

# Lengths of attractors and transients in neuronal networks with random connectivities

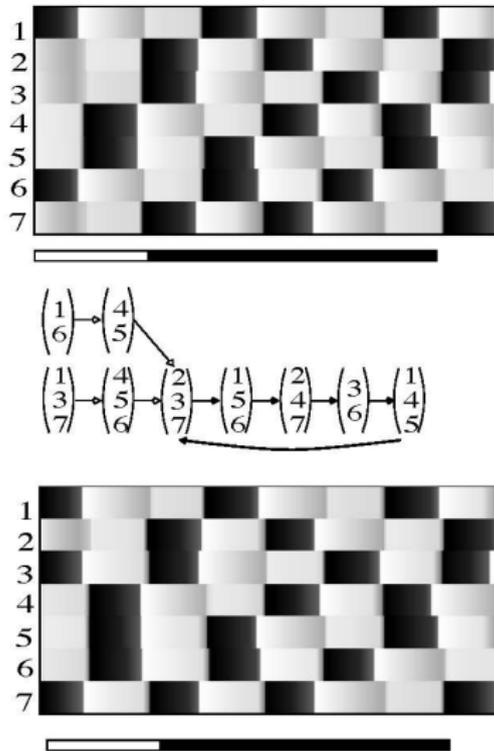
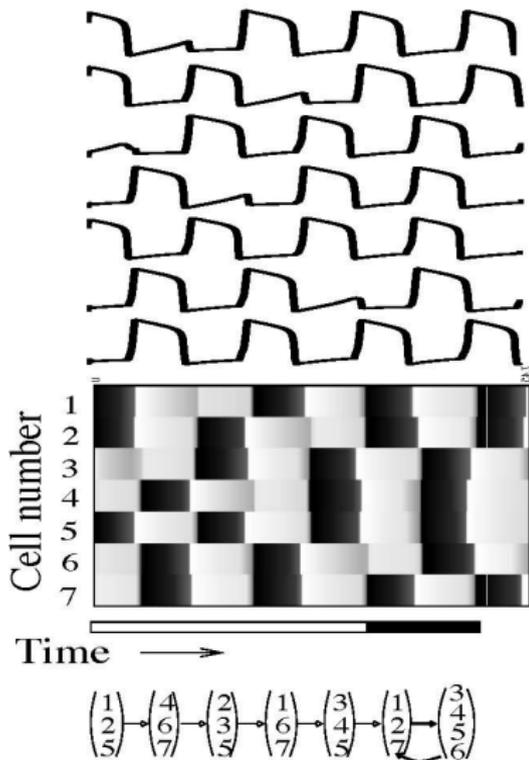
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# A problem from mathematical neuroscience

Some recordings from certain neuronal tissues (of real organisms) reveal the following pattern: Time seems to be partitioned into **episodes** with surprisingly sharp boundaries. During one episode, a group of neurons fires, while other neurons are at rest. In the next episode, a different group of neurons fires. Group membership may vary from episode to episode, a phenomenon called **dynamic clustering**.

# How dynamic clustering looks like



# How to model dynamic clustering

Time seems to be partitioned into episodes with surprisingly sharp boundaries. During one episode, a group of neurons fires, while other neurons are at rest. In the next episode, a different group of neurons fires. Group membership may vary from episode to episode.

**Why? How can we mathematically explain this phenomenon?**

Of course, something like this will occur in many discrete-time dynamical systems, but this does not give an **explanation** as the episodes are built right into the definition of time.

**Does the phenomenon occur in biologically realistic ODE models?**

# An ODE model of neuronal networks

by Terman D, Ahn S, Wang X, Just W, Physica D. 2008

Each excitatory ( $E$ -) cell satisfies

$$\begin{aligned}\frac{dv_i}{dt} &= f(v_i, w_i) - g_{EI} \sum s_j^I (v_i - v_{syn}^I) \\ \frac{dw_i}{dt} &= \epsilon g(v_i, w_i) \\ \frac{ds_i}{dt} &= \alpha(1 - s_i)H(v_i - \theta_E) - \beta s_i.\end{aligned}$$

Each inhibitory ( $I$ -) cell satisfies

$$\begin{aligned}\frac{dv_i^I}{dt} &= f(v_i^I, w_i^I) - g_{IE} \sum s_j (v_i^I - v_{syn}^E) - g_{II} \sum s_j^I (v_i^I - v_{syn}^I) \\ \frac{dw_i^I}{dt} &= \epsilon g(v_i^I, w_i^I) \\ \frac{dx_i^I}{dt} &= \epsilon \alpha_x (1 - x_i^I) H(v_i^I - \theta_x) - \epsilon \beta_x x_i^I \\ \frac{ds_i^I}{dt} &= \alpha_I (1 - s_i^I) H(x_i^I - \theta_x) - \beta_I s_i^I.\end{aligned}$$

# We have a plausible model, but ...

Let us call the model that we just described  $M$ .

- The model  $M$  **does predict** dynamic clustering.
- The architecture involves a layer of excitatory neurons and a layer of inhibitory neurons that mediate the firing of the excitatory neurons.
- Individual neurons are modeled by a version of the Hodgkin-Huxley Equations, which are **nonlinear DEs**.
- These are **difficult** to analyze mathematically even for single neurons, let alone for large networks.

**Can we study the dynamics of  $M$  by means of a simpler, approximate model  $N$ ?**

# Mathematical neuroscience for the rest of us

The following is true in at least some neuronal networks.

- Neurons **fire** or are at rest.
- After a neuron has fired, it has to go through a certain **refractory period** when it cannot fire.
- Neurons are connected via synapses. Through a given synapse, the **presynaptic** neuron may send **firing input** to the **postsynaptic neuron**.
- A neuron will fire when it has reached the end of its refractory period and when it receives firing input from a specified minimal number of other neurons.

This is of course way too simple ...

but let us build a class of simple models  $N$  of neuronal networks based on these facts.

# Discrete dynamical system models $N(D)$

Let  $D = ([n], A_D)$  be a digraph on  $[n] = \{1, \dots, n\}$ .

We describe here only the simplest case when all refractory periods and firing thresholds are 1.

A state  $\vec{s}(t)$  at the discrete time  $t$  is a vector:

$\vec{s}(t) = (s_1(t), \dots, s_n(t))$  where  $s_i(t) \in \{0, 1\}$  for each  $i$ .

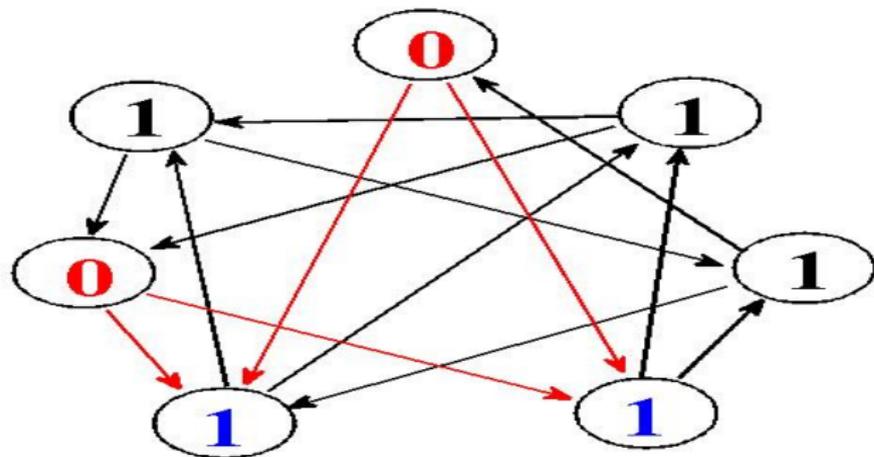
The state  $s_i(t) = 0$  means neuron  $i$  fires at time  $t$ .

Dynamics of  $N(D)$ :

- If  $s_i(t) < 1$ , then  $s_i(t+1) = s_i(t) + 1 = 1$ .
- If  $s_i(t) = 1$ , and there exists at least one neuron  $j$  with  $s_j(t) = 0$  and  $\langle j, i \rangle \in A_D$ , then  $s_i(t+1) = 0$ .
- If  $s_i(t) = 1$  and there does not exist a neuron  $j$  with  $s_j(t) = 0$  and  $\langle j, i \rangle \in A_D$ , then  $s_i(t+1) = 1$ .

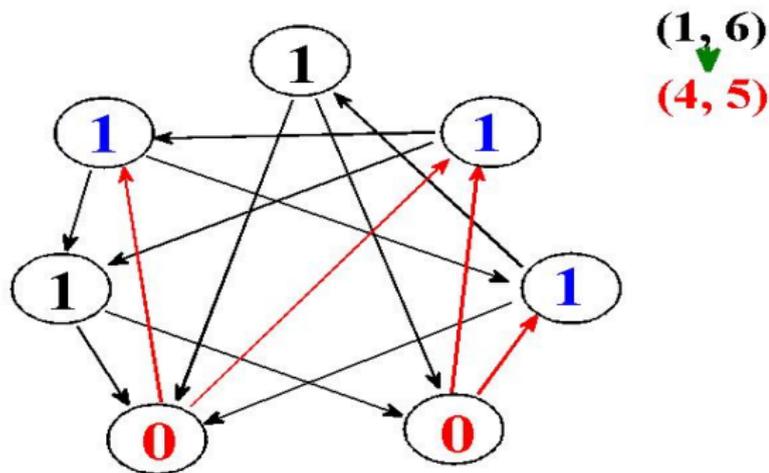
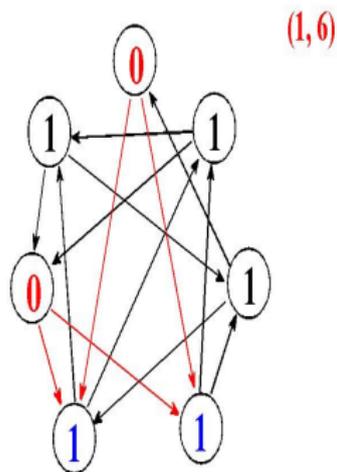
$N(D)$  is a Boolean dynamical system.

# An example

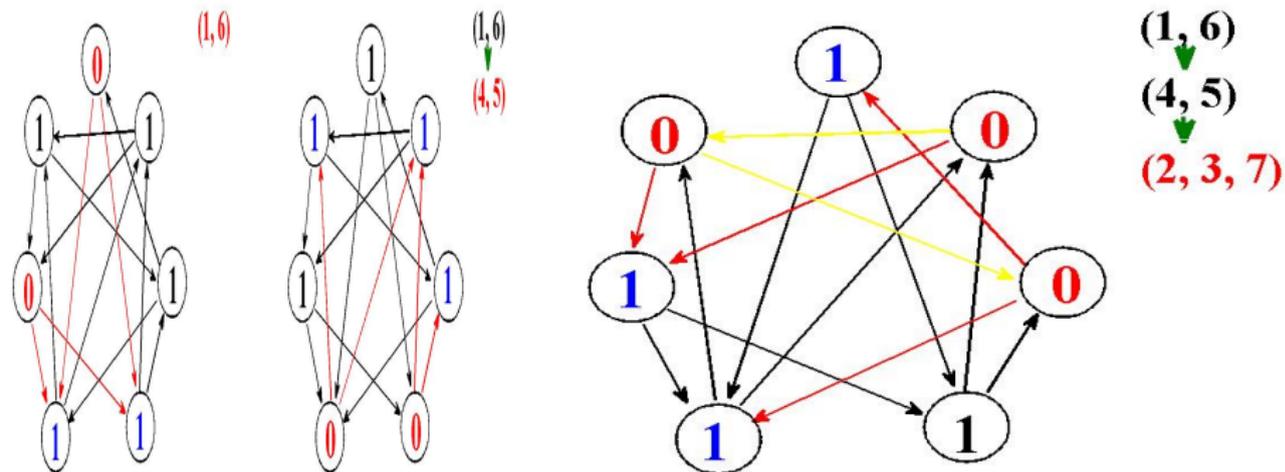


**(1, 6)**

# An example



# An example



# Reducing neuronal networks to discrete dynamics,

by Terman D, Ahn S, Wang X, Just W, Physica D. 2008

## Theorem

*For each ODE model  $M$  of neuronal networks as described above, if the intrinsic and synaptic properties of the cells are chosen appropriately, the dynamics of  $M$  will exhibit dynamic clustering. Moreover, there exists a discrete model  $N = N(D)$  that correctly predicts, for a large region  $U$  of the state space of  $M$  and all times  $t$ , which neurons will fire during which episodes.*

The theorem essentially tells us that as long as  $M$  is a biologically sufficiently realistic model of a given neuronal network, then so is the corresponding model  $N$ .

The discrete models  $N(D)$  are much more tractable than the ODE models  $M$ . In particular, they permit us to **study the dependence of the dynamics on the network connectivity  $D$** .

# The keyword is “more”

I wrote: “The discrete models  $N$  are much **more** tractable than the ODE models  $M$ .”

On the one hand, each such model is a finite object, and in principle each property of the dynamics can be determined by an exhaustive search algorithm.

On the other hand, at least for the version with higher firing thresholds, no **feasible** (polynomial-time) algorithm exists that will even tell you whether a given state  $\vec{s}_*$  will eventually be reached from a given initial state  $\vec{s}(0)$  (W. Just, collected unpublished notes).

In this sense, the dynamics of our **very simple** models  $N(D)$  are already **as complex as the dynamics of any kind** of finite-state discrete models of neuronal dynamics that one could possibly construct.

- W. Just, S. Ahn, and D. Terman (2008); Minimal attractors in digraph system models of neuronal networks. *Physica D* **237**, 3186–3196.  
*Two phase transitions for dense random connectivities.*
- S. Ahn, Ph. D. Thesis (OSU) and S. Ahn and W. Just (2012); Digraphs vs. Dynamics in Discrete Models of Neuronal Networks. *Discrete and Continuous Dynamical Systems - Series B (DCDS-B)* **17**(5) 1365–1381.  
*Characterizes possible dynamics for some basic connectivities.*
- W. Just, S. Ahn, and D. Terman (2013); Neuronal Networks: A Discrete Model. In *Mathematical Concepts and Methods in Modern Biology*. R. Robeva and T. Hodge, eds., Academic Press, 2013, 179–211.  
*Elementary introduction and overview. Suitable as basis for REU.*
- W. Just and S. Ahn (2014); Lengths of attractors and transients in neuronal networks with random connectivities. *Preprint*.  
[arXiv:1404.5536](https://arxiv.org/abs/1404.5536) A shortened journal version has been submitted.

# Why do we want to study this question for random connectivities?

**Amazing fact:** There exists a little roundworm, *Caenorhabditis elegans*, with 302 neurons, for which each single synapse has been mapped!

For higher organisms though, our knowledge of the actual neuronal wiring is only very fragmentary. We may, however, have some information about global network parameters such as the degree distribution. For example, there are about  $10^{12}$  neurons and  $10^{15}$  synaptic connections in the human brain, which gives a mean degree of about 1000 for the network.

The architecture of actual neuronal networks has been shaped by evolution and to some extent by learning, both of which are **stochastic processes**. Thus it is reasonable to assume that the actual architecture exhibits features that are reasonably typical for a **relevant** probability distribution on digraphs.

# Basics of network dynamics

- The **trajectory** of initial state  $\vec{s}(0)$  is the sequence  $(\vec{s}(0), \vec{s}(1), \dots, \vec{s}(t), \dots)$
- States that are visited infinitely often by the trajectory are called **persistent states**. Since the state space is finite, every trajectory must eventually reach a persistent state. The set of these persistent states is called the **attractor** of the trajectory.
- **Transient states** are visited only once. Their sequence is an initial segment of the trajectory, called its **transient (part)**.
- The set  $\{(1, \dots, 1)\}$  is the unique **steady state attractor**. All other attractors, if such exist, are called **periodic attractors**.

# The basic setup

Just W and Ahn S arXiv:1404.5536 (2014)

- Let  $\pi$  be a function that assigns to each positive integer  $n$  a probability  $\pi(n)$ .
- Randomly draw an Erdős-Rényi digraph  $D$  on  $[n]$  where each potential arc is included with probability  $\pi(n)$ .
- Randomly draw an initial condition  $\vec{s}(0)$  in the chosen network.
- Let  $\alpha$  be the length of the attractor and let  $\tau$  be the length of the transient of the trajectory of  $\vec{s}(0)$ .
- Explore how  $\alpha$  and  $\tau$  scale **on average** w.r.t. the number  $n$  of neurons.

# Scaling laws for $\alpha$ and $\tau$

We are interested in how the **medians** and all **fixed percentiles** of  $\alpha$  and  $\tau$  scale as  $n \rightarrow \infty$ .

## Why percentiles?

If the means of  $\alpha$  or  $\tau$  do scale differently from the percentiles, then this must be due to rare outliers. Experimental studies of a actual neuronal networks and simulation studies of their models are unlikely to detect extremely rare outliers.

Thus theoretical results on the scaling of fixed percentiles will in general be better predictors of simulation results than theoretical results on the means.

# Why are these scaling laws relevant?

**Biological relevance:** Several of the neuronal tissues in which dynamic clustering has been observed are part of olfactory systems. There is an ongoing debate among neuroscientists whether odors are coded in the attractors or in the transients of neuronal dynamics. The first coding requires sufficiently many different (long) attractors, the second requires sufficiently long transients.

**Mathematical relevance:** Classes of Boolean systems can be roughly categorized as those exhibiting predominantly **ordered dynamics** and those exhibiting predominantly **chaotic dynamics**. The former are characterized (among other hallmarks) by **relatively short** transients and attractors; the latter by **relatively long** ones. The difference between “short” and “long” often corresponds to **polynomial** vs. **exponential** scaling with system size  $n$ . The capability of the system to perform complex computations appears to require that its dynamics falls into the **critical regime**, right at the boundary between order and chaos.

# Some basic tools for our study

Let  $\gamma$  denote the maximal length  $\gamma$  of a directed path in  $D$ .  
We call  $D$  **supersimple** if it is either acyclic or contains exactly one directed cycle  $C$  and satisfies an additional condition.

## Proposition

*Assume  $D$  is acyclic. Then  $\alpha = 1$  and  $\tau + 1 \leq \gamma$ .*

## Lemma

*Assume  $D$  is supersimple and contains a directed cycle of length  $L$ .  
Then*

- (i)  $\alpha$  is a divisor of  $L$ .*
- (ii) The percentiles of  $\tau$  scale like  $\Theta(\gamma)$ .*

Since we randomly draw initial states, part (ii) takes the form of a scaling law.

# $\alpha$ and $\tau$ for very sparse connectivities

Assume  $\pi(n) = \frac{c}{n}$  for  $c < 1$  (the **subcritical case**).

It is (well) known that in the case **a.a.s.** (**asymptotically almost surely**, that is, with probability approaching 1 as  $n \rightarrow \infty$ ), the upstream and downstream connected components of the corresponding Erdős-Rényi digraph  $D$  are all **simple** (contain at most one directed cycle).

We first extend this result to **supersimple** and then derive the following consequence:

## Theorem (The subcritical case)

*Assume  $\pi(n) = \frac{c}{n}$  with  $c < 1$ . Then*

- (i) Each fixed percentile of  $\alpha$  scales like  $O(1)$ .*
- (ii) Each fixed percentile of  $\tau$  scales like  $\Theta(\log n)$ .*

Thus the subcritical case exhibits hallmarks of **highly ordered dynamics**.

# The critical window

It is also (well) known that when  $\pi(n)$  is increased from  $\frac{c_\ell}{n}$  to  $\frac{c^u}{n}$  for some  $c_\ell < 1 < c^u$ , then a so-called **giant strongly connected component** that comprises a fixed fraction of all nodes appears a.a.s. in the corresponding Erdős-Rényi digraph  $D$ .

There have been detailed studies of the expected structure of  $D$  in the so-called **critical window** where  $\pi(n) \sim \frac{1}{n}$ .

Roughly speaking, these studies have discovered distinct structural properties in the **lower end**, **middle part**, and **upper end** of the critical window.

We made some contributions by showing that in (much of) the lower end a.a.s. the upstream components will remain **supersimple**, but many directed cycles with **distinct** lengths appear.

# The lower end of the critical window

## Theorem (Lower end of the critical case)

Assume  $\pi(n) = \frac{1-n^{-\beta}}{n}$ , where  $0 < \beta < 1/4$ . Then with probability arbitrarily close to 1 as  $n \rightarrow \infty$

(i)  $\tau$  scales like  $O((\log n)n^\beta)$ .

(ii)  $\tau$  scales like  $\Omega(n^\beta)$ .

(iii)  $\alpha \leq e^{\sqrt{n \ln n} + o(1)}$  and thus scales subexponentially.

(iv)  $\alpha \geq e^{\Omega(\log n \log \log n)}$  and hence scales faster than any polynomial function.

We observe one hallmark of the **critical regime** for the dynamics.

# What happens in the middle of the critical window?

One would conjecture that for  $\pi(n) = \frac{1}{n}$  both  $\alpha$  and  $\tau$  scale even faster. Simulations studies indicate as much.

However, our arguments so far relied on having almost perfect control over the dynamics, as the structures that we use as tools (directed cycles in upstream components) remain neatly segregated. Higher up in the critical window we lose all such control.

Thus it seems very challenging to develop good tools for exploring the dynamics of our system deep inside the critical window.

# What happens above the critical window?

When  $\pi(n) = \frac{c}{n}$  for some constant  $c > 1$ , we regain a certain amount of control.

In this case we can assume that there exists a giant strongly connected component. If we remove it together with all nodes downstream of it, the remaining digraph will exhibit the same features as in the subcritical case: small and supersimple upstream components. This essentially reduces the problem to studying what happens inside the giant component.

# Eventually minimally cycling nodes

## Definition

A node  $i$  is **eventually minimally cycling** if there are only finitely many times  $t$  with  $s_i(t) = s_i(t + 1) = 1$ .

Intuitively, a node is eventually minimally cycling if from some time on it will always fire as soon as it has reached the end of its refractory period.

# The supercritical case

## Theorem (The supercritical case)

*There exists a constant  $c_{crit}$  with  $1 \leq c_{crit} \leq 2$  such that if  $\pi(n) = \frac{c}{n}$  for some fixed  $c > c_{crit}$ :*

- (i) A.a.s. all nodes in the giant component will be eventually minimally cycling.*
- (ii) Each fixed percentile of  $\alpha$  scales like  $O(1)$ .*
- (iii) Each fixed percentile of  $\tau$  scales like  $\Omega(\log n)$ .*
- (iv) There exists a constant  $k = k(c) > 0$  such that each fixed percentile of  $\tau$  scales like  $O(n^k)$ .*

We observe hallmarks of **highly ordered** dynamics.

# Open problems: The big one

**Problem 0:** What is  $c_{crit}$ , really?

We showed that  $1 \leq c_{crit} \leq 2$ .

We conjecture that  $c_{crit} = 1$ .

Simulation results indicate as much.

# Open problems: An even bigger one

Define **locally modified Erdős-Rényi (di)-graphs** as follows:

- Consider an algorithm  $A$  that takes as input a (di)graph  $D$  on  $[n]$  with some labeling of the vertices with a fixed set of labels, and outputs another labeled (di)graph  $A(D)$  on  $[n]$ .
- The algorithm decides whether or not  $\langle i, j \rangle$  is an arc (edge) of  $A(D)$  **only** based on the structure and labels of subgraph induced by all nodes that can be reached from  $i$  or  $j$  via a (directed) path of length  $\leq N$ , where  $N$  is fixed and does not depend on  $n$ .
- Let  $D$  be an Erdős-Rényi (di)graph.
- Generate the labels independently, with specified probabilities of assigning a given label.

This defines a family of distributions  $A(D)$ .

**What methods can be used to study such distributions?**

**Problem 1:** Find the exact scaling law for the length  $\tau$  of the transient in the supercritical case, or at least narrow the gap between  $\Omega(\log n)$  and  $O(n^{k(c)})$ .

**Problem 2:** Assume  $\pi(n) = \frac{1-n^{-\beta}}{n}$ , where  $0 < \beta < 1/4$ . Find the exact scaling law for the length  $\tau$  of the transient.

At this time we know that it is between  $\Omega(n^\beta)$  and  $O((\log n)n^\beta)$ .

**Problem 3:** Does there exist  $\pi(n)$  such that  $\tau(n)$  scales faster than any polynomial?

At this time we don't even know whether there exists  $\pi(n)$  where  $\tau(n)$  scales like  $\Omega(n)$ .

**Problem 4:** Does there exist, for any  $n$ , a network  $N(D)$  on  $[n]$  that contains any attractor of length  $\alpha > g(n)$ , where  $g(n) \sim e^{\sqrt{n \ln n} + o(1)}$  is Landau's function?

# Open problems for related systems

**Problem 5:** Investigate  $\alpha$  and  $\tau$  for analogous systems with larger firing thresholds.

We have some results, but a full characterization will require new methods.

**Problem 6:** Investigate the behavior of  $\alpha$  and  $\tau$  for other types of random connectivities.

Some empirical results indicate that the degree distributions in actual neuronal networks may be closer to scale-free than to normal. Thus making  $D$  a random scale-free network may be more relevant to neuroscience. But we had to start our investigations somewhere.

**Problem 7:** Try to generalize our results to systems with other types of rules for the firing of neurons.