Connectivity vs. Dynamics in a Simple Model of Neuronal Networks

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May 22, 2011

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Outline

- Review of the models
- Discrete dynamics for special connectivities
- Discrete dynamics for random connectivities
- Correspondence between ODE dynamics and discrete dynamics

Some empirical observations

Recordings from certain neuronal tissues such as the olfactory bulb of mammals or the antennal lobe of insects 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."

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How can we mathematically explain this phenomenon?

An ODE model of neuronal networks

from 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

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

Some simulation results

Ahn S, Smith BH, Borisyuk A, Terman D, Physica D, 2010

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Can we build a simpler discrete model whose dynamics **reliably reflects** the one of the underlying ODE model?

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.
- 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.

Let us build a simple model of neuronal networks based on these facts.

A discrete dynamical system model

Ahn S, Smith BH, Borisyuk A, Terman D, Physica D, 2010

A directed graph $D = [V_D, A_D]$ and integers n (size of the network), p_i (refractory period), th_i (firing threshold).

A state $\vec{s}(t)$ at the discrete time t is a vector:
$\vec{s}(t) = [s_1(t), \ldots, s_n(t)]$ where $s_i(t) \in \{0, 1, \ldots, p_i\}$ for each i.
The state $s_i(t) = 0$ means neuron i fires at time t.

Dynamics on the discrete network $N =< D, \vec{p}, \vec{th} >$:

- If $s_i(t) < p_i$, then $s_i(t+1) = s_i(t) + 1$.
- If $s_i(t) = p_i$, and there exists at least th_i neurons j with $s_j(k) = 0$ and $< j, i > \ \in A_D$, then $s_i(t+1) = 0$.
- If $s_i(t) = p_i$ and there do not exist th_i neurons j with $s_j(t) = 0$ and $< j, i > \ \in A_D$, then $s_i(t+1) = p_i$.

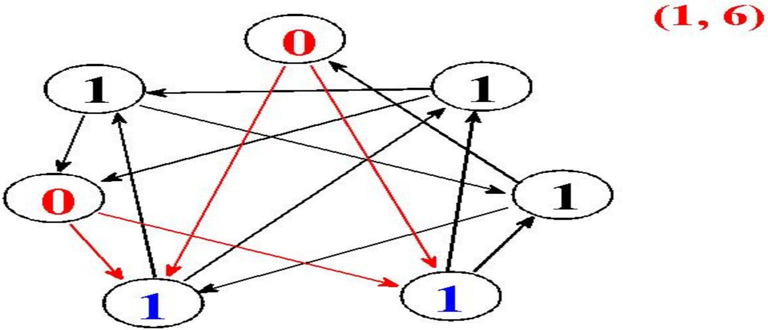
Studying the discrete model

For a given discrete model $N =< D, \vec{p}, \vec{th} >$ we may ask about the (possible, maximal, average)

- lengths of the attractors,
- number of different attractors,
- sizes of their basins of attraction,
- lengths of transients
- ... .

An Example

Assume that refractory period$= 1$ and threshold$= 1$.



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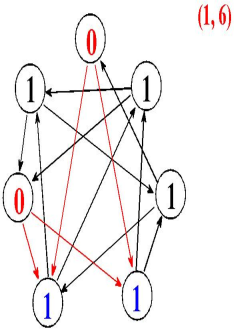

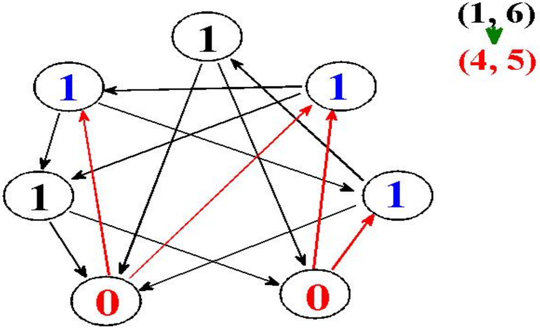

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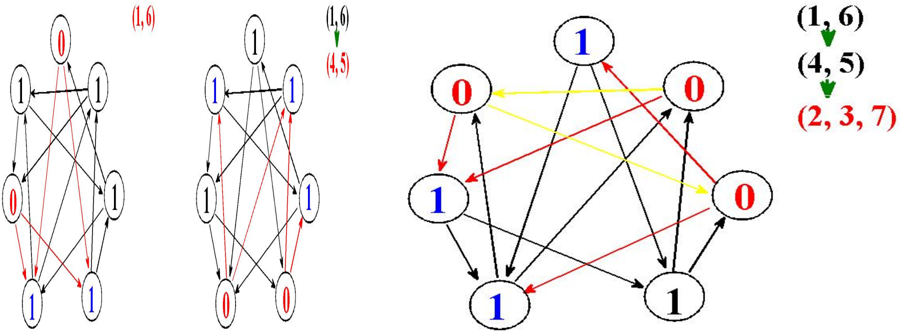

Even the discrete dynamics may be intractable

The problem of deciding for a given discrete model $N = < D, \vec{p}, \vec{th} >$ and a given state $\vec{s}$ whether $\vec{s}$ is transient or persistent is NP-hard.

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For proofs of these and many similar results see
W. Just, *Unpublished research notes,* Fall 2006.

Some special connectivities

- Cyclic digraphs.
- Cyclic digraphs with one shortcut.
- Strongly connected digraphs: There is a directed path from every node to every other node.
- Regular digraphs.
- ...

What kind of dynamical properties are implied by these special connectivities?

Cyclic digraph on n nodes Sungwoo Ahn, Ph. D. Thesis 2010

Theorem

Let $\vec{p} = [p_1, \ldots, p_n], \vec{th} = [1, \ldots, 1] >$*, and* $p^* = \max \vec{p}$*. Then for cyclic digraphs* D *with* n *vertices the system* $N =< D, \vec{p}, \vec{th} >$ *satisfies:*

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- *The length of any attractor is a divisor of n.*
- *The length of any transient is at most $n + 2p^* - 3$.*
- *The number of different attractors is equal to the number of different necklaces consisting of n black or red beads where all the red beads occur in blocks of length that is a multiple of $p^* + 1$. It is equal to*

$$\sum_{k=1}^{\lfloor \frac{n}{p^*+1} \rfloor} \left[\frac{1}{n - kp^*} \sum_{a \in \{\text{divisors of } \gcd(k, n-kp^*)\}} \phi(a) \binom{\frac{n-kp^*}{a}}{\frac{k}{a}} \right] + 1,$$

where ϕ is Euler's phi function.

Attractor lengths in strongly connected digraphs

Ahn, S and Just, W, submitted.

Theorem

Let D be a strongly connected digraph with n vertices that does not have two disjoint directed cycles. Then the length of any attractor in $N = < D, \vec{1}, \vec{1} >$ is bounded by n.

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The complete formulation and proof of the above theorem actually show that strongly connected digraphs for which $N = < D, \vec{1}, \vec{1} >$ has attractors of length $> n$ must have a very special structure. The smallest known example of a Hamiltonian such D has 26 vertices.

Random connectivities

- For given n, we randomly generate a digraph with n nodes by including each possible arc $< i, j >$ with probability $\rho(n)$; independently for all arcs (Erdős-Rényi random digraph).
- We randomly generate many initial conditions.
- We collect statistics on the proportion of initial states for which the dynamics exhibits selected features.
- How do these features depend on $\rho(n)$?

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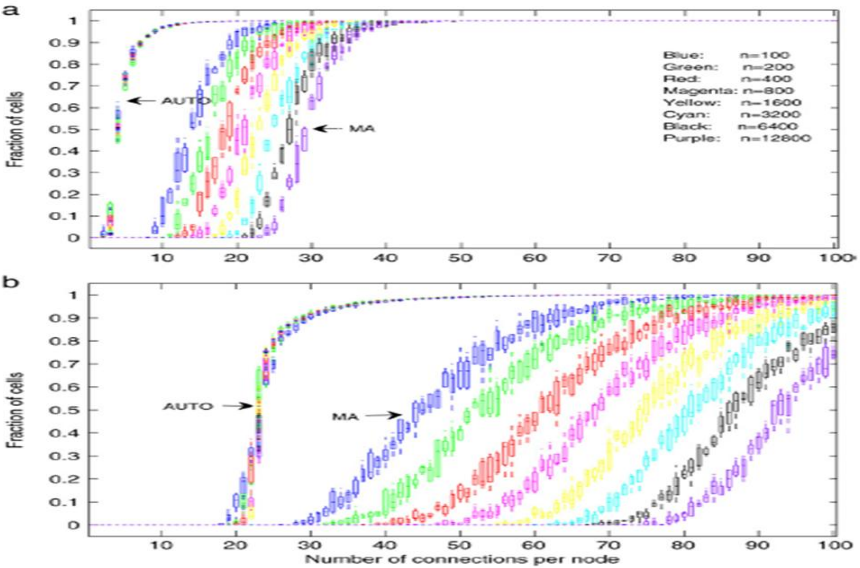
- A *fully active* attractor is one in which every neuron fires at some time.
- An *autonomous set* consists of neurons that fire as soon as they reach the end of their refractory periods, regardless of the dynamics of neurons outside of this set.

Results of the simulations Just W, Ahn S, Terman D, Physica D. 2008



Two phase transitions by Just W, Ahn S, Terman D, Physica D. 2008

Theorem

1. *The first phase transition at* $\rho(n) \sim \frac{\ln n}{n}$*:*
   - *Above this threshold: a generic initial state belongs to a fully active minimal attractor.*
   - *Below this threshold: a generic initial state will not belong to a minimal attractor.*

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2. *The second phase transition at $\rho(n) \sim \frac{c}{n}$:*
    - *Above this threshold: the fraction of nodes that belong to the largest autonomous set will rapidly approach one as ρ increases.*
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3. *Both phase transitions also occur if the digraph is any $k = \lfloor \frac{\rho(n)}{n} \rfloor$ regular digraph.*

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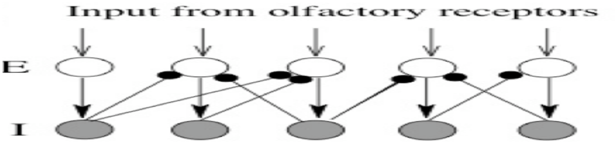
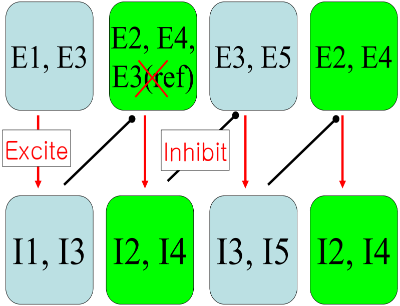
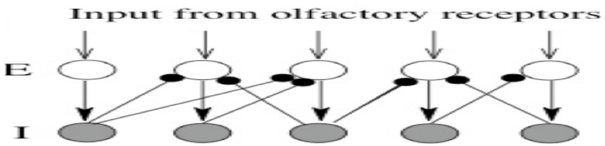
- Explore these phenomena for random digraphs other than Erdős-Rényi random digraphs (e.g., scale-free degree distributions).
- Explore these questions for related discrete models.

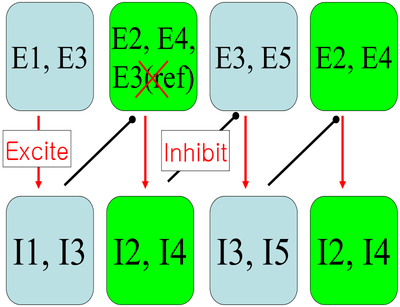
But is the discrete model accurate?

Simulation results show a good correspondence between the dynamics predicted by the discrete model and the underlying more realistic ODE model. But can we rigorously **prove** such a correspondence?


Input from olfactory receptors
E
I


E1, E3
E2, E4, E3(ref)
E3, E5
E2, E4
Excite
Inhibit
I1, I3
I2, I4
I3, I5
I2, I4





$$
\begin{array}{lcl}
E1 & \rightarrow & E2, E3 \\
E2 & \rightarrow & E3 \\
E3 & \rightarrow & E2, E4 \\
E4 & \rightarrow & E5 \\
E5 & \rightarrow & E4
\end{array}
$$

Assume: E-cells can excite one another via interneurons.

Reducing neuronal networks to discrete dynamics,

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

Theorem

For the network architecture described above, if the intrinsic and synaptic properties of the cells are chosen appropriately, then there is an exact correspondence between the trajectories of the continuous and discrete systems for any connectivity between the excitatory and inhibitory cells.

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- For individual trajectories time can be partitioned into subsequent intervals of roughly equal lengths ("episodes").
- Except for slight fuzziness on the boundaries, throughout each episode E-cell number i will reside either in F_i or in R_i.
- The discrete model accurately predicts the movement between F_i and R_i from one episode to the next for all E-cells and all episodes.

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- Phase plane analysis reveals the dynamics of individual neurons.
- The slowest I-neuron in each episode acts as pacemaker.
- Plus a lot more messy details.
- The proof is robust under some noise.

Open problems

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This last question is the current focus of my research (joint project with Todd Young and a group of graduate and undergraduate students at Ohio University).