Synchrony in Stochastic Pulse-coupled Neuronal Network Models

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January 19, 2009

Stochastic Models in Neuroscience
Marseille, France
Motivation and Goals

- **Motivation: Neuronal Model Behavior**
  - Study the most basic point neuron models, network models, and coarse-grained models for use in computations
  - Develop new analytical techniques
  - Look for simple, universal network mechanisms

- **Goals: Understand Oscillatory Dynamics of IF Model**
  - Generalize classical problem of perfectly synchronous Integrate-and-Fire (IF) network oscillations to stochastic setting
  - Quantitative analysis of mechanism sustaining synchrony
  - Lessons for understanding more complicated models and types of oscillations?
Outline

- Network dynamics: model and simulations
- Characterization of mechanism for sustaining stochastically driven synchronized dynamics
- Computation of probability of repeated total firing events
- Computation of firing rates based on first passage time
  - First passage time calculation
  - Approximation of first passage time
Excitatory Neuronal Network

All-to-all connected, current based, integrate-and-fire (IF) network

\[
\frac{dv_i(t)}{dt} = -g_L(v_i(t) - V_R) + I_i(t), \quad i = 1, \ldots, N
\]

\[
I_i(t) = f \sum_k \delta(t - t_{ik}) + \frac{S}{N} \sum_{j \neq i} \sum_k \delta(t - \tilde{t}_{jk})
\]

\( V_R \leq v_i(t) < V_T \)

- \( V_R \): reset potential (\( = 0 \))
- \( V_T \): firing threshold (\( = 1 \))

\( g_L \): leakage rate (\( = 1 \))

\( f \) and \( S \): coupling strengths (\( > 0 \))
Integrate & Fire Dynamics

- $v_i(t)$ evolves according to the voltage ODE until $\tilde{t}_{ik}$, when $v_i(\tilde{t}_{ik}) \geq V_T$
- At $\tilde{t}_{ik}$, $v_i(t)$ is reset to $V_R$: $v_i(\tilde{t}_{ik}^+) = V_R$
- $S/N$ is added to the voltage, $v_j$, for $j = 1, \ldots, N, j \neq i$
Classification by Mean External Driving Strength

Mean voltage driven to \( V_R + f\nu/g_L \) without network coupling

**Superthreshold**
\[ V_R + f\nu/g_L > V_T \]

- \( f = 0.01, \nu = 120 \)
- \( f\nu = 1.2 > 1 \)

**Subthreshold**
\[ V_R + f\nu/g_L < V_T \]

- \( f = 0.01, \nu = 90 \)
- \( f\nu = 0.9 < 1 \)
Classification by Fluctuation Size

Approximate Poisson point process with rate $\nu$ and amplitude $f$ by drift-diffusion process with drift coef $f \nu$ and diffusion coef $f^2 \nu / 2$

**Diffusion Approx. Valid**

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<thead>
<tr>
<th>Poisson Process Driven</th>
<th>Drift-Diffusion Process Driven</th>
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<td><img src="image1" alt="Poisson Process" /></td>
<td><img src="image2" alt="Drift-Diffusion Process" /></td>
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$\nu = 2400$, $f \nu = 1.2$, $N = 1$

**Diffusion Approx. Not Valid**

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<td><img src="image3" alt="Poisson Process" /></td>
<td><img src="image4" alt="Drift-Diffusion Process" /></td>
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$f = 0.005 \ll (V_T - V_R) / g_L$

$\nu = 12$, $f \nu = 1.2$, $N = 1$
Types of Synchronous Firing: Partial Synchrony

All-to-all connected network of $N = 100$ neurons

$f = 0.01, f\nu = 1.2, S = 0.4$
Types of Synchronous Firing: Imperfect Synchrony

All-to-all connected network of $N = 100$ neurons

$f = 0.1, f\nu = 1.2, S = 2.0$
Types of Synchronous Firing: Perfect Synchrony

All-to-all connected network of \( N = 100 \) neurons

Consistent total firing events; “synchronizable network”

\( f = 0.001, f\nu = 1.2, S = 2.0 \)
Model for Self-Sustaining Synchrony

Fluctuations in input desynchronize the network

- Between total firing events $N$ neurons behave independently

Pulse coupling synchronizes the network

- First neuron firing causes cascading event, pulling all other neurons over threshold due to synaptic coupling ($S'$)

After each total firing event, all neurons reset, process repeats

Which systems are synchronous?
What is the mean firing rate of the network?
(1) What is the probability to see repeated total firing events?
Model for Synchronous Firing

Voltages of the other $N - 1$ neurons when the first neuron fires:

Cascade-Susceptible

Not Cascade-Susceptible

$f = 0.008, f\nu = 1.0$

$f = 0.08, f\nu = 1.0$

$S = 2, N = 100$ (Bin size $= S/N$)
For What Parameters is Network Synchronizable?

Neuron will fire in a cascade if instantaneous coupling from other firing neurons pushes its voltage over threshold

Probability all neurons included in cascading event: \( P(C) \)

Cascade-susceptibility described by event:

\[
C = \bigcap_{k=1}^{N-1} C_k \quad \text{where} \quad C_k : V_T - V^{(k)} \leq (N - k) \frac{S}{N}
\]

\( C, C_k \in [V_R, V_T]^N \) and \( V^{(1)} \leq V^{(2)} \leq \cdots \leq V^{(N-1)} \)
Computation of Cascade-Susceptibility Probability

- **Condition upon time of first threshold crossing:**

\[
P(C) = \int_0^\infty P(C \mid T^{(1)} = t) p_{T^{(1)}}(t) \, dt.
\]

- **Approximate condition:** max neuron at threshold at time \(t\)

\[
P(C \mid T^{(1)} = t) \approx P(C \mid V^{(N)}(t) = V_T)
\]

- **Manipulate using elementary probability,**

\[
P(C \mid V^{(N)}(t) = V_T) = 1 - P(C^c \mid V^{(N)}(t) = V_T)
\]

\[
= 1 - \sum_{j=1}^{N-1} P(A_j \mid V^{(N)}(t) = V_T)
\]

where \(A_k \equiv C_k^c \bigcap_{j=k+1}^{N-1} C_j\)

denotes event that cascade fails first at \(k\)th neuron
Computation of $P(A_j \mid V^{(N)}(t) = V_T)$

$A_4$: 

- Reduce to elementary combinatorial calculation of how neurons are distributed in bins (width $S/N$), each independently distributed with

$$p_{v|V^{(N)}}(x, t) \equiv \begin{cases} \frac{p_v(x, t)}{\int_{V_R}^{V_T} p_v(x', t) \, dx'} & \text{for } x \in [V_R, V_T], \\ 0 & \text{otherwise,} \end{cases}$$

- Approximate single-neuron freely evolving voltage pdf $p_v(x, t)$ as Gaussian

- Sum probabilities of each configuration consistent with $A_j$
Probability that Network is Cascade-Susceptible

Larger fluctuations need larger coupling to maintain synchrony

\[ f \nu = 1.2, f = 0.001 \]

\[ f \nu = 1.2, N = 100 \]
Probability that Network is Cascade-Susceptible

What about for networks where connections are not all-to-all?

**Synaptic failure:** \( p_f \)

**Sparsity:** \( p_c \)

\[
N = 100, \ f \nu = 1.2, \ f = 0.001 \quad \text{or} \quad N = 100, \ f \nu = 1.2, \ N = 100
\]

Adjust \( P(C) \) by taking \( p_{v|V(N)}(x,t) \to \left\{ \begin{array}{c} (1-p_f) \\ (1-p_c) \end{array} \right\} p_{v|V(N)}(x,t) \)
Probability that Network is Cascade-Susceptible

What about scale-free networks? Effect of local topology

- Distribution of connections:

  \[ P(K = k) \propto k^{-3} \]

- Account for topology in \( P(A_2) \):

- Consider higher order terms:

  \[ P(k_B) \Rightarrow P(k_B | k_A, A \rightarrow B) \]

![Diagram of network connections]

- Red: only neurons that fire
- Blue: neurons result of clustering
- Neuron A connects to B

\( N = 4000, f\nu = 1.2, f = 0.001 \)

(also with M. Shkarayev)
Probability that Network is Cascade-Susceptible

What about non instantaneous synaptic coupling? \( P(C) = 0 \)

**Synaptic Delay:** \( T_D \)

\[ N = 1000, S = 0.1, \langle T_D \rangle = 0.002 \]

\[ f_\nu = 1.2, f = 0.001 \]

**Synaptic Time Course:** \( H(t) \frac{t}{\tau^2_E} e^{-t/\tau_E} \)

\[ N = 1000, S = 0.1, \tau_E = 0.002 \]

\[ f_\nu = 1.2, f = 0.001, \]
(2) What is the mean time between total firing events?
Synchronous First Exit Problem

▷ $N$ neurons - don’t want to solve $N$-dimensional mean exit time problem!
▷ Obtain PDF of one neuron’s exit time, $p_T(t)$, and find PDF of minimum exit time, $p^{(1)}_T$, of $N$ independent neurons.

Mean first passage time of $N$ neurons

$$\langle t \rangle = \int_0^\infty t p^{(1)}_T(t) dt$$

$$p^{(1)}_T(t) = N p_T(t) (1 - F_T(t))^{N-1}$$
Synchronous First Exit Problem

- Neuron reaches threshold - removed from system (absorbed)
- Probability neuron not fired is probability still in $V_R \rightarrow V_T$

\[ P(T \geq t) = 1 - F_T(t) = \int_{V_R}^{V_T} p_v(x, t) \, dx \]

- $p_v(x, t)$ solves Kolmogorov Forward Equation (KFE)
Single Neuron Kolmogorov Forward Equation

KFE:

\[
\frac{\partial}{\partial t} p_v(x, t) = \frac{\partial}{\partial x} \left[ g_L(x - V_R)p_v(x, t) \right] + \nu \left[ p_v(x - f, t) - p_v(x, t) \right]
\]

Taylor Expand KFE - Diffusion Approximation:

\[
\frac{\partial}{\partial t} p_v(x, t) = \frac{\partial}{\partial x} \left[ (g_L(x - V_R) - f\nu)p_v(x, t) \right] + \frac{f^2\nu}{2} \frac{\partial^2}{\partial x^2} p_v(x, t)
\]

Boundary Conditions:

- absorbing at \( V_T \): \( p_v(V_T, t) = 0 \)
- reflecting at \( V_R \): \( J[p_v](V_R, t) = 0 \)

Flux: \( J[p_v](x, t) = - \left[ (g_L(x - V_R) - f\nu)p_v(x, t) \right] - \frac{f^2\nu}{2} \frac{\partial}{\partial x} p_v(x, t) \)
Solution to Single Neuron KFE

Eigenfunction expansion:

\[ p_v(x, t) = p_s(x) \sum_{n=1}^{\infty} A_n Q_n(x) e^{-\lambda_n t} \]

Define: \( z(x) = \frac{g_L(x-V_R)-f \nu}{f \sqrt{\nu g_L}} \)

Eigenfunctions are Confluent Hypergeometric Functions:

\[ Q_n(x) = \begin{cases} 
  c_1 M \left( \frac{-\lambda_n}{2g_L}, \frac{1}{2}, z^2(x) \right) + c_2 U \left( \frac{-\lambda_n}{2g_L}, \frac{1}{2}, z^2(x) \right) & \text{for } z(x) < 0 \\
  c_3 M \left( \frac{-\lambda_n}{2g_L}, \frac{1}{2}, z^2(x) \right) + c_4 U \left( \frac{-\lambda_n}{2g_L}, \frac{1}{2}, z^2(x) \right) & \text{for } z(x) \geq 0
\end{cases} \]

Stationary Solution: \( p_s(x) = \mathcal{N} e^{-z^2(x)} \)

Initial Conditions: \( p_v(x, 0) = \delta(x - V_R) \) \( A_n = \frac{Q_n(V_R)}{\int_{V_R}^V p_s(x) Q_n^2(x) \, dx} \)
Synchronous Gain Curves

dashed - Gaussian approx.
solid - first passage time
circles - simulations
black - deterministic rate

- Good agreement where diffusion approximation valid
- For fixed (superthreshold) $f \nu$, dependence $\sim \sqrt{f}$

\[ N=100, S=5.0 \]
Synchronous Gain Curves

dashed - Gaussian approx.
solid - first passage time
circles - simulations

For fixed (superthreshold) $f \nu$, dependence $\sim \ln N$

$\ln(N) = 0.01, S = 20.0$
Summary

- Synchronous firing over a wide range of parameters
  - Balance between fluctuations and coupling strength

- Synchronous firing rate in terms of single neuron properties
  - Driven by time first neuron crosses threshold

- Network properties are calculated accurately through exit time problems where diffusion approximation is valid

This work was supported by a NSF graduate fellowship