Research Notes on Self-Coupled Spiking Neural Networks

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Contents

1 The self-coupled SNN Model

Problem Statement

Given:

- A Linear Dynamical System $\frac{dx}{dt} = Ax(t) + Bc(t)$, $x \in \mathbf{R}^d$
- A Decoder Matrix $D \in \mathbf{R}^{d\ x\ N}$ specifying the preferred directions of N neurons in d-dimensional space,

synthesize a spiking neural network that implements the linear dynamical system.

Features

1. ***Long-Term Network Accuracy*** The Deneve network assumes $\hat{x} = x$. We show this assumption produces estimation error between the network and its target system that increases with time. By avoiding this assumption, the self-coupled network remains accurate over time.

2. ***Tuning Curve Rotation*** To most efficiently use neurons, we use orthogonal coding directions via SVD. The dynamics matrix A is diagonalized by an orthonormal basis $\mathcal{U}$ in d-dimensional space, while the decoder matrix D is chosen such that $\mathcal{U}$ gives its singular vectors. This choice of coding directions eliminates the need for coupling.

   At least two neurons per dimension (2d in total) are required since voltage thresholds are strictly positive. N-neuron ensembles can thus represent systems with $\frac{N}{2}$ dimensions or less.

3. ***Post-synaptic Spike Dropping*** At each synapse, neurotransmitter release due to an action potential is probabilistic. We incorporate probabilistic spike transmission by thinning at every synaptic connection. The pre-synaptic neuron's membrane potential is still deterministically reset by an action potential.

4. ***Dimensionless Time*** We describe both the network and target system in dimensionless time. Time is normalized by the synapses' time constant, τ_s. This dimensionless representation ensures consistent numerical simulation independent of simulation timestep. Furthermore, τ_s is implicitly specified as 1, reducing the model's parameters by one.

2 Derivation: Basic Model

1. Let τ_s be the synaptic time constant of each synapse in the network. Define dimensionless time as:

$$\xi \triangleq \frac{t}{\tau_s}.$$

We now assume our Linear Dynamical System is expressed in dimensionless time, i.e

$$\frac{dx}{d\xi} = Ax(\xi) + Bc(\xi). \tag{2.1}$$

To describe the neuron dynamics in dimensionless time, let $o(\xi) \in \mathbf{R}^N$ be the spike trains of N neurons composing the network with components

$$o_j(\xi) = \sum_{k=1}^{n_j \text{ spikes}} \delta(\xi - \xi_j^k),$$

where ξ_j^k is the time at which neuron j makes its k^{th} spike. Define the network's estimate of the state variable as

$$\hat{x}(\xi) \triangleq Dr(\xi), \tag{2.2}$$

where $D \in \mathbf{R}^{d \times N}$ and

$$\frac{dr}{d\xi} = -r + o(\xi). \tag{2.3}$$

When the probability of synaptic transmission is 1, component r_j is the total received post-synaptic current (PSC) from neuron j by the network estimator. Define the network error as

$$e(\xi) \triangleq x(\xi) - \hat{x}(\xi). \tag{2.4}$$

2. From equations (2.3) and (2.2), we have

$$D\dot{r} + Dr = Do$$

$$\implies \dot{\hat{x}} + \hat{x} = Do,$$

where the dot denotes derivative w.r.t dimensionless time ξ.

Subtract $\dot{\hat{x}}$ from $\dot{x}$ to get $\dot{e}$:

$$\begin{aligned}
\dot{e} &= \dot{x} - \dot{\hat{x}} \\
&= (Ax + Bc) - (Do - \hat{x}) \\
&= A\,(e + \hat{x}) + Bc - Do + \hat{x} \\
&= Ae + (A + I)\hat{x} + Bc - Do \\
&= Ae + (A + I)\,(Dr) + Bc - Do \\
\implies A^{-1}\dot{e} &= e + (I + A^{-1})Dr + A^{-1}Bc - A^{-1}Do \\
\implies D^T A^{-1}\dot{e} &= D^T e + D^T(I + A^{-1})Dr + D^T A^{-1}Bc - D^T A^{-1}Do
\end{aligned} \tag{2.5}$$

where the third equality follows from equation (2.4) and the fifth from equation (2.2).

3. Assuming both D and A are full rank, diagonalize each to a common left basis:

$$A = \mathcal{U}\Lambda\mathcal{U}^T = \sum_{j=1}^{d} \Lambda_j \mathcal{U}_j \mathcal{U}_j^T,$$

$$D = \mathcal{U}\,[S \;\; 0]\, V^T = \sum_{j=1}^{d} S_j \mathcal{U}_j V_j^T,$$

$$D^T = V \begin{bmatrix} S \\ 0 \end{bmatrix} \mathcal{U}^T = \sum_{j=1}^{d} S_j V_j \mathcal{U}_j^T,$$

$$D^T D = V \begin{bmatrix} S \\ 0 \end{bmatrix} \begin{bmatrix} S & 0 \end{bmatrix} V^T = \sum_{j=1}^{d} S_j^2 V_j V_j^T,$$

with $\mathcal{U} \in \mathbf{R}^{d \times d}$ and $V \in \mathbf{R}^{N \times N}$, and $S \in \mathbf{R}^{d \times d}$.

To express equation (2.5) with the $\mathcal{U}$ and V bases, first note

$$\begin{aligned} D^T A^{-1} &= V \begin{bmatrix} S \\ 0 \end{bmatrix} \mathcal{U}^T \mathcal{U} \Lambda^{-1} \mathcal{U}^T \\ &= V \begin{bmatrix} S \\ 0 \end{bmatrix} \Lambda^{-1} \mathcal{U}^T \\ &= \sum_{j=1}^{d} \frac{S_j}{\Lambda_j} V_j \mathcal{U}_j^T, \end{aligned}$$

and

$$\begin{aligned} D^T A^{-1} D &= V \begin{bmatrix} S \\ 0 \end{bmatrix} \mathcal{U}^T \mathcal{U} \Lambda^{-1} \mathcal{U}^T \mathcal{U}\,[S\ 0]\, V^T \\ &= V \begin{bmatrix} S \\ 0 \end{bmatrix} \Lambda^{-1}\,[S\ 0]\, V^T \\ &= \sum_{j=1}^{d} \frac{S_j^2}{\Lambda_j} V_j V_j^T. \end{aligned}$$

Consequently,

$$\sum_{j=1}^{d} \frac{S_j}{\Lambda_j} V_j \mathcal{U}_j^T \dot{e} = \sum_{j=1}^{d} S_j V_j \mathcal{U}_j^T e + \sum_{j=1}^{d} S_j^2 (1 + \Lambda_j^{-1}) V_j V_j^T r + \sum_{j=1}^{d} \frac{S_j}{\Lambda_j} V_j \mathcal{U}_j^T B c - \sum_{j=1}^{d} \frac{S_j^2}{\Lambda_j} V_j V_j^T o. \qquad (2.6)$$

Left-multiply both sides of the preceding equation by V_j^T to arrive at the system of equations

$$\frac{S_j}{\Lambda_j}\mathcal{U}_j^T\dot{e} = S_j\mathcal{U}_j^T e + S_j^2(1+\Lambda_j^{-1})V_j^T r + S_j\Lambda_j^{-1}\mathcal{U}_j^T Bc - S_j^2\Lambda_j^{-1}V_j^T o$$

$$\implies \mathcal{U}_j^T\dot{e} = \Lambda_j\mathcal{U}_j^T e + S_j(\Lambda_j+1)V_j^T r + \mathcal{U}_j^T Bc - S_j V_j^T o,$$

for $j = 1, \ldots, d$.

4. To simplify notation, we note that our preceding left-multiply has transformed the equations to the basis V^T. The transformed neuron's fast synaptic inhibition (reset), membrane voltage, slow synaptic excitation, and input weight vector are respectively:

$$\begin{aligned} \Omega_j &\triangleq S_j V_j^T o \\ v_j &\triangleq \mathcal{U}_j^T e, \\ \rho_j &\triangleq S_j V_j^T r \\ \beta_j &\triangleq \mathcal{U}_j^T B. \end{aligned} \tag{2.7}$$

The system of equations simplifies to the membrane voltage dynamics

$$\dot{v}_j = \Lambda_j v_j + (\Lambda_j + 1)\rho_j + \beta_j c - \Omega_j,$$

or in matrix form,

$$\dot{v} = \Lambda v + (\Lambda + I)\rho + \beta c - \Omega. \tag{2.8}$$

Here, v is a d vector which describes the dynamics of the d-neurons needed to implement the dynamical system. The remaining $N - d$ neurons are unused and do not contribute to the network readout at present.
From equation (2.3) the PSC dynamics are

$$\dot{\rho} = -\rho + \Omega. \tag{2.9}$$

Similar to equation (2.8), ρ describes a d-vector.

5. The spike trains are chosen minimize the network estimation error

$$\mathcal{L}(\xi) = ||x(\xi + d\xi) - \hat{x}(\xi + d\xi)||^2. \tag{2.10}$$

The network greedily minimizes $\mathcal{L}$ an instant $d\xi$ ahead in time. Writing $\hat{x}$ in terms of Ω and ρ, equations (2.2) and (2.7) imply

$$
\begin{aligned}
\hat{x} &= Dr \\
&= \sum_{j=1}^{d} S_j \mathcal{U}_j V_j^T r \\
&= \sum_{j=1}^{d} \mathcal{U}_j \rho_j \\
&= \mathcal{U} \rho.
\end{aligned}
$$

If neuron j does not spike, the objective is

$$\mathcal{L}_{ns} = ||x - \hat{x}||^2.$$

If neuron j spikes at time ξ, then $\hat{x} \leftarrow \hat{x} + \hat{U}_j$. The objective is now

$$
\begin{aligned}
\mathcal{L}_{sp} &= ||x - (\hat{x} + \mathcal{U}_j)||^2, \\
&= (x - \hat{x} - \mathcal{U}_j)^T (x - \hat{x} - \mathcal{U}_j) \\
&= x^T x - x^T \hat{x} - x^T \mathcal{U}_j - \hat{x}^T x + \hat{x}^T \hat{x} + \hat{x}^T \mathcal{U}_j - \mathcal{U}_j^T x + \mathcal{U}_j^T \hat{x} + \mathcal{U}_j^T \mathcal{U}_j \\
&= \left(x^T x - 2x^T \hat{x} + \hat{x}^T \hat{x}\right) + 2\mathcal{U}_j^T \left(\hat{x} - x\right) + \mathcal{U}_j^T \mathcal{U}_j \\
&= ||x - \hat{x}|| + 2\mathcal{U}_j^T \left(\hat{x} - x\right) + \mathcal{U}_j^T \mathcal{U}_j \\
&= \mathcal{L}_{ns} + 2\mathcal{U}_j^T \left(\hat{x} - x\right) + \mathcal{U}_j^T \mathcal{U}_j
\end{aligned}
$$

A spike occurs when it lowers the objective more than not spiking. Our spiking condition is therefore

$$
\begin{aligned}
\mathcal{L}_{sp} &< \mathcal{L}_{ns} \\
\implies 2\mathcal{U}_j^T \left(\hat{x} - x\right) + \mathcal{U}_j^T \mathcal{U}_j &< 0 \\
\implies \mathcal{U}_j^T \left(x - \hat{x}\right) &> \frac{\mathcal{U}_j^T \mathcal{U}_j}{2} \\
\implies \mathcal{U}_j^T e &> \frac{\mathcal{U}_j^T \mathcal{U}_j}{2} \\
\implies v_j &> \frac{1}{2},
\end{aligned}
$$

where the last inequality follows from applying the voltage definition from equation (2.7). Thus neuron j spikes when its membrane voltage v_j exceeds the threshold of $v_{th} = \frac{1}{2}$.

6. Equations (2.8) and (2.9) describe how we implement a network with d neurons that produces an accurate estimate $\hat{x}$ of the given target system.

   When neuron j spikes, a vector $\mathcal{U}_j$ is added to the network estimate, $\hat{x}$. A spike has a strictly positive area so that the network is only able to modify its estimate by adding from a fixed set of vectors. This restricts the space representable by the network to strictly positive state-space, or only $\frac{1}{2^d}$ of the desired state-space. To remove this restriction, we add an additional d neurons whose preferred directions $\mathcal{U}_j$ are anti-parallel to neurons j for $j = 1, \dots, d$. Such vectors are required in order to allow subtraction, defined as addition of the additive inverse. Thus the number of neurons required to represent a d-dimensional system is $2d$. We update U, S, Λ and v_{th} to reflect the additional neurons:

$$U \leftarrow [U \quad -U] \in \mathbf{R}^{d \times 2d},$$

$$S \leftarrow \begin{bmatrix} S & 0 \\ 0 & S \end{bmatrix} \in \mathbf{R}^{2d \times 2d},$$

$$\Lambda \leftarrow \begin{bmatrix} \Lambda & 0 \\ 0 & \Lambda \end{bmatrix} \in \mathbf{R}^{2d \times 2d},$$

$$v_{th} \leftarrow \begin{bmatrix} v_{th} \\ v_{th} \end{bmatrix} \in \mathbf{R}^{2d},$$

   and afterward recompute $\beta \in \mathbf{R}^{2d \times d}$.

Simulation of Basic Equations

Here we simulate the above equations (2.8) and (2.9) with the $N = 2d$ neurons. The parameters are

$$A = -\begin{bmatrix} 1 & 0 \\ 0 & 1 \end{bmatrix} = \mathcal{U}\Lambda\mathcal{U}^T,$$

$$B = \begin{bmatrix} 1 & 0 \\ 0 & 1 \end{bmatrix},$$

$$c(\xi) = 10 \begin{bmatrix} cos(\frac{\pi}{4}\xi) \\ sin(\frac{\pi}{4}\xi) \end{bmatrix} \tag{2.11}$$

$$D = \mathcal{U} \begin{bmatrix} S & 0 \end{bmatrix} V^T = \mathcal{U} \begin{bmatrix} I_d & 0 \end{bmatrix} I_N,$$

$$d\xi = 10^{-6},$$

$$N = 4,$$

$$x(0) = \begin{bmatrix} \frac{1}{2} & \frac{1}{2} \end{bmatrix}.$$

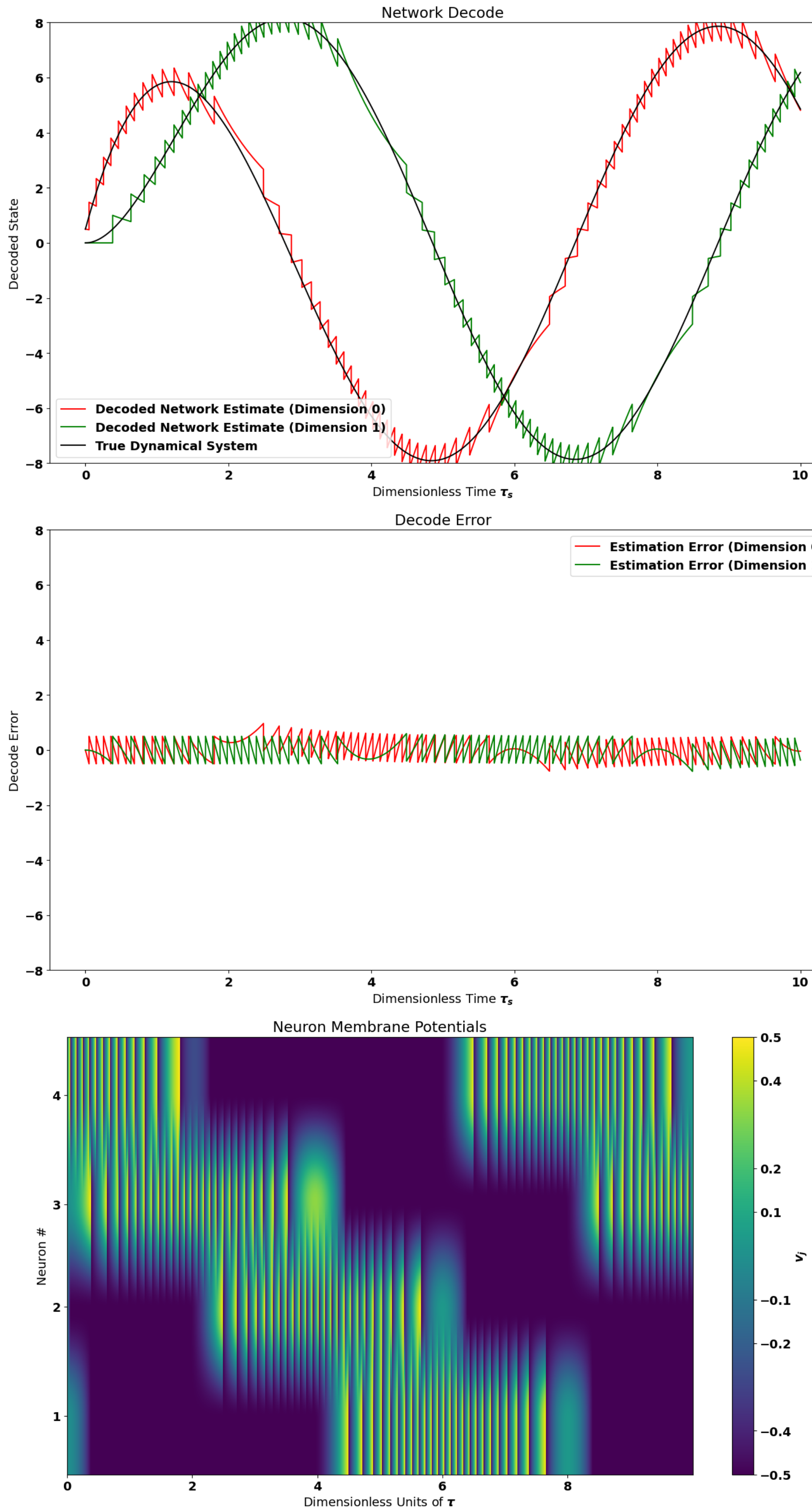

Network Decode
Decoded State
Dimensionless Time τ_s
Decoded Network Estimate (Dimension 0)
Decoded Network Estimate (Dimension 1)
True Dynamical System
Decode Error
Estimation Error (Dimension 0)
Estimation Error (Dimension 1)
Neuron Membrane Potentials
Neuron #
Dimensionless Units of τ
v_j

Figure 1: Simulation of equations (2.8) and (2.9) with parameters listed in equation (2.11). ***Top:*** The decoded network estimate plotted alongside the target dynamical system. ***Middle:*** The estimation error along each state-space dimension. ***Bottom:*** The membrane potentials of the 4 neurons during the same time period.

For the numerical implementation, the matrix exponential was used to integrate the continuous terms over a simulation time step. Continuous terms include all equation terms excepting the delta functions Ω handled separately. After integrating over a timestep, any neuron above threshold was manually reset (action of fast inhibition). If multiple neurons are above threshold, the system is integrated backwards in time until only one neuron is above threshold before spiking. The matrix exponential was computed using a Padé approximation via the Python package Scipy: *scipy.linalg.expm()*.

3 Analysis: RMSE vs Spike Rate for Constant Driving Force

We analyse the network described by equations (2.8) and (2.9 for the case of a constant (in time) driving force $c(\xi) = k\mathcal{U}_j$. First we derive explicit expressions for the network estimate, then we compute the resulting RMSE for various driving strengths k.

1. Let

$$A = -\begin{bmatrix} 1 & 0 \\ 0 & 1 \end{bmatrix},$$

$$B = \begin{bmatrix} 1 & 0 \\ 0 & 1 \end{bmatrix},$$

$$c(\xi) = k\mathcal{U}_1$$

$$d\xi = 10^{-4},$$

$$N = 4,$$

$$x(0) = \begin{bmatrix} \frac{1}{2} & 0 \end{bmatrix}.$$

   With the given initial conditions, $v_j = 0$ for $j \neq 1$ for all ξ. The dynamics simplify to

$$\dot{v_1} = \Lambda_1 v_1 + (\Lambda_1 + 1)\rho_1 + k - \Omega_1.$$

2. We assume that the decoding matrix D is chosen such that $S_1 = 1$. Because A is the negative identity matrix, it is also clear that $\Lambda_1 = -1$. The preceding equation simplifies to

$$\dot{v_1} = -v_1 + k - \Omega_1, \tag{3.1}$$

   which is a form of the well-known Leaky Integrate-and-Fire (LIF) model. Assuming a spike has occurred at $v_{th} = \frac{1}{2}$, the voltage has just been reset so that $v_1(0) = -\frac{1}{2}$. Until the next spike, the neuron's trajectory is integrated as

$$v(\xi) = k - e^{-\xi}(k + \frac{1}{2}).$$

   Neglecting any spike reset, the voltage will asymptotically approach $v_1 = k$. Thus for any spiking to occur, we must have $k \geq v_{th}$. In this case, the time required to reach a spike threshold v_{th} is

$$v_{th} = k - e^{-\xi_{spike}}(k + \frac{1}{2})$$

$$\implies e^{-\xi_{spike}} = \frac{k - v_{th}}{k + \frac{1}{2}}$$

$$= \frac{1 - \frac{v_{th}}{k}}{1 + \frac{1}{2k}}$$

$$\implies \xi_{spike} = -ln\left(\frac{1 - \frac{v_{th}}{k}}{1 + \frac{1}{2k}}\right)$$

$$\implies \frac{1}{\xi_{spike}} = -\frac{1}{ln\left(\frac{1 - \frac{v_{th}}{k}}{1 + \frac{1}{2k}}\right)}$$

$$= \frac{1}{ln\left(1 + \frac{1}{2k}\right) - ln\left(1 - \frac{v_{th}}{k}\right)},$$

which determines the frequency at which the LIF neuron spikes. Denote this frequency as a function of driving strength k by $\phi(k)$:

$$\phi(k) \triangleq \frac{1}{ln\left(1 + \frac{1}{2k}\right) - ln\left(1 - \frac{v_{th}}{k}\right)}. \tag{3.2}$$

The network will encode the constant driving force by spiking at a fixed rate determined by equation (3.2). Figure (2) shows a plot of equation (3.2) along with numerically computed spike rates for a simulated network driven with constant drive strength k. Similar to membrane voltage, the resulting PSC and readout dynamics are reduced to one neuron periodically spiking:

$$\dot{\rho_1} = -\rho_1 + \Omega_1$$

$$\implies \dot{\hat{x}} = -\mathcal{U}_1\rho_1 + \mathcal{U}_1\Omega_1$$

$$= -\hat{x} + \mathcal{U}_1\Omega_1.$$

3. The spike train Ω_1 is a periodic sequence of impulses spaced in time by $\frac{1}{\phi(k)}$. Hence $\Omega_1(\xi) = \sum_{l=0}^{\infty} \delta\left(\xi - \frac{l}{\phi(k)}\right)$. The network estimate therefore has dynamics

$$\dot{\hat{x}} = -\hat{x} + \mathcal{U}_1 \sum_{l=0}^{\infty} \delta\left(\xi - \frac{l}{\phi(k)}\right). \tag{3.3}$$

The target dynamical system is

$$\dot{x} = -x + k\mathcal{U}_1$$
$$x(0) = \begin{bmatrix} \frac{1}{2} & 0 \end{bmatrix},$$

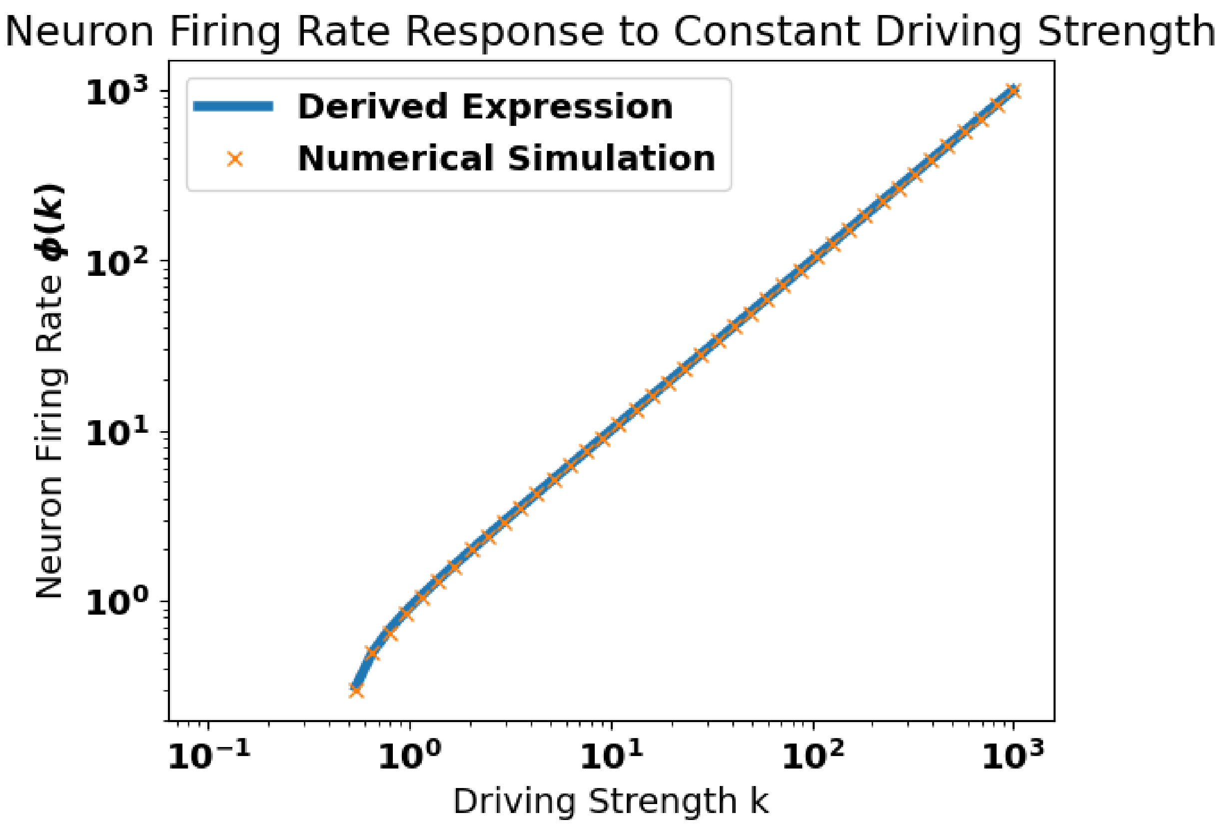


Figure 2: A log-log plot of equation (3.2) alongside the rates measured from numerical simulations. The simulation parameters are described at the beginning of this section, with the decoder matrix D chosen to be the first d rows of the N x N identity matrix. This ensures the singular values $S_j = 1$ as assumed in the derivation. The rate was measured as the number of spike resets divided by the duration of the simulation.

which has a stable fixed point at

$$x = k\mathcal{U}_1. \tag{3.4}$$

4. Equation (3.3) implies that the network estimate $\hat{x}$ will decay until the first spike ξ_1^1 occurs:

$$\hat{x}(\xi) = x(0)e^{-\xi}, \quad 0 \leq \xi < \frac{1}{\phi(k)}.$$

At this instant, the vector $\mathcal{U}_1$ is added to the network estimate.

$$\hat{x}(\frac{1}{\phi(k)}) = x(0)e^{-\frac{1}{\phi(k)}} + \mathcal{U}_1.$$

Decay again occurs until the next spike

$$\hat{x}(\xi) = \hat{x}(\frac{1}{\phi(k)})e^{-(\xi-\frac{1}{\phi(k)})},$$

$$= \left(x(0)e^{-\frac{1}{\phi(k)}} + \mathcal{U}_1\right)e^{-(\xi-\frac{1}{\phi(k)})}, \quad \frac{1}{\phi(k)} \leq \xi < \frac{2}{\phi(k)}$$

$$\implies \hat{x}(\frac{2}{\phi(k)}) = \left(x(0)e^{-\frac{1}{\phi(k)}} + \mathcal{U}_1\right)e^{-(\frac{1}{\phi(k)})} + \mathcal{U}_1$$

$$= x(0)e^{-\frac{2}{\phi(k)}} + \mathcal{U}_1 e^{-\frac{1}{\phi(k)}} + \mathcal{U}_1.$$

The third spike more clearly shows the recursive behavior

$$\hat{x}(\frac{3}{\phi(k)}) = \left[x(0)e^{-\frac{2}{\phi(k)}} + \mathcal{U}_1 e^{-\frac{1}{\phi(k)}} + \mathcal{U}_1\right]e^{-\frac{1}{\phi(k)}} + \mathcal{U}_1$$

$$= x(0)e^{-\frac{3}{\phi(k)}} + \mathcal{U}_1 e^{-\frac{2}{\phi(k)}} + \mathcal{U}_1 e^{-\frac{1}{\phi(k)}} + \mathcal{U}_1$$

Let us consider the n^{th} spike sufficiently far from $\xi = 0$ such that the transient term $x(0)e^{-\frac{n}{\phi(k)}}$ can be neglected. This leads to the expression

$$\hat{x}(\frac{n}{\phi(k)}) = \sum_{l=0}^{n-1} \mathcal{U}_1 e^{-\frac{l}{\phi(k)}}$$

$$= \mathcal{U}_1 \frac{1 - e^{-\frac{n}{\phi(k)}}}{1 - e^{-\frac{1}{\phi(k)}}}.$$

For sufficiently large n, this converges to

$$\hat{x}(\xi_1^n) = \frac{\mathcal{U}_1}{1 - e^{-\frac{1}{\phi(k)}}}. \tag{3.5}$$

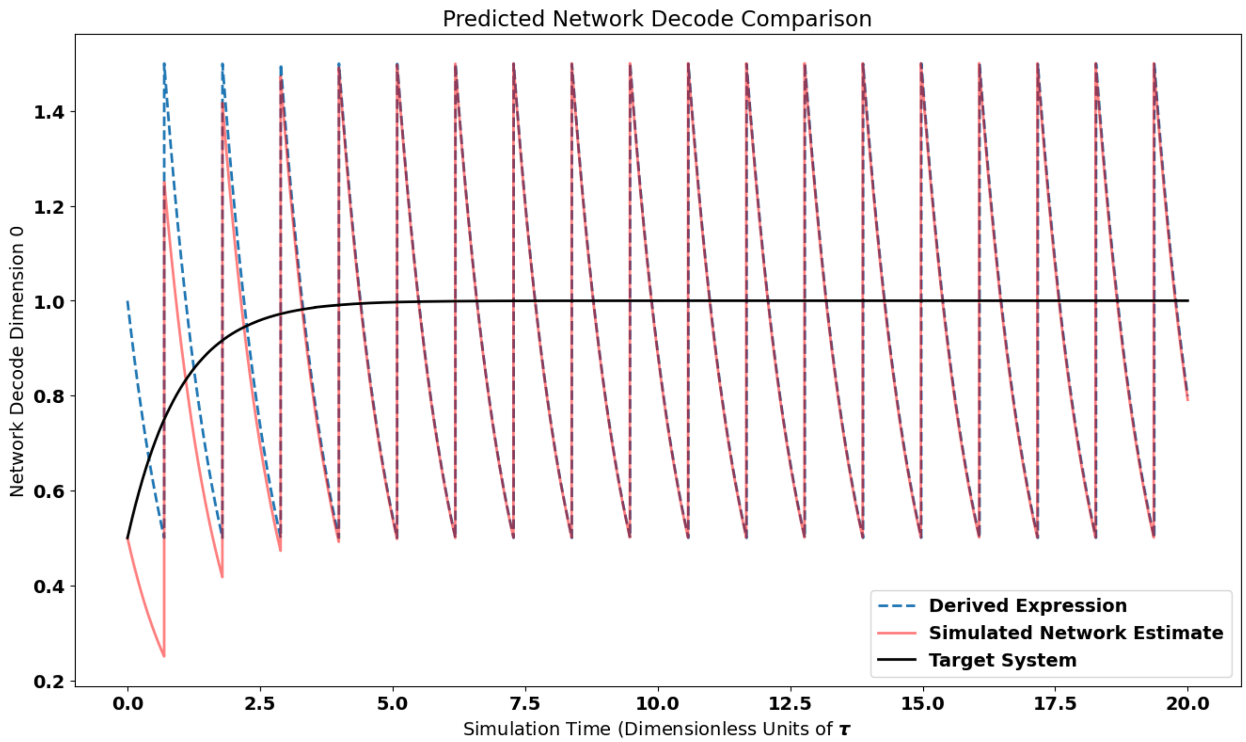


Figure 3: Comparison of the derived long-term network estimate equation (3.6) to numerical simulation. Parameters are the same as the previous figure, with $k = 1$.

5. The preceding argument states that after a transient interval, the network estimate at any spike time ξ_1^n is given by equation (3.5). As shown in figure (3), this convergence occurs after roughly 5 spikes for the case $k = 1$.

   We know from equation (3.3) that the estimate will decay exponentially from this value over an interval $\frac{1}{\phi(k)}$ until a spike returns it returns to the initial value. Thus the network estimate between two consecutive spikes is given by

$$\hat{x}(\xi) = \frac{\mathcal{U}_1}{1 - e^{-\frac{1}{\phi(k)}}} e^{-(\xi - \xi_1^n)}, \quad 0 \leq \xi - \xi_1^n < \frac{1}{\phi(k)}.$$

   Combine this expression with equation (3.5), we have an explicit expression for the long-term behavior of the network estimate given by

$$\hat{x}(\xi) = \frac{\mathcal{U}_1}{1 - e^{-\frac{1}{\phi(k)}}} e^{-(\xi - \xi_1^1) \mod \frac{1}{\phi(k)}}, \tag{3.6}$$

   where $x \mod y$ denotes the fractional remainder of x after division by y.

6. Assume the true system dynamics have settled to their fixed point $x = k\mathcal{U}_1$. From equation (3.6) the network estimate $\hat{x}$ and therefore error $e = x - \hat{x}$ is a periodic function of ξ with period $\frac{1}{\phi(k)}$. The RMSE over any integer number of spike periods is easily calculated from the RMSE over a single spike period.

   We compute the per-spike RMSE of the error signal e by

$$RMSE_{spike} \triangleq \sqrt{\phi(k) \int_0^{\frac{1}{\phi(k)}} ||e(\tau)||^2 \, \mathrm{d}\tau}. \tag{3.7}$$

   The integrand $||e(\tau)||^2$ simplifies to

$$\begin{aligned}
e^T e &= (x - \hat{x})^T (x - \hat{x}) \\
&= x^T x - 2x^T \hat{x} + \hat{x}^T \hat{x} \\
&= k^2 \, \mathcal{U}_1^T \mathcal{U}_1 - 2k \, \mathcal{U}_1^T \mathcal{U}_1 \frac{e^{-\tau}}{1 - e^{-\frac{1}{\phi(k)}}} + \mathcal{U}_1^T \mathcal{U}_1 \left(\frac{e^{-\tau}}{1 - e^{-\frac{1}{\phi(k)}}} \right)^2 \\
&= k^2 - \frac{2k \, e^{-\tau}}{1 - e^{-\frac{1}{\phi(k)}}} + \frac{e^{-2\tau}}{\left(1 - e^{-\frac{1}{\phi(k)}}\right)^2}.
\end{aligned}$$

   Therefore the integral is

$$\begin{aligned}
\phi(k) \int_0^{\frac{1}{\phi(k)}} ||e(\tau)||^2 \, \mathrm{d}\tau &= \phi(k) \int_0^{\frac{1}{\phi(k)}} k^2 - \frac{2k \, e^{-\tau}}{1 - e^{-\frac{1}{\phi(k)}}} + \frac{e^{-2\tau}}{\left(1 - e^{-\frac{1}{\phi(k)}}\right)^2} \, \mathrm{d}\tau \\
&= k^2 + \phi(k) \frac{2k}{1 - e^{-\frac{1}{\phi(k)}}} \left(e^{-\frac{1}{\phi(k)}} - 1 \right) - \phi(k) \frac{1}{2\left(1 - e^{-\frac{1}{\phi(k)}}\right)^2} \left(e^{-\frac{2}{\phi(k)}} - 1 \right) \\
&= k^2 + \phi(k) \left[\frac{1 - e^{-\frac{2}{\phi(k)}}}{2\left(1 - e^{-\frac{1}{\phi(k)}}\right)^2} - 2k \right].
\end{aligned}$$

   The per-spike RMSE of the network estimate as a function of drive strength k is therefore

$$RMSE_{spike}(k) = \sqrt{k^2 + \phi(k) \left[\frac{1 - e^{-\frac{2}{\phi(k)}}}{2\left(1 - e^{-\frac{1}{\phi(k)}}\right)^2} - 2k \right]}. \tag{3.8}$$

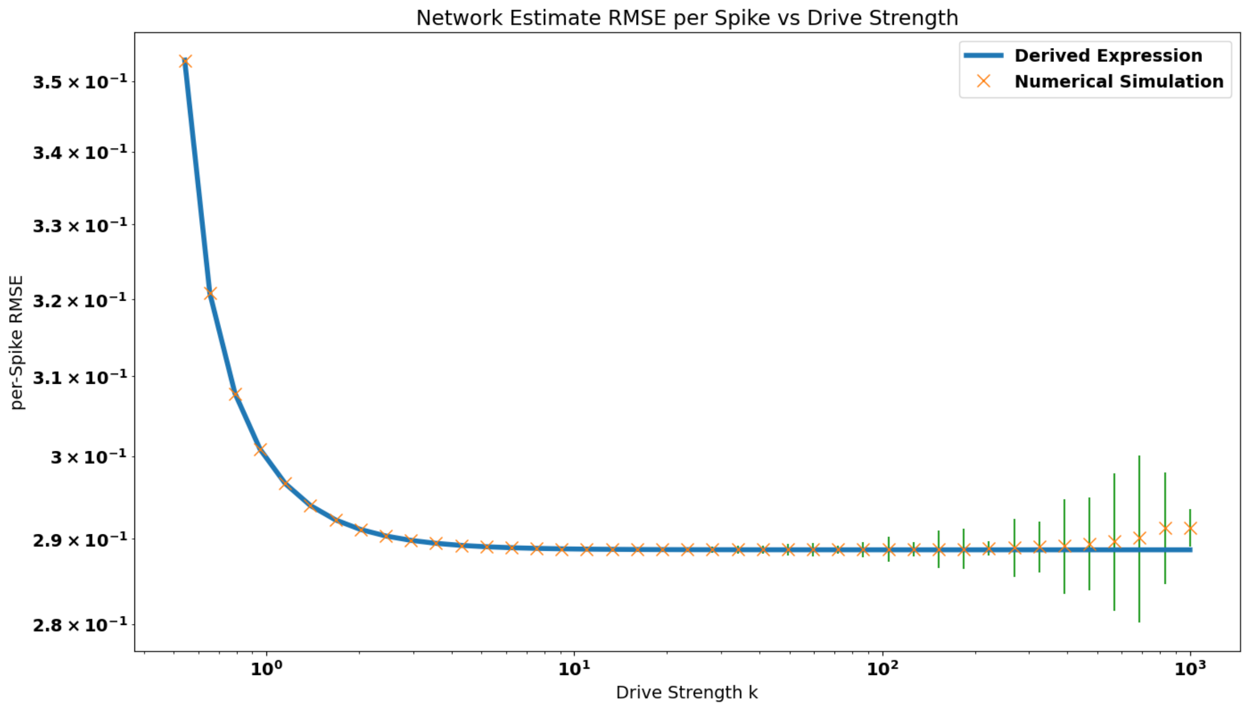
   To write the RMSE explicitly as a function of firing rate $\phi(k)$, we invert equation (3.2) to obtain

$$k(\phi) = \frac{v_{th} + \frac{e^{-\frac{1}{\phi}}}{2}}{1 - e^{-\frac{1}{\phi}}}.$$

Substitute this for k to obtain

$$
\begin{aligned}
RMSE_{spike}(\phi) &= \sqrt{k(\phi)^2 + \phi\left[\frac{1-e^{-\frac{2}{\phi}}}{2\left(1-e^{-\frac{1}{\phi}}\right)^2} - 2k(\phi)\right]} \\
&= \sqrt{\left(\frac{v_{th} + \frac{e^{-\frac{1}{\phi}}}{2}}{1-e^{-\frac{1}{\phi}}}\right)^2 + \phi\left[\frac{1-e^{-\frac{2}{\phi}}}{2\left(1-e^{-\frac{1}{\phi}}\right)^2} - 2\,\frac{v_{th} + \frac{e^{-\frac{1}{\phi}}}{2}}{1-e^{-\frac{1}{\phi}}}\right]}.
\end{aligned}
\tag{3.9}
$$

Equations (3.8) and (3.9) are plotted in figure (4). Note that the drive strength varies the amplitude of the target system's steady state. Thus we have derived the the network performance over its dynamic range of representable state space.



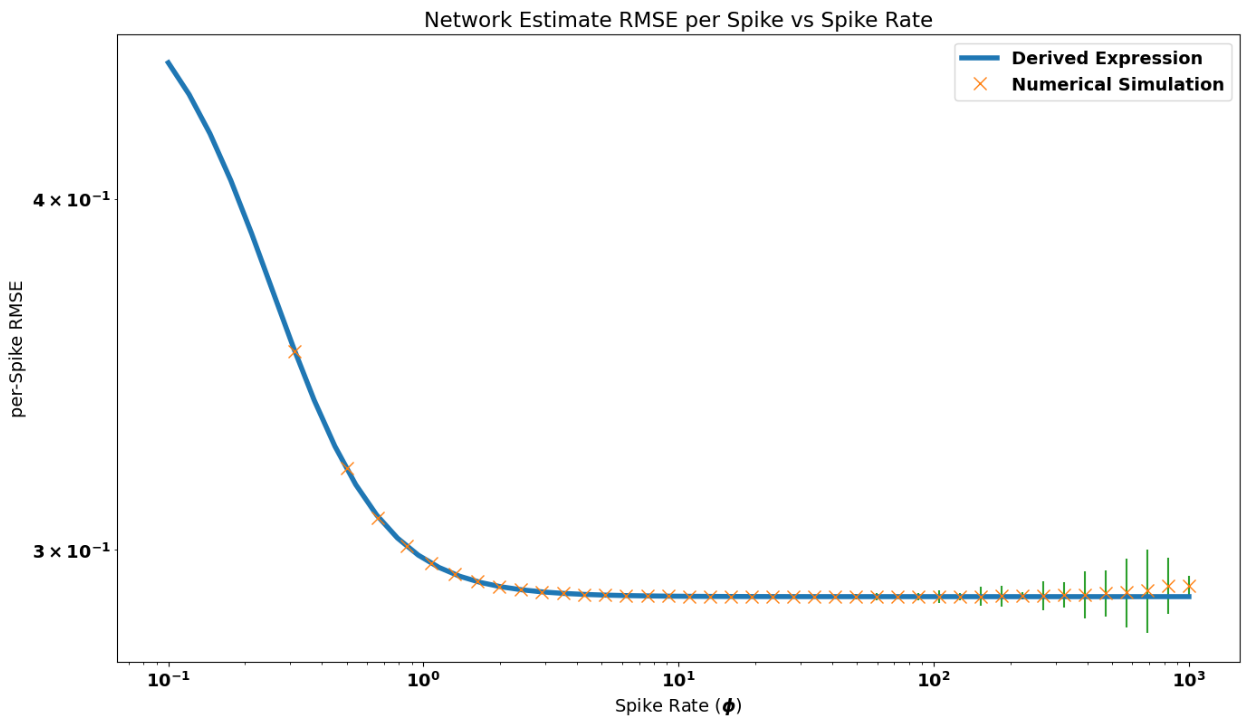


Figure 4: ***Top:*** A log-log plot of equation (3.8). ***Bottom:*** A log-log plot of equation (3.9). ***Both:*** Each simulated data point is the RMSE averaged over all inter-spike intervals in a simulation of length $T = 80\tau_s$ at a constant (in time) drive strength. Between simulations, the spike rates were varied by sweeping drive strength. Green vertical lines towards the larger values are +/- 1 standard deviation. The spike rates $\hat{\phi}$ were computed numerically via dividing the number of spikes in a simulation by the simulation duration. The RMSE between two adjacent spikes was computed by numerical integration as a discrete sum: $R\hat{M}SE = \sqrt{\hat{\phi} \sum_{\tau \text{ between spikes}} e(\xi)^T e(\xi)\, d\xi}$. The increase in standard deviation is due to finite approximation error from numerical integration.

4 Analysis: RMSE vs Spike Rate for a Fixed Dynamical System

Here we derive the RMSE of a signal representing a given dynamical system with a varying spike rate. The RMSE is computed over a constant interval of time for a fixed target system while the spike rate is varied.

1. Our system is described by

$$A = -\begin{bmatrix} 1 & 0 \\ 0 & 1 \end{bmatrix},$$

$$B = \begin{bmatrix} 1 & 0 \\ 0 & 1 \end{bmatrix},$$

$$c(\xi) = \mathcal{U}_1$$

$$d\xi = 10^{-4},$$

$$N = 4,$$

$$x(0) = \begin{bmatrix} \frac{1}{2} & 0 \end{bmatrix}.$$

2. With the given initial conditions, $v_j = 0$ for $j \neq 1$ for all ξ. From equations (2.7) and (2.8), the dynamics simplify to

$$\dot{v_1} = \Lambda_1 v_1 + (\Lambda_1 + 1)\rho_1 + S_1 \mathcal{U}_1^T \mathcal{U}_1 - \Omega_1.$$

It is clear that $\Lambda_1 = -1$ so that

$$\dot{v_1} = -v_1 + S_1 - \Omega_1, \tag{4.1}$$

which is a form of the well-known Leaky Integrate-and-Fire (LIF) model.

3. Assuming a spike has occurred at $v_{th} = \frac{1}{2}$, the voltage has just been reset so that $v_1(0) = -\frac{1}{2}$. Until the next spike, the neuron's trajectory is integrated as

$$v(\xi) = S_1 - e^{-\xi}(S_1 + \frac{1}{2}).$$

The spike occurs at $v(\xi_{spike}) = v_{th}$ or

$$v_{th} = S_1 - e^{-\xi}(S_1 + \frac{1}{2})$$

$$\implies \frac{S_1 - v_{th}}{S_1 + \frac{1}{2}} = e^{-\xi_{spike}}$$

$$\implies \xi_{spike} = ln(S_1 + \frac{1}{2}) - ln(S_1 - v_{th}).$$

The inverse of the preceding expression gives the firing rate of the neuron,

$$\phi(S_1) \triangleq \frac{1}{ln(1+\frac{1}{2\,S_1}) - ln(1-\frac{v_{th}}{S_1})}. \tag{4.2}$$

Equation (4.2) describes the neuron's firing rate as a function of the decode matrix D's singular values. Thus for a given target dynamical system, the decode matrix D determines the neuron's firing rates.

4. From equations (2.9) and (2.2),

$$\dot{\rho} = -\rho + \Omega$$

$$\implies \dot{\hat{x}} = -\hat{x} + \mathcal{U}\Omega$$

$$\implies \dot{\hat{x}} = -\hat{x} + \mathcal{U}_1 \sum_{l=0}^{\infty} \delta\left(\xi - \frac{l}{\phi}\right), \tag{4.3}$$

where the last equality follows from the periodicity of the LIF neuron firing at rate ϕ.

We solve equation (4.3) and inductively derive an explicit expression for its asymptotic behavior in time. Note that equation (4.3) implies that the network estimate $\hat{x}$ will decay until the first spike ξ_1^1 occurs:

$$\hat{x}(\xi) = x(0)e^{-\xi}, \quad 0 \le \xi < \xi_1^1.$$

At this instant, the vector $\mathcal{U}_1$ is added to the network estimate,

$$\hat{x}(\xi_1^1) = x(0)e^{-\xi_1^1} + \mathcal{U}_1.$$

Decay again occurs until the next spike

$$\hat{x}(\xi) = \hat{x}(\xi_1^1)e^{-(\xi-\xi_1^1)},$$

$$= \left(x(0)e^{-\xi_1^1} + \mathcal{U}_1\right)e^{-(\xi-\xi_1^1)}, \quad 0 \le \xi - \xi_1^1 < \frac{1}{\phi}$$

$$\implies \hat{x}(\xi_1^1 + \frac{1}{\phi}) = \left(x(0)e^{-\xi_1^1} + \mathcal{U}_1\right)e^{-\frac{1}{\phi}} + \mathcal{U}_1$$

$$= x(0)e^{-\left(\xi_1^1+\frac{1}{\phi}\right)} + \mathcal{U}_1 e^{-\frac{1}{\phi}} + \mathcal{U}_1.$$

The third spike more clearly shows the recursive behavior

$$\hat{x}(\xi_1^1 + \frac{2}{\phi}) = \left[x(0)e^{-\left(\xi_1^1+\frac{1}{\phi}\right)} + \mathcal{U}_1 e^{-\frac{1}{\phi}} + \mathcal{U}_1.\right]e^{-\frac{1}{\phi}} + \mathcal{U}_1$$

$$= x(0)e^{-\left(\xi_1^1+\frac{2}{\phi}\right)} + \mathcal{U}_1 e^{-\frac{2}{\phi}} + \mathcal{U}_1 e^{-\frac{1}{\phi}} + \mathcal{U}_1.$$

Let us consider the n^{th} spike sufficiently far from $\xi = 0$ such that the transient term $x(0)e^{-\left(\xi_1^1+\frac{n-1}{\phi}\right)}$ can be neglected. This leads to the expression

$$\hat{x}\left(\xi_1^1 + \frac{n}{\phi}\right) = \sum_{l=0}^{n-1} \mathcal{U}_1 e^{-\frac{l}{\phi}}$$

$$= \mathcal{U}_1 \frac{1 - e^{-\frac{n}{\phi}}}{1 - e^{-\frac{1}{\phi}}}.$$

For sufficiently large n, this converges to

$$\hat{x}\left(\xi_1^1 + \xi_1^n\right) = \frac{\mathcal{U}_1}{1 - e^{-\frac{1}{\phi}}}.$$

Between two spikes, the dynamics are exponential decay

$$\hat{x}\left(\xi\right) = \frac{\mathcal{U}_1}{1 - e^{-\frac{1}{\phi}}} e^{-\left(\xi - \xi_1^n\right)}, \quad 0 \leq \xi - \xi_1^n < \frac{1}{\phi},$$

so that the long term network estimate is

$$\hat{x}\left(\xi\right) = \frac{\mathcal{U}_1}{1 - e^{-\frac{1}{\phi}}} e^{-\left(\xi - \xi_1^1\right) \mod \frac{1}{\phi}}.$$

Applying equation (4.2),

$$
\begin{aligned}
e^{-\frac{1}{\phi}} &= e^{ln\left(1-\frac{v_{th}}{S_1}\right)-ln\left(1+\frac{1}{2\,S_1}\right)} \\
&= \frac{1-\frac{v_{th}}{S_1}}{1+\frac{1}{2\,S_1}} \\
\implies 1-e^{-\frac{1}{\phi}} &= 1-\frac{1-\frac{v_{th}}{S_1}}{1+\frac{1}{2\,S_1}} \\
&= \frac{1+\frac{1}{2\,S_1}-1+\frac{v_{th}}{S_1}}{1+\frac{1}{2\,S_1}} \\
&= \frac{\frac{1}{S_1}\left(\frac{1}{2}+v_{th}\right)}{1+\frac{1}{2\,S_1}} \\
&= \frac{\frac{1}{2}+v_{th}}{S_1+\frac{1}{2}}s \\
\implies \frac{S_1^{-1}}{1-e^{-\frac{1}{\phi}}} &= \frac{1}{S_1}\frac{S_1+\frac{1}{2}}{\frac{1}{2}+v_{th}} \\
&= \frac{1+\frac{1}{2\,S_1}}{\frac{1}{2}+v_{th}} \\
&= 1+\frac{1}{2\,S_1},
\end{aligned}
$$

where the last equality uses the fact that $v_{th} = \frac{1}{2}$. The network estimate is therefore

$$\hat{x}(\xi) = \left(1+\frac{1}{2\,S_1}\right)e^{-\ \left(\xi-\xi_1^1\right) \mod \frac{1}{\phi}}\ \mathcal{U}_1 \tag{4.4}$$

Equation (4.4) is plotted in figure (5). The trajectories converge indefinitely at $\tau \simeq 5$.

5. Suppose the systems have settled so that equation (4.4) holds. To compute the RMSE of the estimate, consider the interval between two successive spikes. The RMSE over this period is

$$RMSE_{spike} \triangleq \sqrt{\phi\int_0^{\frac{1}{\phi}} e^T e(\tau)\ \mathrm{d}\tau}.$$

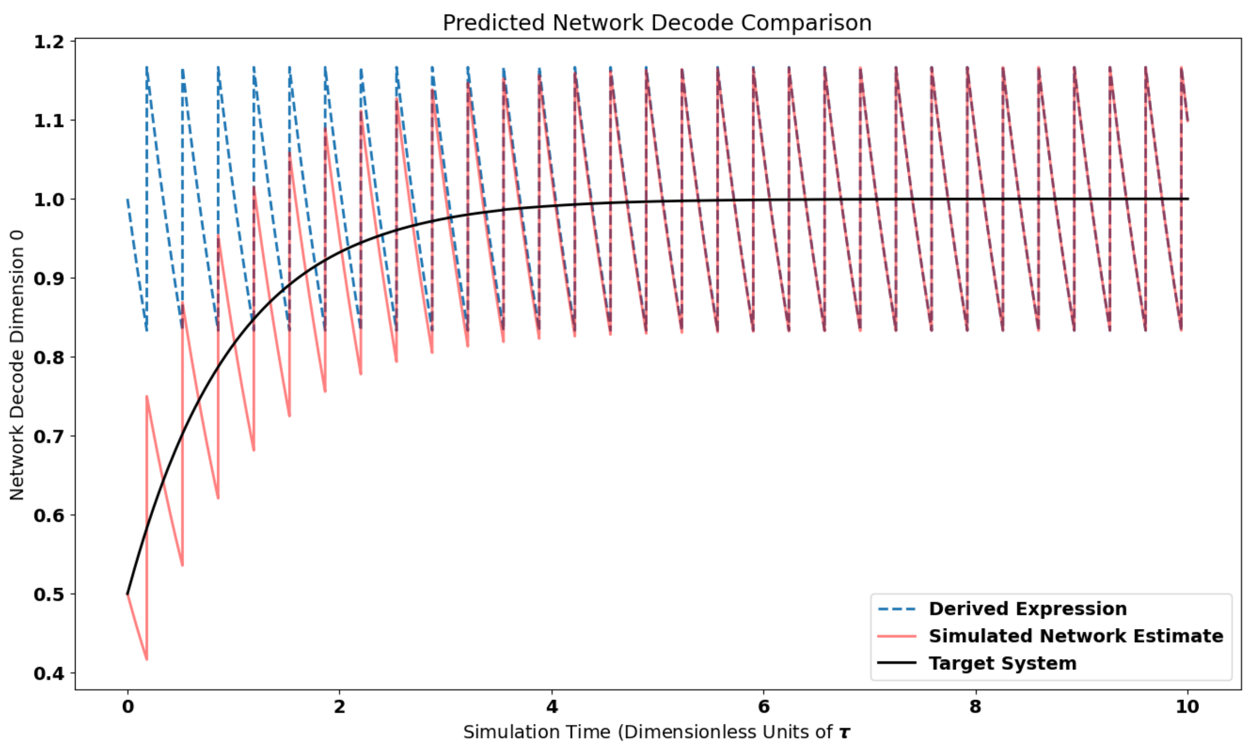


Figure 5: Comparison of the derived long-term network estimate equation (4.4) to numerical simulation. The simulation parameters are described at the beginning of this section, with the decoder matrix D chosen to be the first $d = 2$ rows of the N x N identity matrix, scaled by 3. This ensures the singular value $S_1 = 3$. Using the rate computed by equation (4.2), the derived estimate is computed then overlaid on the numerical simulation after offsetting time by the first spike arrival, ξ_1^1.

Note that the target dynamical system settles to a fixed point $x = \mathcal{U}_1$ so that

$$\begin{aligned}
e(\tau) &= x(\tau) - \hat{x}(\tau) \\
&= \mathcal{U}_1 - \left(1 + \frac{1}{2\,S_1}\right) e^{-\tau}\, \mathcal{U}_1 \\
&= \mathcal{U}_1 \left[1 - e^{-\tau}\left(1 + \frac{1}{2\,S_1}\right)\right] \\
\implies e^T e\,(\tau) &= \left[1 - e^{-\tau}\left(1 + \frac{1}{2\,S_1}\right)\right]^2 \\
&= 1 - 2\,e^{-\tau}\left(1 + \frac{1}{2\,S_1}\right) + e^{-2\,\tau}\left(1 + \frac{1}{S_1} + \frac{1}{4\,S_1^2}\right).
\end{aligned}$$

The integral is therefore

$$\begin{aligned}
\int_0^{\frac{1}{\phi}} e^T e(\tau)\ \mathrm{d}\tau &= \frac{1}{\phi} - 2\left(1 + \frac{1}{2\,S_1}\right)\frac{\frac{1}{2} + v_{th}}{S_1 + \frac{1}{2}} + \frac{1}{2}\left(1 + \frac{1}{S_1} + \frac{1}{4\,S_1^2}\right)\left(1 - e^{\frac{2}{\phi}}\right) \\
&= \frac{1}{\phi} - 2\frac{1}{S_1}\left(S_1 + \frac{1}{2}\right)\frac{\frac{1}{2} + v_{th}}{S_1 + \frac{1}{2}} + \frac{1}{2}\left(1 + \frac{1}{S_1} + \frac{1}{4\,S_1^2}\right)\left(1 - e^{\frac{2}{\phi}}\right) \\
&= \frac{1}{\phi} - \frac{1 + 2\,v_{th}}{S_1} + \frac{1}{2}\left(1 + \frac{1}{S_1} + \frac{1}{4\,S_1^2}\right)\left(1 - e^{\frac{2}{\phi}}\right), \\
&= \frac{1}{\phi} - \frac{1 + 2\,v_{th}}{S_1} + \frac{1}{2}\frac{1}{S_1}\left(1 + \frac{1}{4\,S_1} + 2\,v_{th} - \frac{v_{th}^2}{S_1}\right) \\
&= \frac{1}{\phi} - \frac{1 + 2\,v_{th} - \frac{1}{S_1}\left(\frac{1}{4} - v_{th}^2\right)}{2\,S_1} \\
&= \frac{1}{\phi} - \frac{1}{S_1},
\end{aligned}$$

where we have used the earlier result

$$\frac{S_1^{-1}}{1 - e^{\frac{1}{\phi}}} = 1 + \frac{1}{2\,S_1},$$

and

$$e^{-\frac{2}{\phi}} = \frac{\left(1 - \frac{v_{th}}{S_1}\right)^2}{\left(1 + \frac{1}{2S_1}\right)^2}$$

$$= \frac{1 - 2\,\frac{v_{th}}{S_1} + \frac{v_{th}^2}{S_1^2}}{1 + \frac{1}{S_1} + \frac{1}{4\,S_1^2}}$$

$$\implies 1 - e^{-\frac{2}{\phi}} = \frac{1 + \frac{1}{S_1} + \frac{1}{4\,S_1^2} - 1 + 2\,\frac{v_{th}}{S_1} - \frac{v_{th}^2}{S_1^2}}{1 + \frac{1}{S_1} + \frac{1}{4\,S_1^2}}$$

$$= \frac{\frac{1}{S_1}\left(1 + \frac{1}{4\,S_1} + 2\,v_{th} - \frac{v_{th}^2}{S_1}\right)}{1 + \frac{1}{S_1} + \frac{1}{4\,S_1^2}}.$$

Consequently the per-spike RMSE of the network estimate is given by

$$RMSE_{spike}(s, \phi(s)) = \sqrt{1 - \frac{\phi}{S_1}}. \tag{4.5}$$

To write the above equation as a function of only ϕ, we invert equation (4.2) to obtain

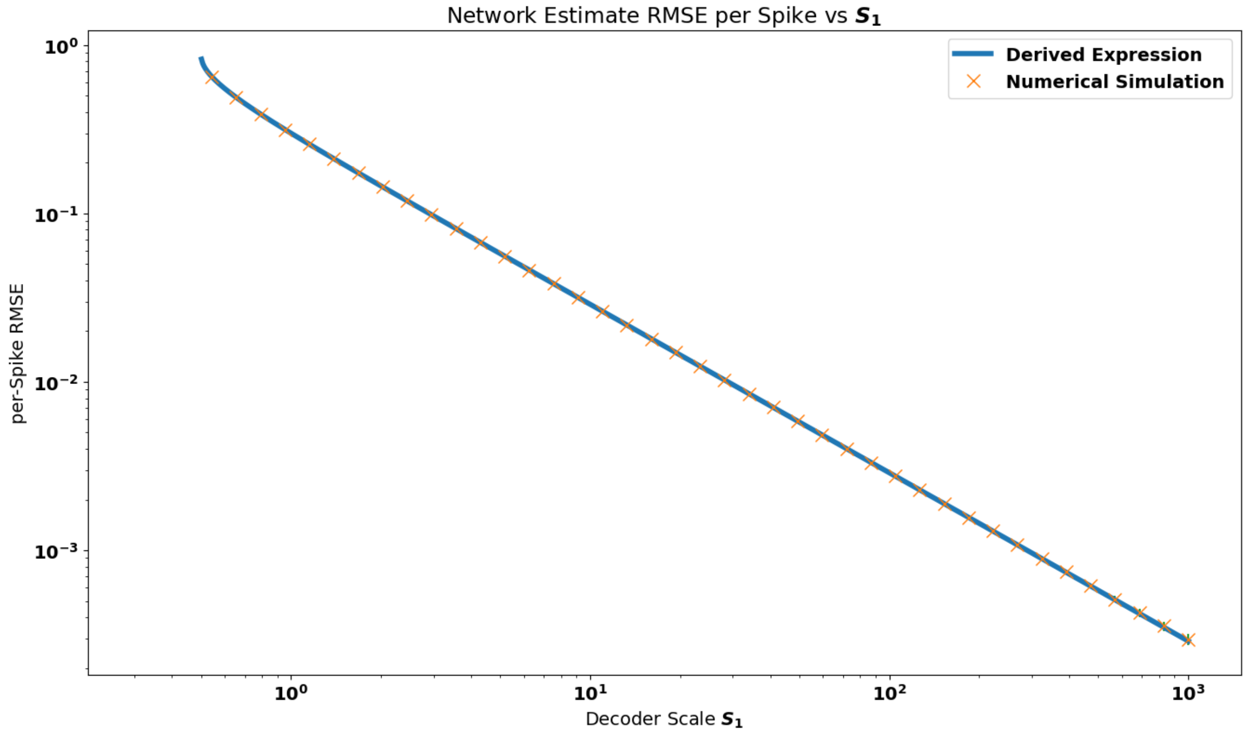
$$S_1(\phi) = \frac{v_{th} + \frac{e^{-\frac{1}{\phi}}}{2}}{1 - e^{-\frac{1}{\phi}}}$$

$$\implies RMSE_{spike} = \sqrt{1 - \phi\left(\frac{1 - e^{-\frac{1}{\phi}}}{v_{th} + \frac{1}{2}e^{-\frac{1}{\phi}}}\right)}$$

$$= \sqrt{1 + 2\phi\left(\frac{e^{-\frac{1}{\phi}} - 1}{e^{-\frac{1}{\phi}} + 1}\right)}$$

$$= \sqrt{1 - 2\phi \tanh\frac{1}{2\,\phi}}. \tag{4.6}$$

The preceding equation is plotted in figure (6). Above spikes rates of $\phi = 1$, the relationship is linearly decreasing on a logarithmic scale.



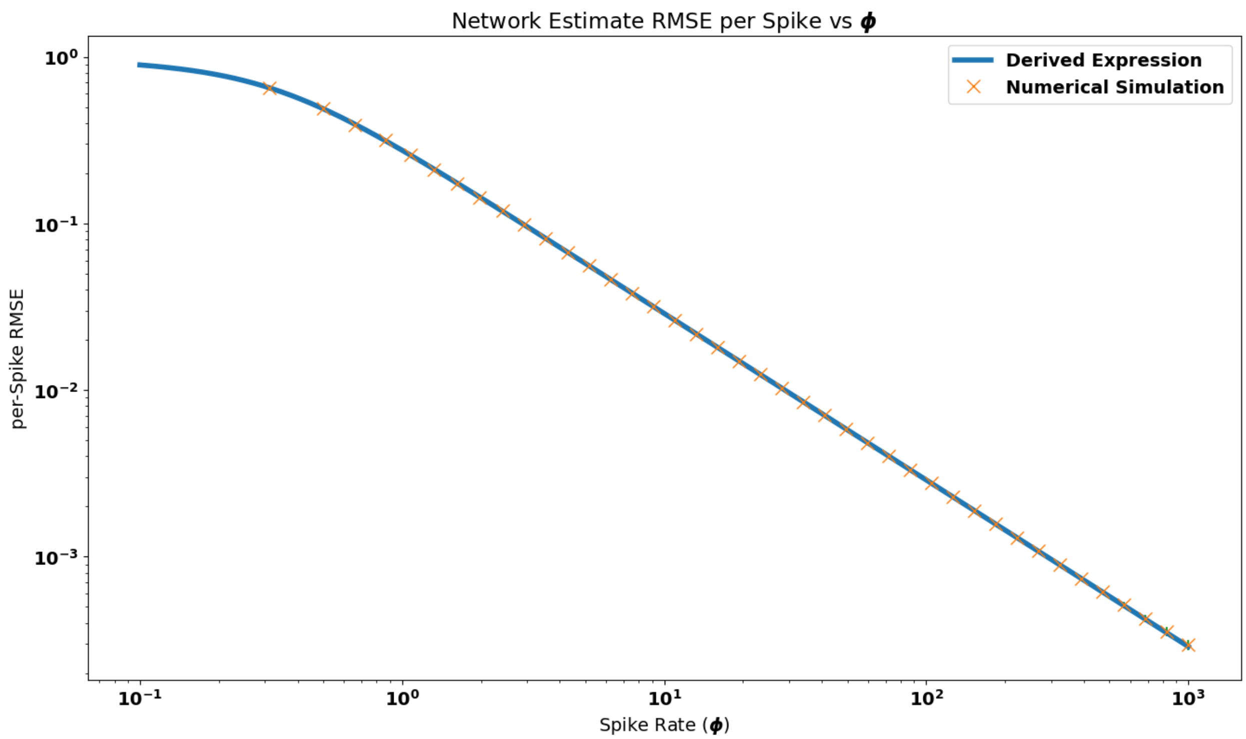


Figure 6: ***Top:*** A log-log plot of equation (4.5) compared with numerical measurements. ***Bottom:*** A log-log plot of equation (4.6). ***Both:*** Each simulated data point is the RMSE averaged over all inter-spike intervals in a simulation of length $T = 80\tau_s$ with $d\xi = 10^{-4}$. Green vertical lines visible towards the larger values are +/- 1 standard deviation over the number of inter-spike intervals in a given simulation. The spike rates $\hat{\phi}$ were computed numerically via dividing the number of spikes in a simulation by the simulation duration. The RMSE between two adjacent spikes was computed by numerical integration as a discrete sum: $R\hat{M}SE = \sqrt{\hat{\phi} \sum_{\tau \text{ between spikes}} e(\xi)^T e(\xi)\ d\xi}$.

5 Derivation: The Predictive Coding Framework and Gap-Junction Network

Here we derive the a form of the predictive coding framework (PCF) as defined in Boerlin & Deneve, 2013. We note an assumption in this model that we later show leads to errant behavior in the network estimate. The correction of this assumption produces an intermittent mode featuring direct membrane voltage coupling. We loosely term this a gap-junction network. We compare the network estimate of all three models (PCF, gap-junction, and self-coupled) for the case of a constant driving stimulus.

1. ***The Predictive Coding Framework (PCF):*** The PCF synthesizes a spiking neural network that implements a given dynamical system. It is briefly derived as follows:

   Assume the following are given:

   - A Linear Dynamical System $\dot{x}(\xi) = Ax(\xi) + Bc(\xi)$, $x \in \mathbf{R}^d$
   - A Decoder Matrix $D \in \mathbf{R}^{d\ x\ N}$ specifying The tuning curve of N neurons in d-dimensional space.

   Let $o(t) \in \mathbf{R}^N$ describe the spike trains whose j^{th} component is given by

   $$o_j(t) \triangleq \sum_{k=0}^{\infty} \delta(t - t_j^k),$$

   where t_j^k is the time of the k^{th} spike of neuron j. Define the time-varying firing rate of the neurons by

   $$\frac{dr}{dt}(t) \triangleq -\tau_s^{-1} r(t) + \tau_s^{-1} o(t),$$

   where $\tau_s{-1}$ is the decay rate of $r(t)$ given by the inverse synaptic time constant τ_s. For consistency across models, we transform the preceding two equations to dimensionless time via $\xi = \frac{t}{\tau_s} \implies \tau_s\, d\xi = dt$. This gives

   $$o_j(\xi) \triangleq \sum_{k=0}^{\infty} \delta(\xi - \xi_j^k), \tag{5.1}$$

   where ξ_j^k is the k^{th} spike of neuron j in dimensionless time, and

   $$\frac{dr}{dt}(t) = -\tau_s^{-1} r(t) + \tau_s^{-1} o(t),$$

   $$\implies \frac{dr}{\tau_s\, d\xi}(\xi) = -\tau_s^{-1} r(\xi) + \tau_s^{-1} o(\xi),$$

   $$\implies \frac{dr}{d\xi}(\xi) = -r(\xi) + o(\xi).$$

   Letting $[\ \dot{}\ ]$ denote differentiation w.r.t. dimensionless time ξ, we arrive at

   $$\dot{r}(\xi) \triangleq -r(\xi) + o(\xi). \tag{5.2}$$

   The network estimate is defined as

   $$\hat{x}(\xi) \triangleq Dr(\xi), \tag{5.3}$$

which gives rise to the network estimation error

$$e(\xi) \triangleq x(\xi) - \hat{x}(\xi). \tag{5.4}$$

The network chooses spike times ξ_j^k to greedily optimize the objective function

$$\mathcal{L}(\xi) = ||x(\xi + d\xi) - \hat{x}(\xi + d\xi)||^2.$$

The PCF features regularized rate terms $r(\xi)$ for the sake of biological plausibility. At present we ignore these terms. They only increase the network estimation error e by sacrificing accuracy to minimize $r(\xi)$. Using an identical approach to the derivation of the self-coupled network in section (2), we arrive at

$$d_j^T (x - \hat{x}) = \frac{d_j^T d_j}{2}$$

where d_j is the j^{th} column of D. We define membrane voltage to get the spiking condition:

$$\begin{aligned} v_j &\triangleq d_j^T (x - \hat{x}) \\ \implies d_j^T e &= v_{th}, \end{aligned} \tag{5.5}$$

where $v^{th} = \frac{d_j^T d_j}{2}$.

Deriving the dynamics, the preceding equation defines voltage, which in matrix form is given by

$$\begin{aligned} V &= D^T (x - \hat{x}) \\ \implies \dot{V} &= D^T \dot{x} - D^T \dot{\hat{x}} \\ &= D^T (Ax + Bc) - D^T (D\dot{r}) \\ &= D^T Ax + D^T Bc - D^T D (-r + o). \end{aligned}$$

The PCF makes the assumption that when the network performs correctly, $x = \hat{x}$. We later quantify the estimation error introduced by this assumption and correct it to form the gap-junction model. For now make the assumed substitution $x = \hat{x} = Dr$.

$$\begin{aligned} \dot{V} &= D^T A (Dr) + D^T Bc + D^T Dr - D^T Do \\ &= D^T (A + I) Dr + D^T Bc - D^T Do. \end{aligned}$$

The model is finalized by the addition of a voltage leakage term to ensure stability, giving the final dynamics equation

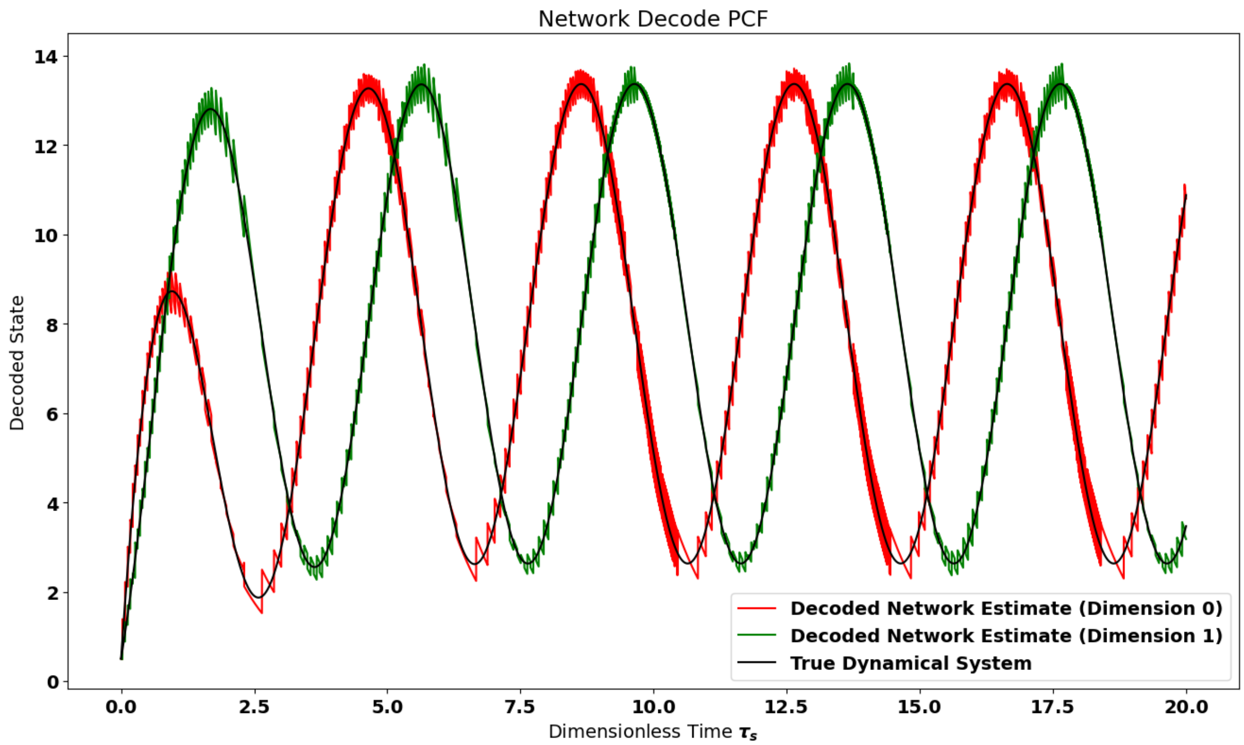
$$\dot{V} = -v + D^T (A + I) Dr + D^T Bc - D^T Do. \tag{5.6}$$

Equation (5.6) scales the spike train o_j by $d_j^T d_j$. Thus the spiking behavior is described by

$$
\begin{aligned}
& v_{th} = \frac{d_j^T d_j}{2} \\
& \text{if } v_j > v_j^{th}, \\
& \text{then } v_j^{'} = v_j - d_j^T d_j \int \delta(\tau)\, d\tau, \\
& \text{and } r_j^{'} = r_j + \int \delta(\tau)\, d\tau.
\end{aligned}
\tag{5.7}
$$

Equations (5.6) and (5.7) specify the PCF model we compare against. Figure (7) shows simulations of the PCF model with the following parameters:

$$
\begin{aligned}
A &= -\begin{bmatrix} 1 & 0 \\ 0 & 1 \end{bmatrix}, \\
B &= \begin{bmatrix} 1 & 0 \\ 0 & 1 \end{bmatrix}, \\
c(\xi) &= 10 \begin{bmatrix} cos(\frac{\pi}{2}\xi) \\ sin(\frac{\pi}{2}\xi) \end{bmatrix} + 8 \\
D_{\text{ij}} &\sim \mathcal{N}(0,1) \text{ Columns Normalized to Unit Length} \\
d\xi &= 10^{-5}, \\
N &= 32, \\
x(0) &= \begin{bmatrix} \frac{1}{2} & \frac{1}{2} \end{bmatrix}.
\end{aligned}
\tag{5.8}
$$



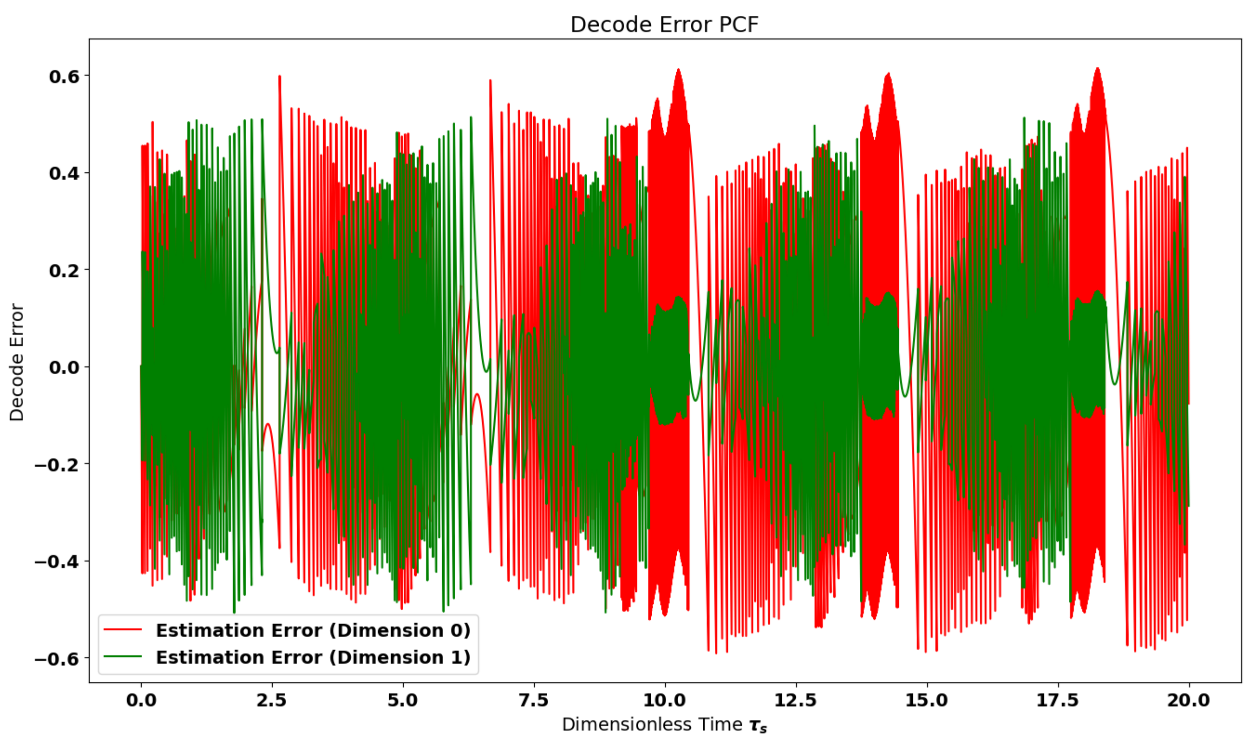


Figure 7: Simulation of PCF model given by equations (5.7) and (5.6). ***Top:*** Network estimate given by equation (5.3). ***Bottom:*** Estimation Error for PCF network from equation (5.4). The simulation parameters are given in equation (5.8). The numerical implementation is identical to that in section (2). A Padé approximation is used to compute a matrix exponential, then used to integrate the continuous terms of the differential equations. The spikes are handled separately at each time step by manually changing the values of neurons above threshold. For reasons of numerical stability, only one spike per time-step is allowed in the PCF model.

2. ***The Gap-Junction Correction:*** Here we correct the assumption that $\hat{x} = x$ made in the PCF model. We restart the previous derivation from this point and derive more a accurate form of equation (5.6) termed the gap-junction model.
The derivation is identical as the PCF until we derive the voltage dynamics.

$$\dot{V} = D^T Ax + D^T Bc + D^T Dr - D^T Do.$$

Instead of assuming $x = \hat{x}$, we apply the definition of voltage, equation (5.5) in matrix form.

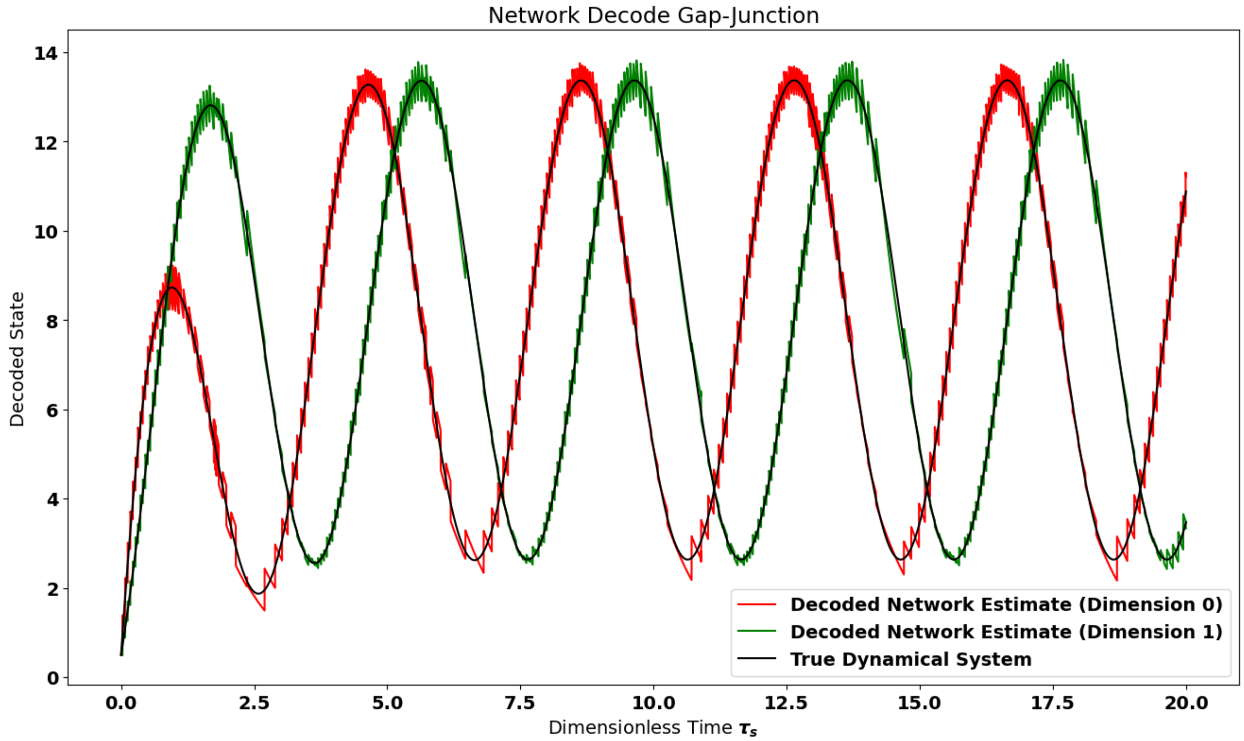
$$\begin{aligned} v_j &= d_j^T e \\ \implies V &= D^T e \\ &= D^T (x - \hat{x}) \\ \implies x &= D^{T\dagger} V + \hat{x} \\ &= D^{T\dagger} V + Dr, \end{aligned}$$

where $D^{T\dagger}$ is the left Moore-Penrose pseudo-inverse of D^T. Substitute this for x in $\dot{V}$ above to get

$$\dot{V} = D^T A \left(D^{T\dagger} V + Dr \right) + D^T Dr + D^T Bc - D^T Do$$

$$\implies \dot{V} = D^T A D^{T\dagger} V + D^T (A + I) Dr + D^T Bc - D^T Do. \tag{5.9}$$

Equation (5.9) in conjunction with an identical spiking rule from PCF, equation (5.7) specifies the gap-junction model. It is simulated in figure (8). While the two simulations are similar, there are noticeable differences in their behavior e.g. $\tau_s \simeq 10$, 13.



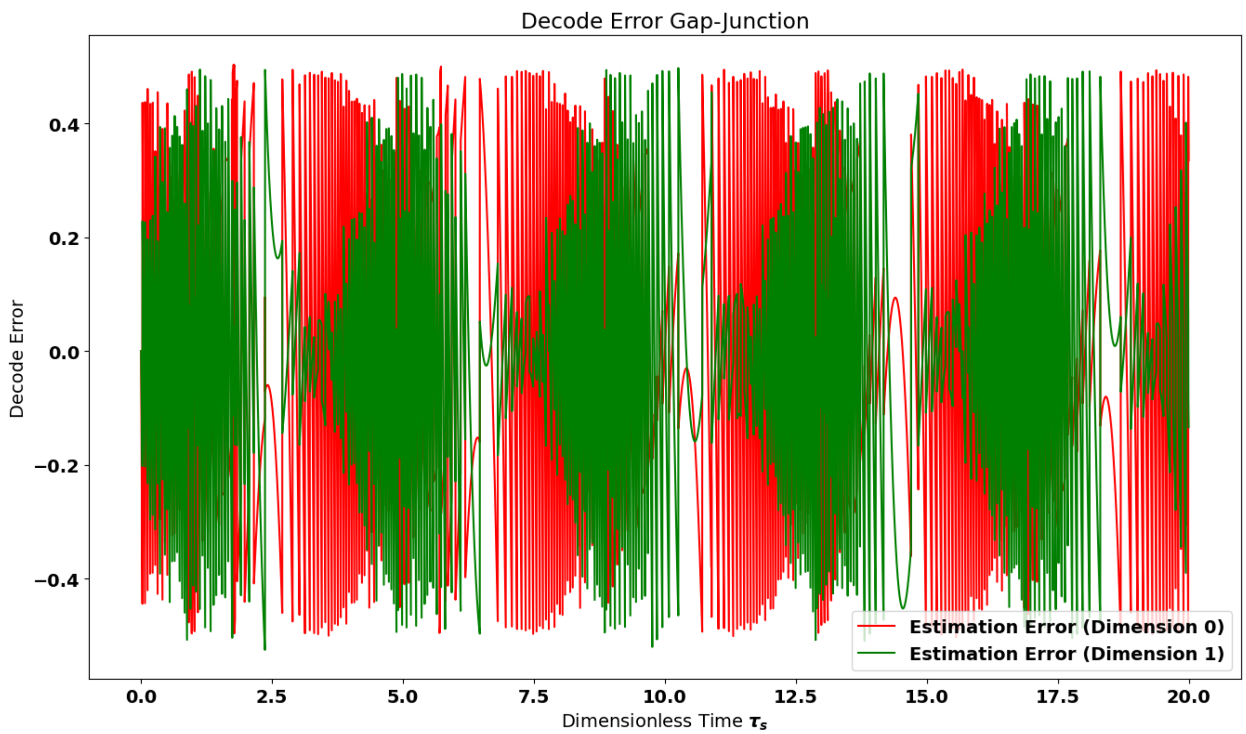


Figure 8: Simulation of the Gap-Junction model given by equations (5.7) and (5.9). ***Top:*** Network estimate given by equation (5.3). ***Bottom:*** Estimation Error for the Gap-Junction network from equation (5.4). The simulation parameters are the same as the previous figure. As with the PCF model, the network is only numerically stable if spikes are restricted to one per time step.

6 Analysis: PCF and Gap-Junction Response to Constant Stimulus

We compare the network estimate of all three models (PCF, gap-junction, and self-coupled) for the case of a constant driving stimulus.
Let all 3 models have the same parameters as given by equation (5.8) with the exception that

$$c(\xi) = c = \begin{bmatrix} 1 \\ 0 \end{bmatrix},$$

and $x(0) = \begin{bmatrix} \frac{1}{2} & 0 \end{bmatrix}$.

1. ***PCF Network Response to Constant Stimulus:***
   From equation (5.6), the PCF dynamics become

$$\dot{V}_{pcf} = -V_{pcf} + D^T\left(-I + I\right)D^T r + D^T \begin{bmatrix} 1 \\ 0 \end{bmatrix} - D^T D o$$

$$= -V_{pcf} + D^T \begin{bmatrix} 1 \\ 0 \end{bmatrix} - D^T D o.$$

   All voltages are initially 0. From equation (5.7) the thresholds are identically $\frac{1}{2}$. Until the first spike, neuron j's voltage integrates the quantity $d_j^T \begin{bmatrix} 1 \\ 0 \end{bmatrix}$. Denote the neuron j whose tuning curve d_j is closest in angle to c by

$$j_{max} \triangleq \underset{i \in [1,\ldots,N]}{argmax} \quad d_j^T c.$$

   Neuron j_{max} will receive the highest driving force and will therefore reach its threshold before any other neuron. It will then be reset by 1 to $-\frac{1}{2}$. Each other neuron k will also be reset (decremented) by $d_k^T d_{j_{max}}$, proportional to their angle relative to both neuron j_{max} and the driving strength c. This sequence will repeat periodically so that only neuron j_{max} fires at a constant rate.
   We write the PCF network as the one-dimensional equation

$$v_{pcf} = -v_{pcf} + d_{j_{max}}^T c - o_{j_{max}}.$$

   This is a form of the leaky integrate-and-fire (LIF) model, with drive term $d_j^T c(\xi)$. The neuron is driven by inner product $d_{j_{max}}^T c$. Note from equation (5.7) that the threshold voltage varies with $||d_{j_{max}}||^2$. For clarity, we drop the subscripts j, j_{max} in the following equations. It is understood that we are referring to the solely spiking neuron j_{max}. With initial condition $v_{pcf}(0) = -\frac{||d||^2}{2}$, the neuron's trajectory is integrated as

$$v_{pcf}(\xi) = d^T c - e^{-\xi}\left(d^T c + \frac{||d||^2}{2}\right). \tag{6.1}$$

   The neuron spikes when it reaches the threshold $v_{pcf} = ||d||^2$. To compare with the self-coupled network, we note that the singular value associated with neuron j of the decoder matrix $S = ||d||^2$.

From the preceding equation with voltage at threshold $\frac{||d||^2}{2}$,

$$\frac{||d||^2}{2} = d^T c - e^{-\xi_{spike}} \left(d^T c + \frac{||d||^2}{2} \right)$$

$$\implies e^{-\xi_{spike}} = \frac{d^T c - \frac{||d||^2}{2}}{d^T c + \frac{||d||^2}{2}}$$

$$\implies \xi_{spike} = ln \left(d^T c + \frac{||d||^2}{2} \right) - ln \left(d^T c - \frac{||d||^2}{2} \right)$$

This leads to a firing rate

$$\phi_{pcf}(d) = \frac{1}{ln \left(d^T c + \frac{||d||^2}{2} \right) - ln \left(d^T c - \frac{||d||^2}{2} \right)} \tag{6.2}$$

A self-coupled neuron spike adds U_1 to its network estimate. Using an identical analysis to this case as done in section (4), we substitute d for U_1 to arrive at the steady state network estimate of the PCF network:

$$\hat{x}_{pcf}(\xi) = \left(1 + \frac{1}{2\, d^T c} \right) e^{-\ \left(\xi - \xi_1^1\right) \mod \frac{1}{\phi}}\ d. \tag{6.3}$$

2. ***Gap-Junction Network Response to Constant Stimulus:*** Here we derive the decoded estimate of a gap-junction network driven by a constant stimulus, $c(\xi) = \begin{bmatrix} 1 & 0 \end{bmatrix}$. All other parameters are identical to those in equation (5.8).

   From the dynamics equation (5.9) gap-junction voltages are continuously coupled to one another via $D^T A D^{T\dagger}$. We thus need to solve the entire system between spikes rather than reducing it to a single dimension. Let $\tilde{[]}$ denote the Laplace transform of a variable. Assume neuron j has just spiked so that

$$V(0) = -\frac{1}{2} \begin{bmatrix} d_1^T d_j \\ \vdots \\ d_j^T d_j \\ \vdots \\ d_N^T d_j \end{bmatrix}.$$

   Since $c(\xi) = \begin{bmatrix} 1 \\ 0 \end{bmatrix}$, $B = I$, and $o(\xi) = 0$ between spikes, we have

$$\dot{V} = D^T A D^{T\dagger} V + D^T (A + I) D r + d_1,$$

   where d_1 is the first column of D. Apply the one-sided Laplace Transform to both sides and use the

Laplace derivative property:

$$s\tilde{V} - V(0) = D^T A D^{T\dagger} \tilde{V} + D^T (A + I)\, o D\tilde{r} + \mathcal{L}[d_1]$$

$$\implies \left(s\,I - D^T A D^{T\dagger}\right)\tilde{V} = V(0) + D^T (A + I)\, D\tilde{r} + \tilde{d}_1$$

$$\implies \tilde{V} = \left(s\,I - D^T A D^{T\dagger}\right)^{-1}\left[V(0) + D^T (A + I)\, D\tilde{r} + \tilde{d}_1\right]$$

$$= \left(sI - D^T A D^{T\dagger}\right)^{-1} V(0) + \left(sI - D^T A D^{T\dagger}\right)^{-1} D^T (A + I)\, D\tilde{r} + \tilde{(}d_1).$$

Now apply the inverse Laplace transform. Note that by definition of matrix exponential,

$$\mathcal{L}^{-1}\left(sI - D^T A D^{T\dagger}\right)^{-1} = e^{\xi D^T A D^{T\dagger}}.$$

Therefore,

$$V(\xi) = e^{\xi D^T A D^{T\dagger}} V(0) + \mathcal{L}^{-1}\left[\left(sI - D^T A D^{T\dagger}\right)^{-1} D^T B\tilde{c}\right] + \mathcal{L}^{-1}\left[\left(sI - D^T A D^{T\dagger}\right)^{-1} D^T (A + I)\, D\tilde{r}\right]. \quad (6.4)$$

To simplify the second term of equation (6.4), use the convolution-product property of the Laplace transform to get

$$\mathcal{L}^{-1}\left[\left(sI - D^T A D^{T\dagger}\right)^{-1} D^T B\tilde{c}\right] = \mathcal{L}^{-1}\left[\left(sI - D^T A D^{T\dagger}\right)^{-1}\right] * \mathcal{L}^{-1}\left[D^T B\tilde{c}\right].$$

Note $c(\xi) = \begin{bmatrix} 1 \\ 0 \end{bmatrix}$, and $B = I$. Therefore,

$$\mathcal{L}^{-1}\left[D^T B\tilde{c}\right] = D^T B c = d_1,$$

where d_1 is the first column of D. The entire second term in $V(\xi)$ above becomes

$$\mathcal{L}^{-1}\left[\left(sI - D^T A D^{T\dagger}\right)^{-1} D^T B\tilde{c}\right] = e^{\xi D^T A D^{T\dagger}} * d_1.$$

Evaluating the convolution, bring d_1 outside the integral, a linear operator:

$$e^{\xi D^T A D^{T\dagger}} * d_1(\xi) = \int_{\tau=-\infty}^{\infty} e^{(\xi-\tau) D^T A D^{T\dagger}}\, d\tau\, d_1.$$

The state $V(\xi)$ depends only on the past up to $V(0)$ so that $0 < \xi - \tau \leq \xi$:

$$e^{\xi D^T A D^{T\dagger}} * d_1(\xi) = \int_{\tau=0}^{\xi} e^{(\xi-\tau) D^T A D^{T\dagger}}\, d\tau\, d_1.$$

The integral of the matrix exponential $\int_{t=0}^{T} e^{tX}\, dt = X^{-1}\left(e^{Tx} - I\right)$. Thus,

$$\mathcal{L}^{-1}\left[\left(sI - D^T A D^{T\dagger}\right)^{-1} D^T B\tilde{c}\right] = \left(D^T A D^{T\dagger}\right)^{-1}\left(e^{\xi D^T A D^{T\dagger}} - I\right) d. \quad (6.5)$$

Note the notation $d = D^T Bc$. Looking at the final term of equation (6.4), assume the network estimate is periodic with period $\frac{1}{\phi}$, where ϕ is the unknown spike rate. Between spikes, the dynamics of $r(\xi)$ are known from equation (5.2) solved as

$$r(\xi) = e^{-\xi I} r(0), \quad 0 < \xi \leq \frac{1}{\phi}.$$

Hence,

$$\begin{aligned}
\mathcal{L}^{-1}\left[\left(sI - D^T A D^{T\dagger}\right)^{-1} D^T (A+I) D\tilde{r}\right] &= \mathcal{L}^{-1}\left[\left(sI - D^T A D^{T\dagger}\right)^{-1}\right] * \mathcal{L}^{-1}\left[D^T (A+I) D\tilde{r}\right] \\
&= e^{\xi D^T A D^{T\dagger}} * D^T (A+I) D\, e^{-\xi\, I}\, r(0) \\
&= e^{\xi D^T A D^{T\dagger}} * \left(D^T A D e^{-\xi\, I}\, r(0) + D^T D e^{-\xi\, I}\, r(0)\right) \\
&= e^{\xi D^T A D^{T\dagger}} * D^T A D e^{-\xi\, I}\, r(0) + e^{\xi D^T A D^{T\dagger}} * D^T D e^{-\xi\, I}\, r(0).
\end{aligned}$$

The two convolutions are nearly identical so we solve the simpler of the two:

$$e^{\xi D^T A D^{T\dagger}} * D^T D e^{-\xi\, I}\, r(0) = \int_{\tau=0}^{\xi} e^{(\xi-\tau) D^T A D^{T\dagger}} D^T D e^{-\tau\, I}\, r(0)\, d\tau.$$

Note that $e^{-\tau\, I}$ simplifies as

$$\begin{aligned}
e^{-\tau\, I} &= \sum_{k=0}^{\infty} \frac{(-\tau I)^k}{k!} \\
&= \left(\sum_{k=0}^{\infty} \frac{(-\tau^k)}{k!}\right) I \\
&= e^{-\tau} I.
\end{aligned}$$

The scalar and identity matrix can both move to the beginning of the integral and reformed into a matrix:

$$\begin{aligned}
\int_{\tau=0}^{\xi} e^{(\xi-\tau) D^T A D^{T\dagger}} D^T D e^{-\tau\, I}\, r(0)\, d\tau &= \int_{\tau=0}^{\xi} e^{-\tau\, I} e^{(\xi-\tau) D^T A D^{T\dagger}} D^T D\, r(0)\, d\tau \\
&= e^{\xi D^T A D^{T\dagger}} \int_{\tau=0}^{\xi} e^{-\tau\left(I + D^T A D^{T\dagger}\right)}\, d\tau\ \ D^T D\, r(0) \\
&= e^{\xi D^T A D^{T\dagger}} \left(I + D^T A D^{T\dagger}\right)^{-1} \left(e^{\xi\left(I + D^T A D^{T\dagger}\right)} - I\right) D^T D\, r(0).
\end{aligned}$$

From this expression it follows that

$$e^{\xi D^T A D^{T\dagger}} * D^T (A+I) D\, e^{-\xi\, I}\, r(0) = e^{\xi D^T A D^{T\dagger}} \left(I + D^T A D^{T\dagger}\right)^{-1} \left(e^{\xi\left(I + D^T A D^{T\dagger}\right)} - I\right) D^T (A+I) D\, r(0).$$

Hence,

$$\mathcal{L}^{-1}\left[\left(sI - D^T A D^{T\dagger}\right)^{-1} D^T \left(A+I\right) D\tilde{r}\right] = e^{\xi D^T A D^{T\dagger}} \left(I + D^T A D^{T\dagger}\right)^{-1} \left(e^{\xi\left(I + D^T A D^{T\dagger}\right)} - I\right) D^T (A+I) D\, r(0). \tag{6.6}$$

Using equations (6.5) and (6.6), the voltage trajectory equation (6.4) becomes

$$\begin{aligned} V(\xi) = & \\ & e^{\xi D^T A D^{T\dagger}} V(0) \\ & + \left(D^T A D^{T\dagger}\right)^{-1} \left(e^{\xi D^T A D^{T\dagger}} - I\right) d \\ & + e^{\xi D^T A D^{T\dagger}} \left(I + D^T A D^{T\dagger}\right)^{-1} \left(e^{\xi\left(I + D^T A D^{T\dagger}\right)} - I\right) D^T (A+I) D\, r(0). \end{aligned} \tag{6.7}$$

In the case $A = -I$, equation (6.7) simplifies considerably:

$$V(\xi) = e^{-\xi D^T D^{T\dagger}} V(0) + \left(D^T D^{T\dagger}\right)^{-1} \left(I - e^{-\xi D^T D^{T\dagger}}\right) d. \tag{6.8}$$

Simplify the matrix $D^T D^{T\dagger}$ via its SVD:

$$\begin{aligned} D^T &= V \begin{bmatrix} S \\ 0 \end{bmatrix} \mathcal{U}^T, \\ \implies D^{T\dagger} &= \mathcal{U} \begin{bmatrix} S & 0 \end{bmatrix} V^T \\ \implies D^T D^{T\dagger} &= V \begin{bmatrix} S \\ 0 \end{bmatrix} \mathcal{U}^T \mathcal{U} \begin{bmatrix} S & 0 \end{bmatrix} V^T \\ &= V \begin{bmatrix} S \\ 0 \end{bmatrix} \begin{bmatrix} S & 0 \end{bmatrix} V^T \\ &= V \begin{bmatrix} I_d & 0 \\ 0 & 0 \end{bmatrix} V^T \\ &= \begin{bmatrix} I_d & 0 \\ 0 & 0 \end{bmatrix} \in \mathbf{R}^{N \text{ x } N}, \end{aligned}$$

where I_d denotes the d-dimensional identity matrix. Equation (6.8) becomes

$$V(\xi) = e^{-\xi I_d} V(0) + \begin{bmatrix} I_d & 0 \\ 0 & 0 \end{bmatrix}^{-1} \left(I - e^{-\xi I_d}\right) d.$$

The matrix $\begin{bmatrix} I_d & 0 \\ 0 & 0 \end{bmatrix}$ is not invertible. Consider instead only the first d equations of the preceding system.

$$V_j(\xi) = e^{-\xi} V_j(0) + \left(1 - e^{-\xi}\right) d_j, \quad j = 1, \ldots, d.$$

Note that $d_j = d^T c$, and consider neuron $j_{max} = j$ the first to reach the spike threshold. Recall its initial condition $v(0) = -\frac{||d||^2}{2}$ to arrive at

$$V(\xi) = -e^{-\xi} \frac{||d||^2}{2} + \left(1 - e^{-\xi}\right) d^T c$$

Compare with the corresponding PCF trajectory, equation (6.1). The preceding equation rearranges to

$$V(\xi) = d^T c - e^{-\xi} \left(d^T c + \frac{||d||^2}{2} \right),$$

which is identical to equation (6.1). Since only one neuron spikes, $r(\xi)$ and thus $\hat{x}(\xi)$ are identical for both PCF and gap-junction networks. The preceding, somewhat painful analysis shows that if the PCF and gap-junction models begin on their steady-state trajectories with the same initial conditions, their network estimates are identical in time. The statement is limited to the case of a constant driving stimulus. It does not, for example, show which network reaches the steady state trajectory first.