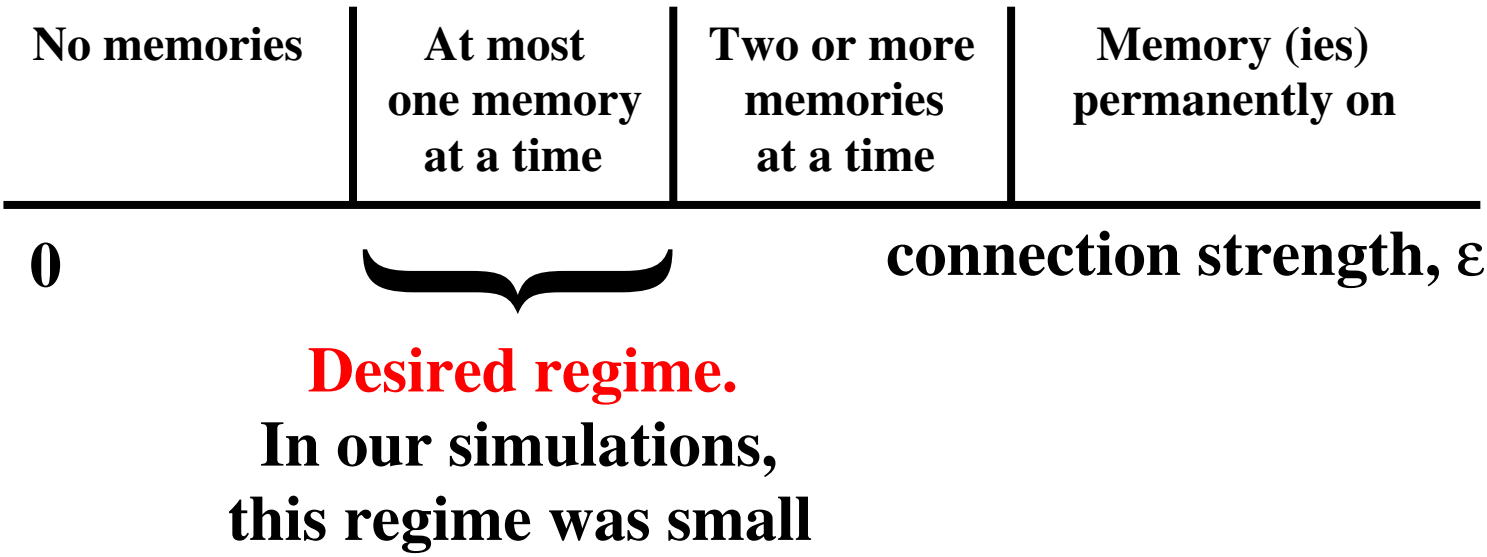
> 90% of the memory neurons must be activated
< 15% of non-memory neurons can be activated

Summary

- **Can embed memories if 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:



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:

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

- W_{ij}: Sparse, random connectivity matrix
- c_{ij}: Sparse, random matrix of 0s and 1s.
- N_μ: Number of neurons in memory μ
- ε_μ: Strength of memory
- η_i^μ: Determines which neurons are active during memory μ (vector of 1s and 0s)
- f_μ: 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:

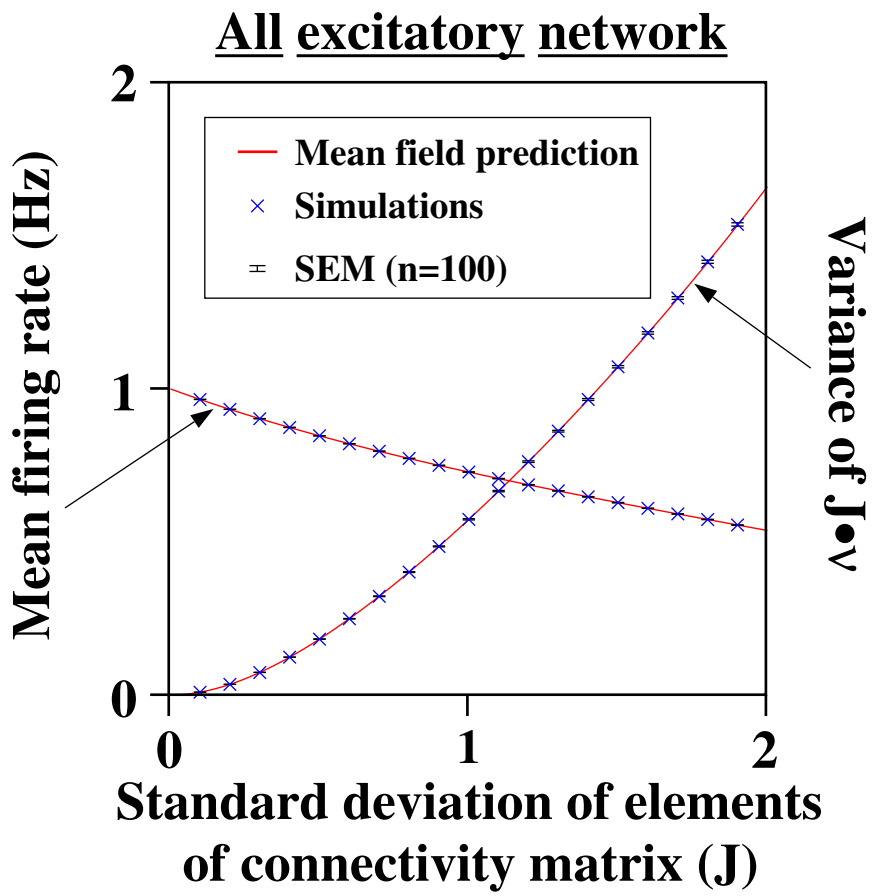
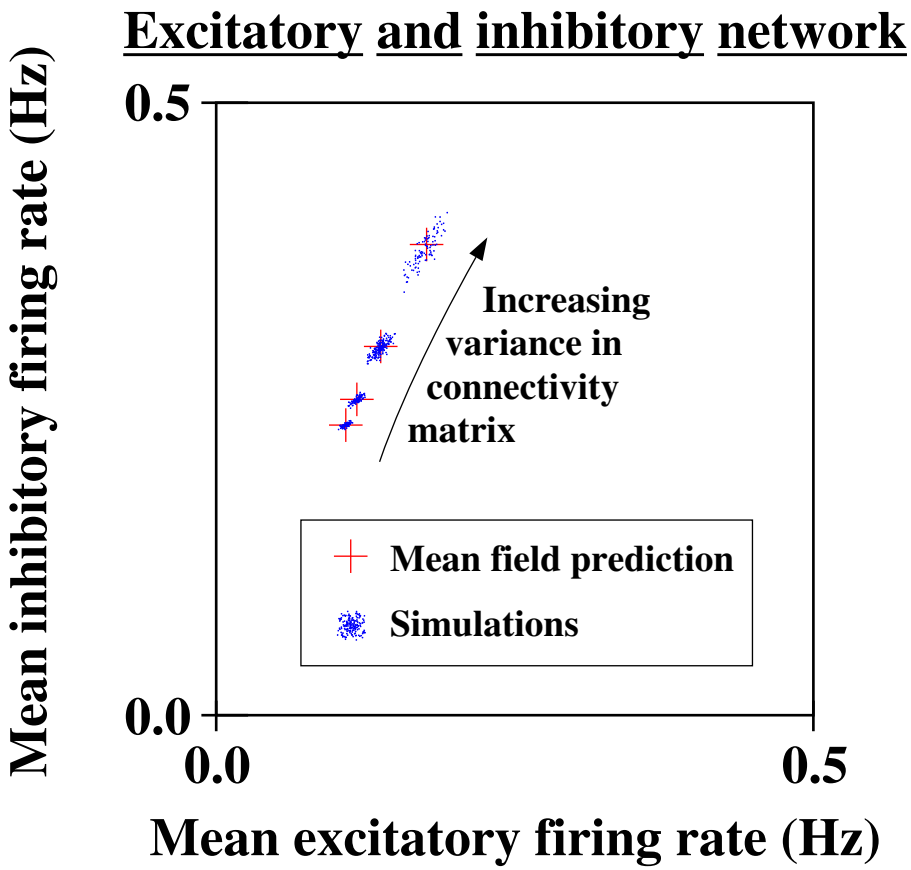
$$m^{\mu} = N_{\mu}^{-1} \sum_{i} \eta_i^{\mu} \nu_i$$

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