Discrete vs. Indiscrete Models of Network Dynamics

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Outline

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- Broader implications for undergraduate instruction: (How) should we teach the modeling of models?

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- Broader implications for undergraduate instruction: (How) should we teach the modeling of models?
- Some (perhaps not so challenging) research problems for your undergraduate students

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?
- If so, would this explain the observations?
- (Why, when) does the discrete dynamics **reliably reflect** the underlying ODE dynamics?

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).

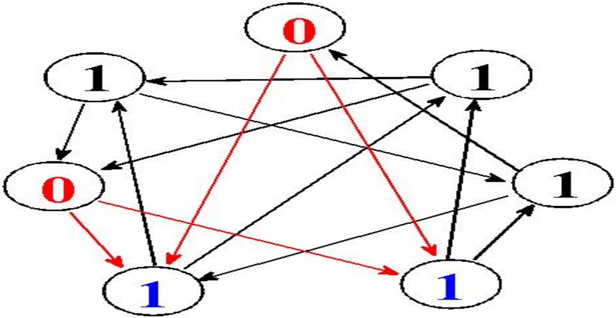
A state $\vec{s}(t)$ at the discrete time t is a vector:
$\vec{s}(t) = [s_1(t), \ldots, s_n(t)]$ where $s_i(t) \in \{0, 1, \ldots, p_i\}$ for each i.
The state $s_i(t) = 0$ means neuron i fires at time t.

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 $s_i(t+1) = p_i$.

An Example

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



(1, 6)

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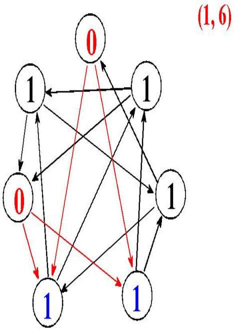

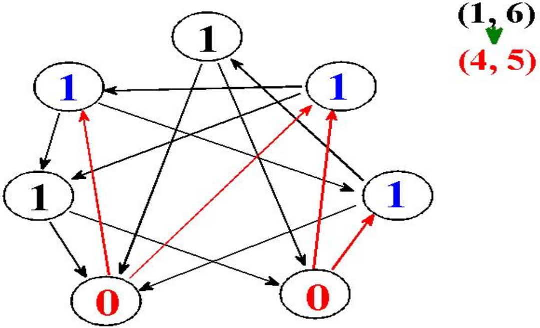

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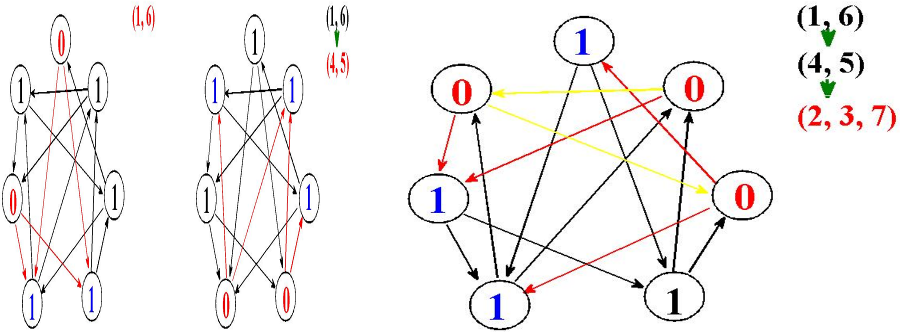
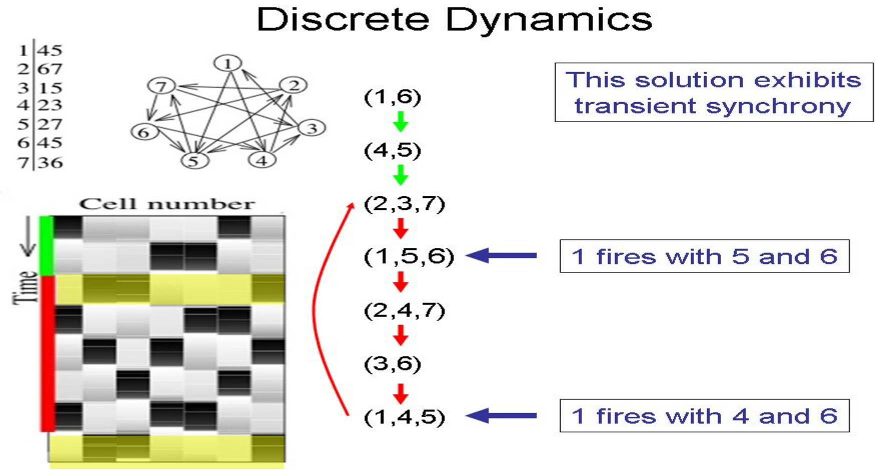


Continuous and Discrete Models

Assume that refractory period= 1 and threshold= 1.



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?

Reducing neuronal networks to discrete dynamics,

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

Theorem

For excitatory-inhibitory networks with a certain architecture, 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.

Open Problem

In general, under which conditions does there exist an "exact correspondence" between an ODE system and a Boolean system?

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For more on this question, come see my poster on Friday.

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We usually think of a **mathematical model** as an idealization of some **real-world systems.** In the research described above, the discrete model can be thought of as a **simpler model of the underlying ODE model.**

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(How, to what extent) should we teach about approximating (modeling) of complicated models by simpler ones?

Bad idea. Forget it.

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Teaching about models only as idealizations of real biological systems is hard enough. Talking about the relation between two or more different models will confuse students even more.

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- Sometimes it is difficult to discern whether a model really explains a phenomenon (like dynamic clustering) or whether the phenomenon is simply built into the model by the choice of modeling paradigm without considering multiple models.
- A paradigm of studying complex systems with a "suite" of models appears to be emerging (C. Jones, UNC, Chapel Hill). This may be especially important in climate modeling, and perhaps the modeling of evolution, where our possibilities for running experiments are severely limited.

Studying the discrete model

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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
- ... .

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.
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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* $n + 2p^* - 3$*.*

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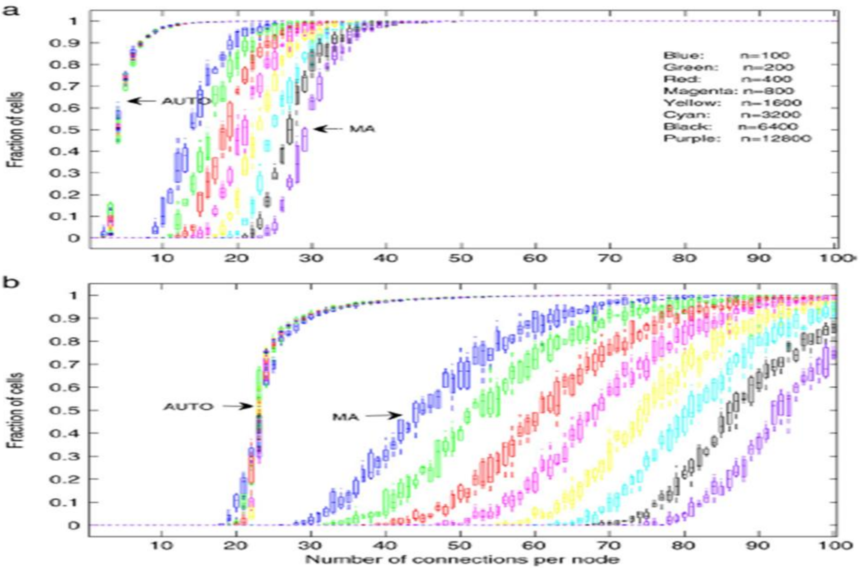
The complete formulation and proof of the above theorem actually show that strongly connected digraphs for which $N = < D, \vec{1}, \vec{1} >$ has attractors of length $> n$ must have a very special structure. The smallest known example of a Hamiltonian such D has 26 vertices.

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 $\rho(n)$?

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



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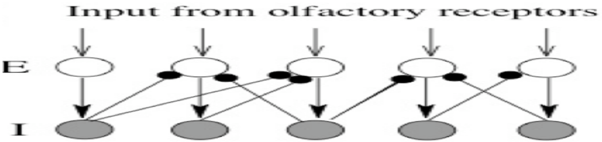
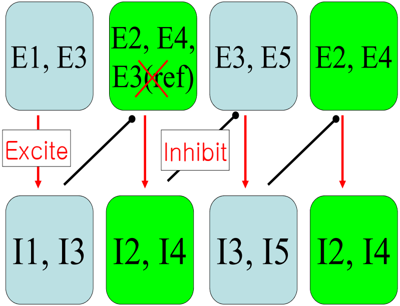
- Explore these phenomena for random digraphs other than Erdős-Rényi random digraphs (e.g., scale-free degree distributions).
- Explore these questions for other special connectivities.
- Explore these questions for related discrete models.

An Architecture





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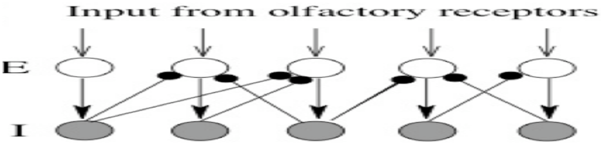

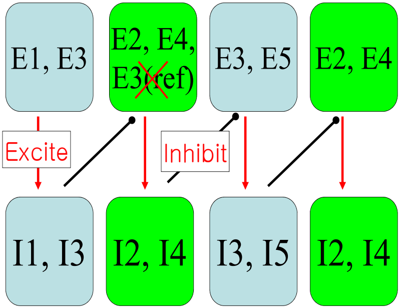

$$\begin{array}{lcl} E1 & \to & E2, E3 \\ E2 & \to & E3 \\ E3 & \to & E2, E4 \\ E4 & \to & E5 \\ E5 & \to & E4 \end{array}$$

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

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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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- 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.