Research Notes on Self-Coupled Spiking Neural Networks

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today

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 $D \in \mathbf{R}^{d \times N}$ 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 left singular vectors. This choice of coding directions eliminates connectivity between neurons with orthogonal encoding directions.

   At least two neurons per dimension (2d in total) are required since spikes, the encoding quanta, have positive unit-area. 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 of the Basic Model

2.1 Predecessor: PCF Voltage Dynamics

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 $\dot{e}$:

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

The quantity $D^T e$ defines the membrane voltage of the predictive coding framework (PCF), a precursor to this model:

$$v_{pcf} \triangleq D^T e.$$

Note that the definition implies $e = D^{T\dagger} v_{pcf}$. The voltage dynamics are thus

$$\dot{v}_{pcf} = D^T A D^{T\dagger} v_{pcf} + D^T (A + I)(Dr) + D^T Bc - D^T Do, \tag{2.5}$$

where $D^{T\dagger}$ is the left pseudo-inverse of $D^T \in \mathbf{R}^{N \times d}$. The PCF thus defines a mapping between two vector spaces: the d-dimensional state space of the target system, and the N-dimensional voltage space of the spiking neural network. This mapping is visualized in figure (1).

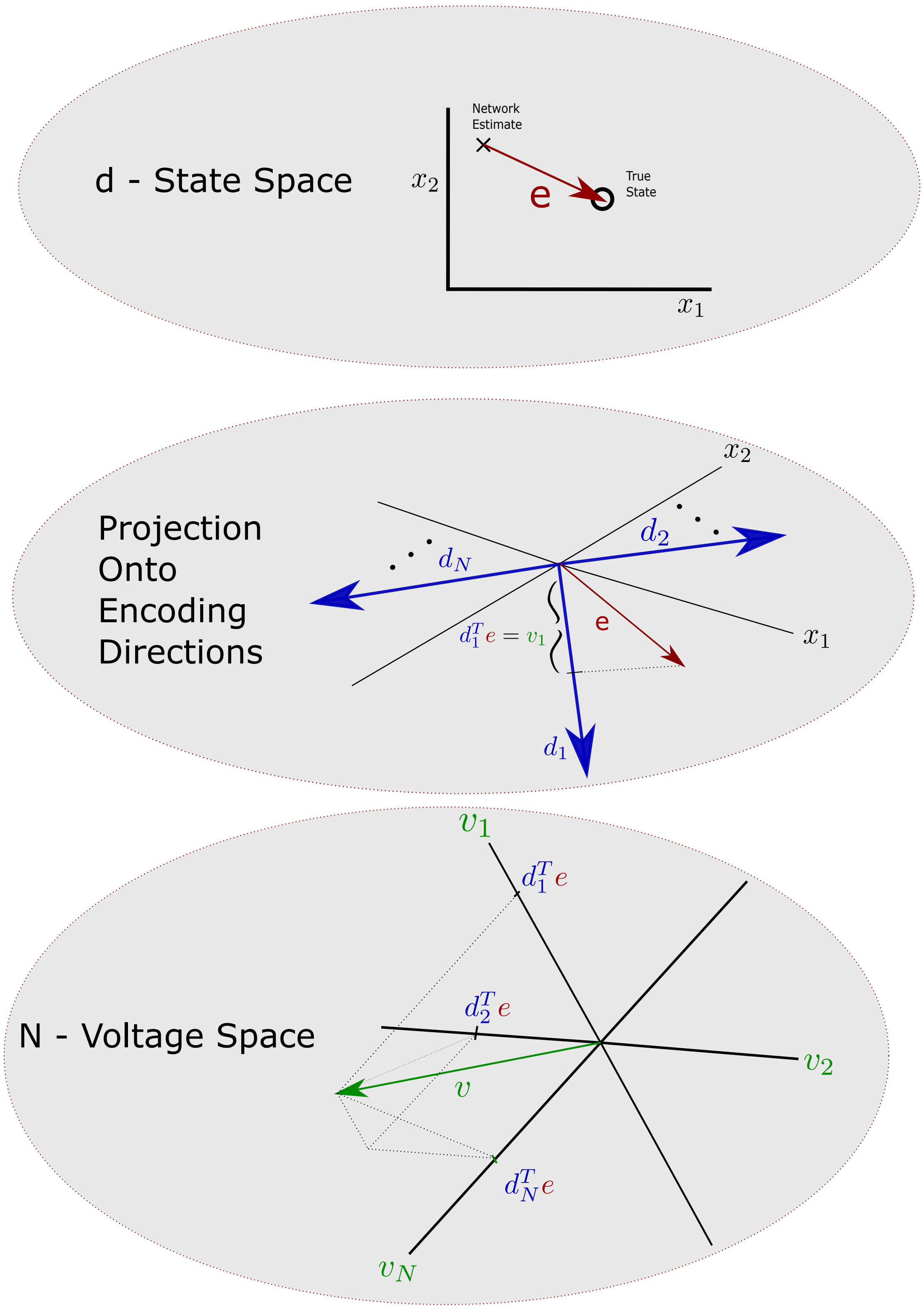


Figure 1: Mapping Between State and Voltage Spaces: ***Top:*** The estimation error e is computed by comparing the decoded network estimate to the true state of the target dynamical system. ***Middle:*** The e is projected onto the encoding directions of the neurons composing the network. The projection of error onto encoding direction j gives the membrane voltage of neuron j, $v_j = d_j^T e$. ***Bottom:*** The voltages form a N-dimensional vector contained in voltage space.

2.2 The Self-Coupled Model is PCF in an Orthonormal Basis

1. The self-coupled network is derived from the PCF via a change of bases. Assuming both D and A are full rank, diagonalize each to a common left basis:

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

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

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

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

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

In the original basis, the state is x. In the rotated basis we denote this quantity as y. It is the projection of x onto the d-dimensional $\mathcal{U}$ basis:

$$y \triangleq \mathcal{U}^T x \tag{2.6}$$

The rotated target dynamics are thus

$$\begin{aligned} \dot{y} &= \mathcal{U}^T \dot{x} \\ &= \Lambda y(\xi) + \mathcal{U}^T B c(\xi) \\ &= \Lambda y(\xi) + \mathcal{U}^T B \mathcal{U}\mathcal{U}^T c(\xi) \\ &= \Lambda y(\xi) + \beta \tilde{c}(\xi) \end{aligned} \tag{2.7}$$

where

$$\beta \triangleq \mathcal{U}^T B \mathcal{U},$$

and

$$\tilde{c} \triangleq \mathcal{U}^T c,$$

give the projections of B and c respectively. The network estimate in the rotated basis is

$$\hat{y} \triangleq \mathcal{U}^T \hat{x}.$$

From equation (2.2),

$$
\begin{aligned}
\hat{y} &= \mathcal{U}^T \hat{x} \\
&= \mathcal{U}^T D r \\
&= \begin{bmatrix} S & 0 \end{bmatrix} V^T r \\
&= \begin{bmatrix} S & 0 \end{bmatrix} \rho \\
\implies \dot{\hat{y}} &= \begin{bmatrix} S & 0 \end{bmatrix} V^T \dot{r} \\
&= \begin{bmatrix} S & 0 \end{bmatrix} \left(-V^T r + V^T o \right).
\end{aligned}
$$

Note that $V^T r$ and $V^T o$ are projections of the N-neuron network's post-synaptic current and spike train respectively onto the rotated basis, denoted by

$$\rho \triangleq V^T r, \tag{2.8}$$

$$\tilde{o} \triangleq V^T o. \tag{2.9}$$

The preceding equality also gives $\hat{y}$ in terms of ρ:

$$\hat{y} = \begin{bmatrix} S & 0 \end{bmatrix} \rho. \tag{2.10}$$

With these definitions, the last equality above also implies

$$\dot{\rho} = -\rho + \tilde{o}. \tag{2.11}$$

To finish describing the basic network quantities in terms of the rotated basis, let ϵ be the error in the rotated basis:

$$
\begin{aligned}
\epsilon &\triangleq y - \hat{y} \\
&= \mathcal{U}^T e.
\end{aligned} \tag{2.12}
$$

2. Repeat the derivation of equation (2.5) but with y, $\hat{y}$, and ϵ:

$$\begin{aligned}
\dot{\epsilon} &= \dot{y} - \dot{\hat{y}} \\
&= \Lambda y + \beta c - \begin{bmatrix} S & 0 \end{bmatrix} \left(-\rho + \tilde{o}\right) \\
&= \Lambda \left(\epsilon + \begin{bmatrix} S & 0 \end{bmatrix} \rho\right) + \beta tildec - \begin{bmatrix} S & 0 \end{bmatrix} \left(-\rho + \tilde{o}\right) \\
&= \Lambda \epsilon + \left(\Lambda + I\right) \begin{bmatrix} S & 0 \end{bmatrix} \rho + \beta \tilde{c} - \begin{bmatrix} S & 0 \end{bmatrix} \tilde{o}
\end{aligned}$$

$$\implies \begin{bmatrix} S \\ 0 \end{bmatrix} \dot{\epsilon} = \begin{bmatrix} S \\ 0 \end{bmatrix} \Lambda \epsilon + \begin{bmatrix} S \\ 0 \end{bmatrix} \left(\Lambda + I\right) \begin{bmatrix} S & 0 \end{bmatrix} \rho + \begin{bmatrix} S \\ 0 \end{bmatrix} \beta \tilde{c} - \begin{bmatrix} S \\ 0 \end{bmatrix} \begin{bmatrix} S & 0 \end{bmatrix} \tilde{o}.$$

The last equality gives a system of N equations of which only d are nontrivial. A comparison with equation (2.5) suggests the N-dimensional rotated membrane potential v is best defined as:

$$v \triangleq \begin{bmatrix} S \\ 0 \end{bmatrix} \epsilon \in \mathbf{R}^N. \tag{2.13}$$

This mapping is invertible from v to ϵ if we write

$$\epsilon = \begin{bmatrix} S^{-1} & 0 \end{bmatrix}.$$

This gives a well-defined $d-$vector. whose first d elements are well defined, and the remaining components of v are assumed to be zero. Using a similar abuse for the ρ and $\tilde{o}$ terms, we arrive at the system of N equations describing the network voltage dynamics:

$$\dot{v} = \begin{bmatrix} \Lambda & 0 \\ 0 & 0 \end{bmatrix} v + \begin{bmatrix} S\left(\Lambda + I_d\right) S & 0 \\ 0 & 0 \end{bmatrix} \rho + \begin{bmatrix} S \\ 0 \end{bmatrix} \beta \tilde{c} - \begin{bmatrix} S^2 & 0 \\ 0 & 0 \end{bmatrix} \tilde{o}. \tag{2.14}$$

To summarize conceptually, there are 4 vector spaces in total: the error space which tracks the dynamical system and the network estimate, the voltage space which tracks the membrane potentials, and the transformed counterparts of each in the $\mathcal{U} - V$ bases. Figure (2) shows the relationships derived between these subspaces.

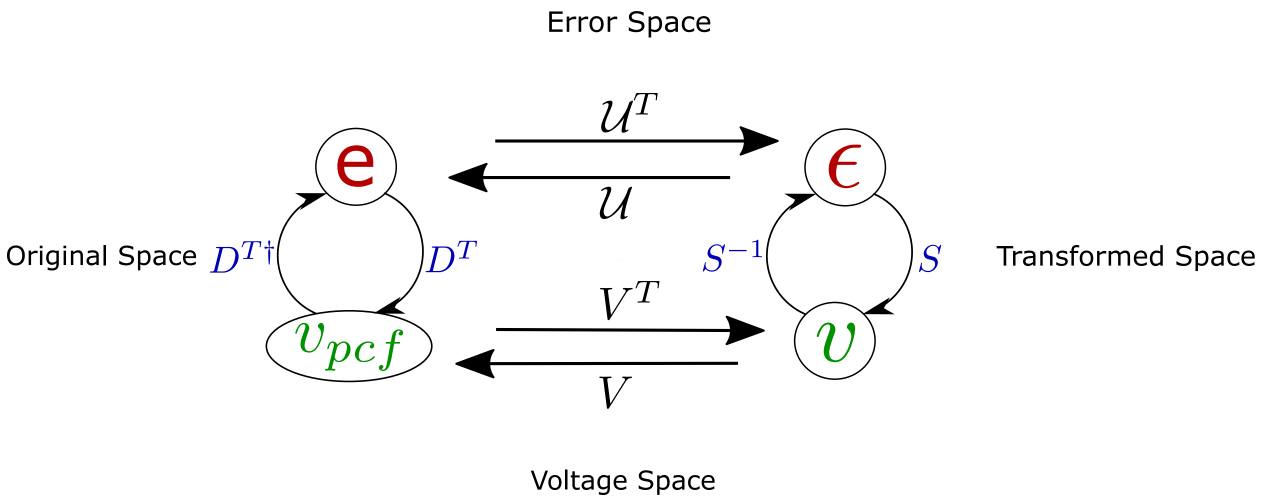


Figure 2: Depiction of the relationship between original and transformed spaces and their respective error and voltage spaces. An arrow represents left multiplication by the given matrix. The zeros in the full $N \times N$ matrices mapping between v and ϵ are omitted for clarity.

2.3 Optimizing Spike-Timing: From PCF to Self-Coupled

1. In PCF, the spike trains o are chosen minimize the network estimation error

$$\mathcal{L}(\xi) = ||x(\xi + d\xi) - \hat{x}(\xi + d\xi)||^2. \tag{2.15}$$

   The network greedily minimizes $\mathcal{L}(\xi)$ an instant $d\xi$ ahead in time. If no spike occurs at time ξ, then the objective is given above. If neuron j spikes, the estimate $\hat{x} \leftarrow \hat{x} + d_j$, where d_j is column j of D. The objective is now

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

   where $\mathcal{L}_{ns}(\xi)$ is the objective if no spike occurs. Spiking occurs when the objective decreases or

$$\begin{aligned}
& \mathcal{L}_{sp} < \mathcal{L}_{ns} \\
\implies & -2d_j^T (x - \hat{x}) + d_j^T d_j < 0 \\
\implies & d_j^T (x - \hat{x}) > \frac{||d_j||^2}{2}.
\end{aligned}$$

   Since $d_j^T (x - \hat{x}) = d_j^T e$ is already defined as membrane voltage, the right hand side gives neuron $j's$ spike threshold voltage $v_t h$,

$$v_{th}^{pcf} = \frac{1}{2} \begin{bmatrix} d_1^T d_1 \\ \vdots \\ d_N^T d_N \end{bmatrix}.$$

2. For the rotated network, note $\mathcal{U}^T$ is an orthonormal matrix by definition. Thus it is norm-preserving:

$$\begin{aligned}
\mathcal{L}_{sp}(\xi) &= ||x - \hat{x}||^2 \\
&= ||\mathcal{U}^T (x - \hat{x})||^2 \\
&= ||y - \hat{y}||^2.
\end{aligned}$$

   If we define the rotated network objective as

$$\tilde{L}(\xi) \triangleq ||y(\xi + d\xi) - \hat{y}(\xi + d\xi)||^2,$$

it is equal to the original network objective when no spike occurs. However, a spike alters the readout by $\hat{y} \leftarrow \hat{y} + S_l$, where S_l is the l^{th} column of $\begin{bmatrix} S & 0 \end{bmatrix}$. With the same approach as above, the objective when neuron l spikes is

$$\tilde{L}_{sp} = \tilde{L}_{ns} + 2S_l^T \epsilon + S_l^T S_l$$

$$\implies v_l > \frac{||S_l||^2}{2}.$$

This leads to voltage thresholds

$$v_{th} = \frac{1}{2} \begin{bmatrix} S_1^T S_1 \\ \vdots \\ S_d^T S_d \\ 0 \\ \vdots \\ 0 \end{bmatrix}.$$

2.4 Consequences of Positive Unit-Area Spikes

1. The voltage thresholds are nonnegative, such that neuron j will only spike if

$$v_l = S_l^T \epsilon > v_{th} > 0.$$

The spike form neuron l corrects the network error ϵ by adding S_l to the estimate $\hat{y}$. The nonnegative voltage implies it is impossible for neuron l to correct antiparallel errors $(-S_l)$, since

$$S_l^T(\epsilon) = S_l^T(-S_l) = -||S_l||^2 < 0 < v_{th}.$$

To illustrate consider the space of errors $\epsilon \in \mathbf{R}^d$ which satisfy the voltage threshold of neuron l, i.e

$$\epsilon_{sp} = \left\{ \epsilon \in \mathbf{R}^d \mid S_l^T \epsilon > v_{th} \right\}.$$

In $\mathbf{R}^2$, ϵ_{sp} is the half-plane formed by the line normal to S_l shifted v_{th} from the origin along S_l as in figure (3). This excludes $-S_l$. The optimization thus tells us that neuron l spikes when the projection $S_l^T \epsilon$ exceeds v_{th}.

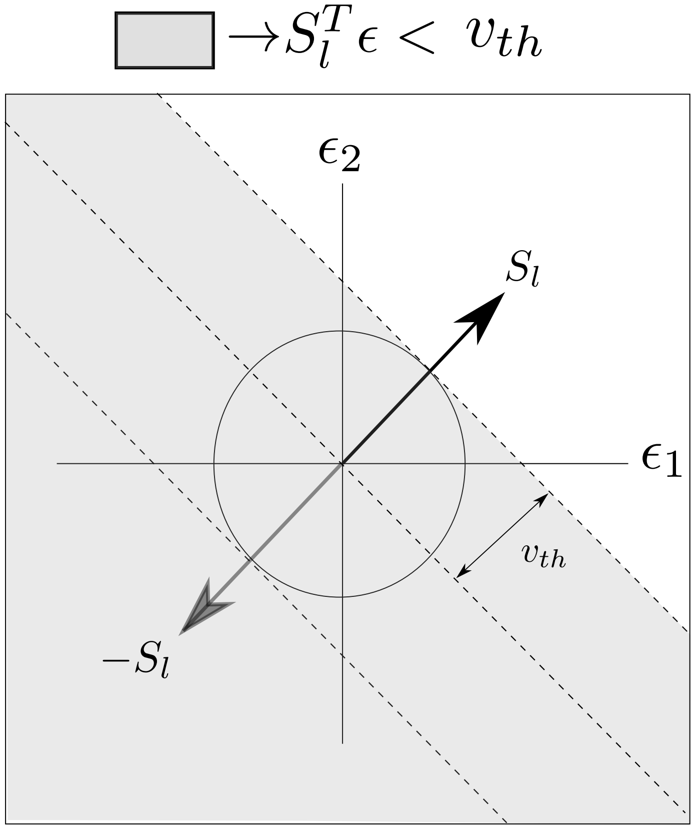


Figure 3: Sketch of the Encoding space ϵ_{sp} of neuron l with direction $S_l \in \mathbf{R}^2$. The radius of the circle is $v_{th} = \frac{||S_l||^2}{2}$. (Vector S_l not drawn to scale).

2. Equations (2.14) and (2.11) describe how we implement a network with d neurons that produces an estimate $\hat{y}$ of the given target system. As written, the network can only encode vectors y with strictly nonnegative elements. To see why we return to the optimization procedure performed by the network.

   The network optimizes the objective

$$\mathcal{L} = ||y - \hat{y}||,$$

   by choosing spike times $\tilde{o}$. The spikes are integrated into a post-synaptic feedback ρ. This feedback vector is scaled by S to generate the estimate $\hat{y}$ that minimizes the objective at time ξ. In other words, the network performs the optimization

$$\underset{\rho \in \mathbf{R}^{d+}}{min} ||y - S\rho||^2,$$

   where $\mathbf{R}^{d+}$ denotes the real $d-$vectors with nonnegative components. The components must be nonnegative because the spikes $\tilde{o}$ have nonnegative area when integrated, and their dynamics will not decay below zero otherwise. In using a greedy approach with only one spike at a given time step, the network more specifically performs

$$\underset{x \in \mathbf{Z}^{d+} : \sum_j Z_j = 1}{min} ||y - S\left(\rho + x\right)||^2.$$

   I.e, it must choose one neuron to spike with unit area 1, which adds precisely one column of S to the estimate $\hat{y}$.

   It is easier to analyze the former optimization of $\rho \in \mathbf{R}^{d+}$, and we do so here. Because $\left\{x \in \mathbf{Z}^{d+} \ : \ \sum_j Z_j = 1\right\} \subset \mathbf{R}^{d+}$, it is always the case that

$$\underset{\rho \in \mathbf{R}^{d+}}{min} ||y - S\rho||^2 \leq \underset{x \in \mathbf{Z}^{d+} : \sum_j Z_j = 1}{min} ||y - S\left(\rho + x\right)||^2,$$

   i.e optimizing over arbitrary $\rho \in \mathbf{R}^{d+}$ will always give just as low or lower objectives than under the single-greedy spike optimization.

   We're interested in the range of vectors representable by the network. That is the set

$$X^* = \left\{x \in \mathbf{R}^{d+} \ : \ Sx = y\right\}.$$

   Over this set, the objective function is 0, i.e.

$$X^* = \left\{x \in \mathbf{R}^{d+} \ : \ \mathcal{L} = ||y - Sx||^2 = 0\right\}.$$

   Let $x \in X^*$, and consider its negative $-x$. It follows that

$$\begin{aligned} & x = S\rho \\ \implies & -x = -S\rho \\ & \quad = S\left(-\rho\right). \end{aligned}$$

   However if $\rho \in \mathbf{R}^{d+}$, then it is impossible for $-\rho \in \mathbf{R}^{d+}$ to also be true. Thus $-\rho \notin X^*$ so that $\mathcal{L} > 0$. We conclude that for any vector $\hat{y}$, the network can represent with $\mathcal{L} = 0$, there exists a negative vector that the network cannot represent with $\mathcal{L} = 0$. This is undesirable as it restricts the set of vectors the network can reconstruct within a given error tolerance. In $\mathbf{R}^2$ for example, network representation where $\mathcal{L} = 0$ is restricted to the first quadrant. This restriction applies equally to the greedy single-spike optimization.

This issue is unique to the self-coupled network and does not occur in the original PCF network even through its spikes must also have positive unit area. The difference arises when we take the SVD of the decoder matrix.

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

The SVD decomposes D into orthonormal bases $\mathcal{U}$ and V which are mapped to one another by singular values S, as in figure (4). By rotating into the $\mathcal{U} - V$ bases, we preemptively perform the first and last mappings, leaving only multiplication by a diagonal matrix. This eliminates linearly dependent encoding vectors, keeping only the orthonormal. For example, suppose $x = Dy = \mathcal{U} \begin{bmatrix} S & 0 \end{bmatrix} V^T y$. For an orthonormal basis, $-x$ is obtainable by $\mathcal{U} \begin{bmatrix} S & 0 \end{bmatrix} V^T(-y)$. However the constraint that spikes have positive unit area prevents a vector $\rho = -y$ from being reachable by the network as written. We consider two options to address this below.

$$D : \mathbf{R}^N \to \mathbf{R}^D = \mathcal{U} \begin{bmatrix} S & 0 \end{bmatrix} V^T$$

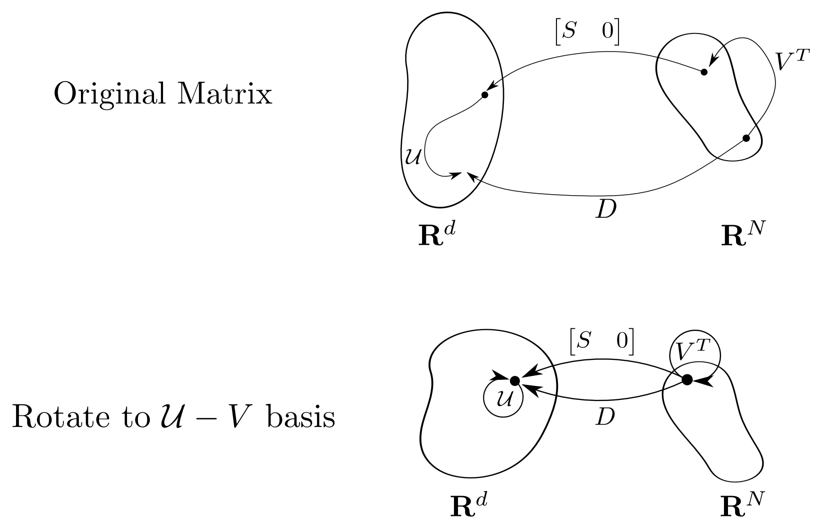


Figure 4: Visualizing D as a sequence of linear maps between subspaces. ***Top:*** The matrix $D \in \mathbf{R}^{d \times N}$ is decomposed via SVD into a sequence of 3 linear maps (matrices). The rightmost matrix $V^T \in \mathbf{R}^{N \times N}$ projects a vector x to give coefficients for the expansion in the basis V. The center matrix $\begin{bmatrix} S & 0 \end{bmatrix} \in \mathbf{R}^{d \times N}$ maps vectors from the V basis to a vector in $\mathbf{R}^d$ by scaling and truncation. The leftmost matrix $\mathcal{U} \in \mathbf{R}^{d \times d}$ gives the resultant vector $Dx \in \mathbf{R}^d$ by using the scaled vector $\begin{bmatrix} S & 0 \end{bmatrix} V^T$ as coefficients for a basis expansion in $\mathcal{U}$. ***Bottom:*** We rotate the basis for vectors in $\mathbf{R}^N$ and $\mathbf{R}^d$ to the $\mathcal{U}$ and V bases respectively. This negates the need of D to preemptively project and afterward rotate a vector, leaving only scaling by a diagonal matrix. The mapping D performs on a vector y simplifies to multiplication by a diagonal matrix S of y's first d components.

3. For the network decoder to fully span the state space of interest, it must have anti-parallel encoding directions even in the rotated orthonormal basis. To do so we augment the rotated bases by adding an antiparallel set so they are no longer orthonormal. We consider two methods of adding antiparallel bases:

   Method A: Separate Antiparallel Networks One solution is to form a separate network of d neurons whose encoding directions are the antiparallel set $-\mathcal{U}$. That is, we form an identical network except the decode matrix is
$$-D = -\mathcal{U}\begin{bmatrix} S & 0 \end{bmatrix} V^T.$$

   We then add the output of the two networks to recover the encoded state.

   We divide the error into its positive and negative components and encode each in a separate network. Let
$$\epsilon^+ = \epsilon \geq 0,$$
   be the nonnegative component of ϵ. Note that the original estimate, e may contain negative or positive components, but the projection ϵ^+ does not. Similarly define the negative error by
$$\epsilon^- = -\epsilon < 0.$$
   Note
$$\epsilon^- \neq -\epsilon^+.$$
   Rather,
$$\epsilon = \epsilon^+ - \epsilon^-.$$
   The relationship between ϵ^+ and ϵ^- resembles two orthogonal subspaces. The preceding relation is analogous to a direct sum.

   Let
$$v^+ = S^T \epsilon^+,$$
   be the voltage induced by projecting ϵ^+ onto the orthonormal bases given by $D = \mathcal{U}\begin{bmatrix} S & 0 \end{bmatrix} V^T$, and
$$v^- = S^T \epsilon^-$$
   be the respective projection onto the antiparallel orthonormal bases, $D = \mathcal{U}\begin{bmatrix} -S & 0 \end{bmatrix} V^T$.

   Note that
$$v^- \neq -v^+.$$
   Rather,
$$v = v^+ - v^-,$$
   where v is the voltage of an idealized neuron capable of positive and negative area spikes. Note that both v_j^+ and v_j^- are bounded by thresholds $v_{th} = \frac{||S_j||^2}{2}$, so that the idealized neuron is always within the voltage range $v \in [-v_{th}, v_{th}]$. This is equivalent to asserting the error along each encoding direction S_j is contained within the polytope $S_j^T \epsilon \leq \frac{||S_j||^2}{2}$.

   Let ρ^+ and $\tilde{o}^+$ be the slow synaptic feedback and spike trains of the positive neurons, with ρ^- and $\tilde{o}^-$ defined similarly for the negative neurons. Finally split $\tilde{c} = \tilde{c}^+ - \tilde{c}^-$ into positive and negative components as with ϵ.

We now have two $d-$dimensional systems of equations.

$$\dot{v}^+ = \begin{bmatrix} \Lambda & 0 \\ 0 & 0 \end{bmatrix} v^+ + \begin{bmatrix} S\left(\Lambda + I_d\right)S & 0 \\ 0 & 0 \end{bmatrix} \rho^+ + \begin{bmatrix} S \\ 0 \end{bmatrix} \beta \tilde{c}^+ - \begin{bmatrix} S^2 & 0 \\ 0 & 0 \end{bmatrix} \tilde{o}^+,$$

$$\dot{v}^- = \begin{bmatrix} \Lambda & 0 \\ 0 & 0 \end{bmatrix} v^- + \begin{bmatrix} S\left(\Lambda + I_d\right)S & 0 \\ 0 & 0 \end{bmatrix} \rho^- + \begin{bmatrix} S \\ 0 \end{bmatrix} \beta \tilde{c}^- - \begin{bmatrix} S^2 & 0 \\ 0 & 0 \end{bmatrix} \tilde{o}^-.$$

These equations each produce estimates

$$\hat{y}^+ = S\rho^+,$$

$$\hat{y}^- = S\rho^-,$$

which give the network estimate

$$\hat{y} = \hat{y}^+ - \hat{y}^-.$$

Writing the above as a single network, assume $N = 2d$ so we need not fill with zeros:

$$\begin{bmatrix} \dot{v}^+ \\ \dot{v}^- \end{bmatrix} = \begin{bmatrix} \Lambda & 0 \\ 0 & \Lambda \end{bmatrix} \begin{bmatrix} v^+ \\ v^- \end{bmatrix} + \begin{bmatrix} S\left(\Lambda + I_d\right)S & 0 \\ 0 & S\left(\Lambda + I_d\right)S \end{bmatrix} \begin{bmatrix} \rho^+ \\ \rho^- \end{bmatrix} + \begin{bmatrix} S & 0 \\ 0 & S \end{bmatrix} \beta \begin{bmatrix} \tilde{c}^+ \\ \tilde{c}^- \end{bmatrix} - \begin{bmatrix} S^2 & 0 \\ 0 & S^2 \end{bmatrix} \begin{bmatrix} \tilde{o}^+ \\ \tilde{o}^- \end{bmatrix}.$$

We simplify this by writing

$$\dot{v} = \Lambda v + S\left(\Lambda + I_{2d}\right)S\rho + S\beta\tilde{c} - S^2\tilde{o},$$

where we have made the following substitutions:

$$v \leftarrow \begin{bmatrix} v^+ \\ v^- \end{bmatrix} \in \mathbf{R}^{2d},$$

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

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

$$\rho \leftarrow \begin{bmatrix} \rho^+ \\ \rho^- \end{bmatrix} \in \mathbf{R}^{2d},$$

$$\tilde{o} \leftarrow \begin{bmatrix} \tilde{o}^+ \\ \tilde{o}^- \end{bmatrix} \in \mathbf{R}^{2d},$$

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

$$\tilde{c} \leftarrow \begin{bmatrix} \tilde{c}^+ \\ \tilde{c}^- \end{bmatrix} \in \mathbf{R}^{2d},$$

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

To decode from the network to the $d-$dimensional estimate, we multiply by $\begin{bmatrix} \mathcal{U} & -\mathcal{U} \end{bmatrix} \in \mathbf{R}^{d \times 2d}$, i.e

$$\hat{y} = \hat{y}^+ - \hat{y}^- = \begin{bmatrix} \mathcal{U} & -\mathcal{U} \end{bmatrix} \rho.$$

This approach suggests a balance between excitatory and inhibitory neurons when coding an oscillatory signal that inhabits the full $d-$dimensional state space. To illustrate, consider a 2 neuron network as in figure (5). An input $\tilde{c}(\xi) = sin(\omega\xi)$ drives the neurons which encode v^+ and v^- respectively. A readout neuron performs leaky integration of the spike trains from the two driven neurons. Consider how a received spike changes the voltage of the readout neuron. A spike from one neuron will increase the readout neuron's membrane potential (excitatory input), while a spike from the other neuron must symmetrically decrease the readout neuron's potential (inhibitory input). In this case, we observe equal levels of excitatory (and inhibitory input from the two neurons, suggesting a tight balance. Note also this ensures consistency with Dale's law, which states that a neuron cannot both excite and inhibit other neurons.

Note also that the fast coupling matrix preceding $\tilde{o}$ is diagonal. This implies that when a neuron j spikes, its antiparallel neuron is unchanged. In the PCF, a neuron spike resets its threshold to $-v_{th}$, but likewise sets a neuron antiparallel to it to v_{th}. Next, the antiparallel neuron spikes and likewise resets the neuron. This cycle repeats itself causing the network estimate to oscillate uncontrollably in a catastrophic network failure termed "ping-ponging". The PCF addresses this through regularization terms applied to the network objective $\mathcal{L}$ and added noise, (Boerlin 2013) both of which are unnecessary in this case.

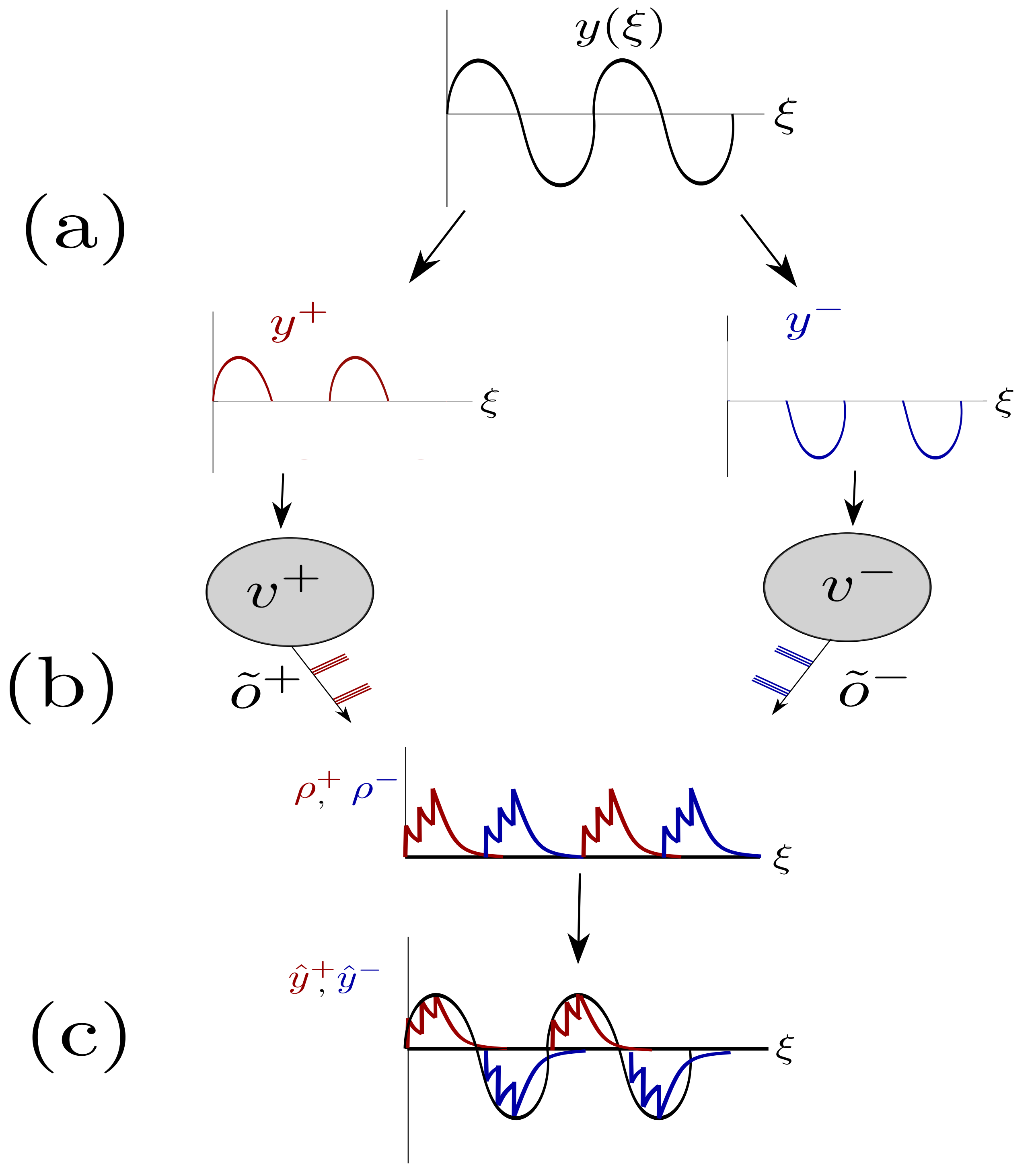


Figure 5: Balance Between Excitatory and Inhibitory Activity for Oscilllatory Input. ***(a):*** A sinusoidal input y is divided into its positive (excitatory) and negative (inhibitory) components. ***(b):*** Each neuron encodes its respective input by spiking to produce a nonnegative filtered spike train ρ. ***(c):*** The network estimate is the sum of activity from excitatory and inhibitory filtered spike trains. For oscillatory input, both neurons must spike in equal amounts so that the amplitude of oscillation remains bounded.

Method B: Fast-Coupling Between Antiparallel Neurons The other method we consider maintains the fast-coupling relationship between a neuron and its opposite as described in PCF. Fast-coupling implies that when a neuron i with encoding direction d_i spikes, neuron j's voltage changes by $-d_j^T d_i$. This is visible in the spiking ($D^T Do$) term in PCF's voltage equation (2.5). If $d_j = -d_i$, then a spike in d_j decreases j's voltage by $||d_j||^2$, while simultaneously increasing neuron i's voltage by the same.

1. Previously we used a subset of d neurons from the decoder matrix,
$$D = \mathcal{U} \begin{bmatrix} S & 0 \end{bmatrix} V^T \in \mathbf{R}^{d \times N}.$$
In adding d antiparallel neurons, we assume $N \geq 2d$ and instead use $2d$ neurons, i.e. we write
$$D = \begin{bmatrix} \mathcal{U} & -\mathcal{U} \end{bmatrix}^T \begin{bmatrix} S & 0 & 0 \\ 0 & S & 0 \end{bmatrix} V^T \in \mathbf{R}^{d \times N}.$$
The first and second d neurons have encoding directions $\mathcal{U}$ and $-\mathcal{U}$ respectively. Before the first d right eigenvectors V_j were scaled by σ_j and mapped to $\mathcal{U}_j$, with the remaining V_j mapped to 0. In adding d antiparallel vectors, we scale an additional d right eigenvectors V_{j+d} by σ_j and map them to $-\mathcal{U}_j$.
The dynamical system remains the same, i.e.
$$\dot{y} = \Lambda y + \beta \tilde{c}.$$

2. The network estimation
$$\hat{y} = \mathcal{U}^T D \hat{x} = \begin{bmatrix} S & 0 \end{bmatrix} \rho$$
is now
$$\hat{y} = \mathcal{U}^T \begin{bmatrix} \mathcal{U} & -\mathcal{U} \end{bmatrix} \begin{bmatrix} S & 0 & 0 \\ 0 & S & 0 \end{bmatrix} \rho$$
$$= \begin{bmatrix} S & -S & 0 \end{bmatrix} \rho.$$
We rederive the error dynamics
$$\dot{\epsilon} = \dot{y} - \dot{\hat{y}}$$
$$= \Lambda y + \beta \tilde{c} - \begin{bmatrix} S & -S & 0 \end{bmatrix} (-\rho + \tilde{o})$$
$$= \Lambda (\epsilon + \hat{y}) + \begin{bmatrix} S & -S & 0 \end{bmatrix} \rho + \beta \tilde{c} - \begin{bmatrix} S & -S & 0 \end{bmatrix} \tilde{o}$$
$$= \Lambda \epsilon + (I + \Lambda) \begin{bmatrix} S & -S & 0 \end{bmatrix} \rho + \beta \tilde{c} - \begin{bmatrix} S & -S & 0 \end{bmatrix} \tilde{o}$$

3. We previously obtained voltage by optimizing the objective
$$\mathcal{L} = ||y - \hat{y}||^2.$$
For the first d neurons this was
$$v_j = S_j^T \epsilon \quad \text{if } j \in [1, \ldots, d].$$

We now add an addition d neurons with antiparallel directions. For each neuron j we add an additional neuron $j+d$ with oppositve encoding direction, and therefore opposite voltage. The voltage is now

$$\begin{cases} v_j = S_j^T \epsilon & \text{for } j \in [1, \dots, d] \\ -S_{j-d}^T \epsilon & \text{for } j \in [d+1, \dots, 2d] \end{cases}.$$

In matrix form,

$$v = \begin{bmatrix} S \\ -S \end{bmatrix} \epsilon.$$

From the error dynamics above, we get

$$\dot{v} = \begin{bmatrix} \Lambda & 0 \\ 0 & \Lambda \end{bmatrix} v + \begin{bmatrix} S \\ -S \end{bmatrix} (I + \Lambda) \begin{bmatrix} S & -S & 0 \end{bmatrix} \rho + \begin{bmatrix} S \\ -S \end{bmatrix} \beta \tilde{c} - \begin{bmatrix} S^2 & -S^2 & 0 \\ -S^2 & S^2 & 0 \end{bmatrix} \tilde{o}. \tag{2.16}$$

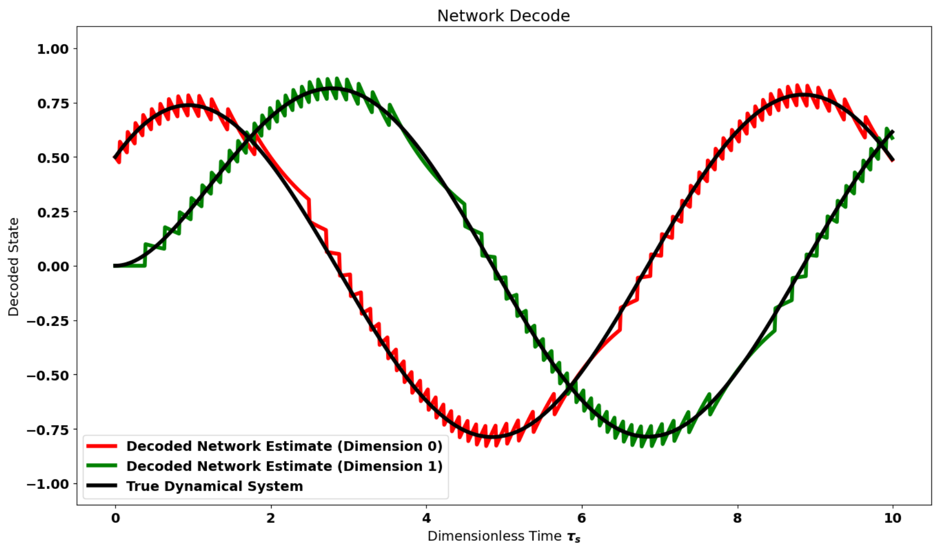
Equation (2.16) gives the voltage dynamics of $2d$ neurons.

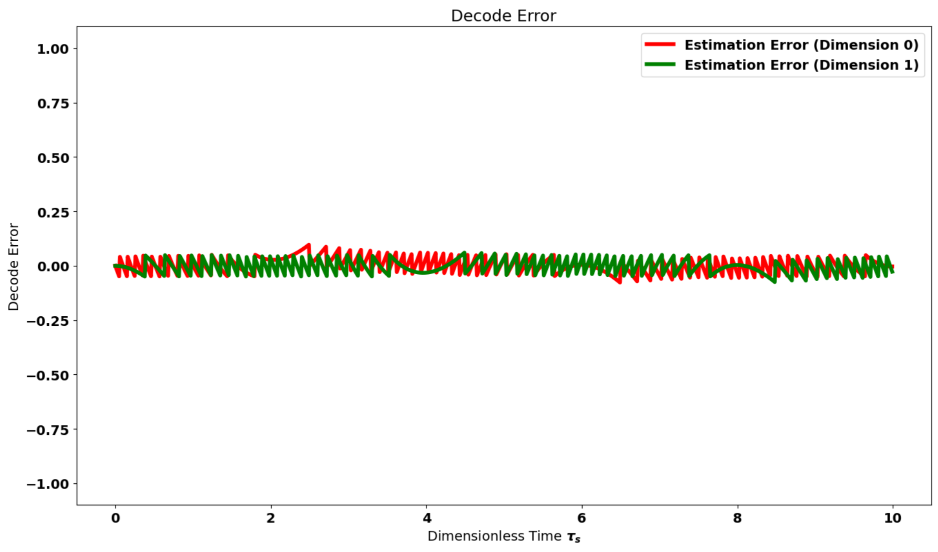
4. To facilitate comparison between the self-coupled network and original PCF model, we will use this method (B) hereafter. Method A is a viable alternative, however it is fundamentally different than the original PCF model because antiparallel neurons do not interact in contrast with PCF and method B. We investigate method A later.

2.5 Simulation of Basic Equations

Here we simulate the above equations (2.14) and (2.11) with the $N = 2d$ neurons. The parameters are

$$\begin{aligned}
A &= \; -\begin{bmatrix} 1 & 0 \\ 0 & 1 \end{bmatrix} = \mathcal{U}\Lambda\mathcal{U}^T, \\
B &= \begin{bmatrix} 1 & 0 \\ 0 & 1 \end{bmatrix}, \\
c(\xi) &= \begin{bmatrix} cos(\frac{\pi}{4}\xi) \\ sin(\frac{\pi}{4}\xi) \end{bmatrix} \\
D &= \mathcal{U}\begin{bmatrix} S & 0 \end{bmatrix} V^T = \mathcal{U}\begin{bmatrix} .1\, I_d & 0 \end{bmatrix} I_N, \\
d\xi &= 10^{-6}, \\
N &= 4, \\
x(0) &= \begin{bmatrix} \frac{1}{2} & \frac{1}{2} \end{bmatrix}.
\end{aligned} \tag{2.17}$$


Network Decode
Decoded State
Dimensionless Time τ_s
Decoded Network Estimate (Dimension 0)
Decoded Network Estimate (Dimension 1)
True Dynamical System


Decode Error
Decode Error
Dimensionless Time τ_s
Estimation Error (Dimension 0)
Estimation Error (Dimension 1)

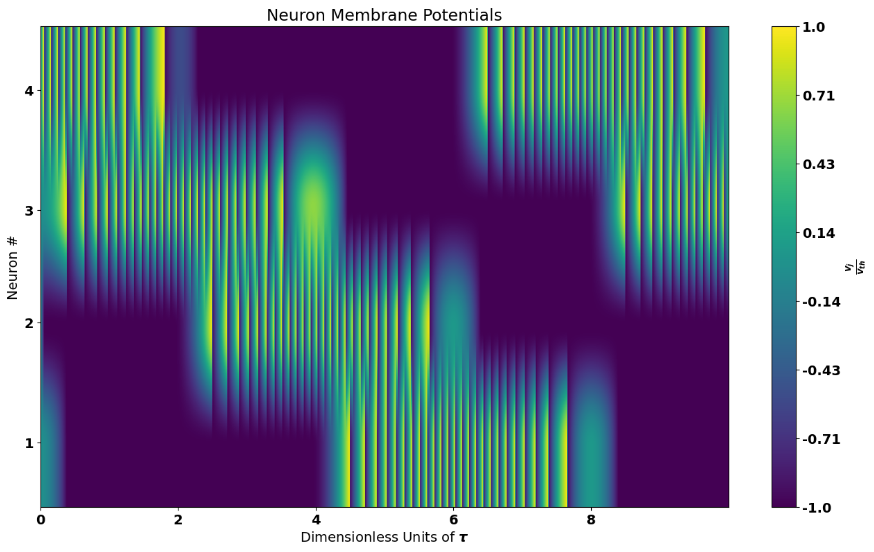

Neuron Membrane Potentials
Neuron #
Dimensionless Units of τ
$\frac{v_j}{v_{th}}$

Figure 6: Simulation of equations (2.14) and (2.11) with parameters listed in equation (2.17). ***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 RMSE vs Spike Rate for Constant Driving Force

We analyse the network described by equations (2.14) and (2.11) for the case of a constant (in time) driving force $\tilde{c}(\xi) = \tilde{c}$.

3.1 Ideal Network

We assume the network

3.2 Neuron Trajectories

Consider the dynamical system

$$\dot{y} = \Lambda y + \beta \tilde{c}, \quad y(0) = y_0$$

as implemented by the network of N neurons whose encoding directions are

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

where

$$S = \begin{bmatrix} S_1 & \dots & S_d \end{bmatrix} \in \mathbf{R}^{d \times d}$$

is a diagonal matrix.

Let

$$\tilde{c} = k\hat{u} \in \mathbf{R}^d$$

such that

$$-\Lambda^{-1}\beta(k\hat{u}) = k\frac{S_j}{||S_j||}$$

$$\implies \tilde{c} = -\frac{k}{||S_j||}\beta^{-1}\Lambda S_j.$$

With this choice of $\tilde{c}$, if we assume neuron j spikes periodically at a rate ϕ_j.

3.3 Solution for the Periodically Spiking Network

Assume the spike train $\tilde{o}_j$ is a periodic sequence of impulses spaced in time by $\frac{1}{\phi_j}$. If the first spike occurs at $\xi_j^0 = 0$, then $\tilde{o}_j(\xi) = \sum_{l=0}^{\infty} \delta\left(\xi - \frac{l}{\phi_j}\right)$. By our choice of k, only neuron j will spike so that

$$\dot{\hat{y}}(\xi) = -\hat{y} + \sum_{l=0}^{\infty} \delta\left(\xi_j^k - \frac{l}{\phi_j}\right) S_j. \tag{3.1}$$

Equation (3.1) implies that the network estimate $\hat{y}$ will decay until j's first spike occurs at $\xi_j^1 = \frac{1}{\phi_j}$.

$$\hat{y}(\xi) = \hat{y}(0)e^{-\xi}, \quad 0 \le \xi < \frac{1}{\phi_j}.$$

At this instant, S_j is added to neuron j's component of the estimate.

$$\hat{y}(\frac{1}{\phi}) = \hat{y}(0)e^{-\frac{1}{\phi}} + S_j.$$

Decay again occurs until the next spike

$$\hat{y}(\xi) = \hat{y}(\frac{1}{\phi_j})e^{-(\xi - \frac{1}{\phi_j})},$$

$$= \left(\hat{y}(0)e^{-\frac{1}{\phi_j}} + S_j\right) e^{-(\xi-\frac{1}{\phi_j})}, \quad \frac{1}{\phi_j} \leq \xi < \frac{2}{\phi_j}$$

$$\implies \hat{y}(\frac{2}{\phi_j}) = \left(\hat{y}(0)e^{-\frac{1}{\phi_j}} + S_j\right) e^{-\frac{1}{\phi_j}} + S_j$$

$$= x(0)e^{-\frac{2}{\phi}} + S_j e^{-\frac{1}{\phi_j}} + S_j.$$

The third spike more clearly shows the recursive behavior

$$\hat{y}(\frac{3}{\phi_j}) = \left[\hat{y}(0)e^{-\frac{2}{\phi_j}} + S_j e^{-\frac{1}{\phi_j}} + S_j\right] e^{-\frac{1}{\phi_j}} + S_j$$

$$= \hat{y}(0)e^{-\frac{3}{\phi_j}} + S_j e^{-\frac{2}{\phi_j}} + S_j e^{-\frac{1}{\phi_j}} + S_j$$

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

$$\hat{y}(\frac{n}{\phi_j}) = \sum_{l=0}^{n-1} S_j e^{-\frac{l}{\phi_j}}$$

$$= S_j \frac{1 - e^{-\frac{n}{\phi_j}}}{1 - e^{-\frac{1}{\phi_j}}}.$$

For sufficiently large n, this converges to

$$\hat{y}(\xi_1^n) = \frac{S_j}{1 - e^{-\frac{1}{\phi_j}}}.$$

We know from equation (3.1) that the estimate will decay exponentially from this value over an interval $\frac{1}{\phi_j}$ until a spike returns it returns to the initial value. Thus we have an explicit expression for the long-term behavior given by

$$\hat{y}(\xi) = \frac{S_j}{1 - e^{-\frac{1}{\phi_j}}} e^{-(\xi) \mod \frac{1}{\phi_j}}, \tag{3.2}$$

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

3.4 RMSE for Periodic Spiking

From equation (3.2) the error $\epsilon = y - \hat{y}$ is a periodic function of ξ with period $\frac{1}{\phi_j}$.

Assume

$$\dot{y} = 0$$

$$\implies y(\xi) = k \frac{S_j}{||S_j||}.$$

We compute the RMSE of the error signal ϵ by

$$RMSE = \sqrt{\phi_j \int_0^{\frac{1}{\phi_j}} ||\epsilon(\tau)||^2 \, \mathrm{d}\tau}. \tag{3.3}$$

The integrand simplifies to

$$\begin{aligned} ||\epsilon||^2 &= (y_j - \hat{y})^2 \\ &= ||y||^2 - 2y^T \hat{y} + ||\hat{y}||^2 \\ &= k^2 - 2\frac{k\,||S_j||}{1 - e^{-\frac{1}{\phi_j}}} e^{-\tau} + \frac{||S_j||^2}{\left(1 - e^{-\frac{1}{\phi_j}}\right)^2} e^{-2\tau} \end{aligned}$$

Note that

$$\int_0^{\frac{1}{\phi_j}} e^{-\tau} \, \mathrm{d}\tau = 1 - e^{-\frac{1}{\phi_j}},$$

while

$$\begin{aligned} \int_0^{\frac{1}{\phi_j}} \left(e^{-\tau}\right)^2 &= \frac{1 - e^{-\frac{2}{\phi_j}}}{2} \\ &= \frac{1}{2}\left(1 - e^{-\frac{1}{\phi_j}}\right)\left(1 + e^{-\frac{1}{\phi_j}}\right). \end{aligned}$$

Therefore the integral is

$$\phi \int_0^{\frac{1}{\phi}} \epsilon_j(\tau)^2 \, \mathrm{d}\tau = k^2 - 2\phi\, k\, ||S_j|| + \phi_j \frac{||S_j||^2}{2} \frac{1 + e^{-\frac{1}{\phi_j}}}{1 - e^{-\frac{1}{\phi_j}}}.$$

The RMSE of the network estimate is thus

$$RMSE = \sqrt{k^2 - 2\phi\, k\, ||S_j|| + \phi_j \frac{||S_j||^2}{2} \frac{1 + e^{-\frac{1}{\phi_j}}}{1 - e^{-\frac{1}{\phi_j}}}}. \tag{3.4}$$

Note ϕ_j is dependent on the remaining parameters. We wish to reduce equation (3.4) to a function of independent variables. The rate ϕ_j had no analytic solution from the voltage trajectory, but can be deduced from equation (3.2). Consider the network estimate immediately before a spike occurs, i.e

$$\hat{y}(\xi^-) = \frac{S_j}{1-e^{-\frac{1}{\phi}}} e^{-\frac{1}{\phi}}.$$

At this point, the error induces a spike in neuron j, i.e.

$$v(\xi) = S_j \epsilon = v_{th} = \frac{||S_j||^2}{2}.$$

This implies

$$\frac{||S_j||^2}{2} = S_j^T\,(y - \hat{y})$$

$$= ||S_j||^2 \left(\frac{k}{||S_j||} - \frac{e^{-\frac{1}{\phi_j}}}{1-e^{-\frac{1}{\phi_j}}} \right).$$

$$= ||S_j||^2 \left(\frac{k}{||S_j||} - \frac{1}{e^{\frac{1}{\phi_j}} - 1} \right).$$

$$\implies e^{\frac{1}{\phi}} - 1 = \frac{1}{\frac{k}{||S_j||} - \frac{1}{2}}$$

$$\implies \frac{1+e^{-\frac{1}{\phi}}}{1-e^{-\frac{1}{\phi}}} = \frac{2\,k}{||S_j||}.$$

Substitute this last expression into equation (3.4) to get

$$RMSE_j = \sqrt{k^2 - 4\,\phi\,k^2 \frac{1-e^{-\frac{1}{\phi_j}}}{1+e^{-\frac{1}{\phi_j}}} + 2\,\phi_j\,k^2\,\frac{1-e^{-\frac{1}{\phi_j}}}{1+e^{-\frac{1}{\phi_j}}}}$$

$$= k\sqrt{1 - 2\,\phi_j\,tanh\left(\frac{1}{2\phi_j}\right)}.$$

Finally, we can normalize by k to obtain the NRMSE that is both dimensionless and solely dependent on the firing rate.

$$NRMSE_j(\phi_j) = \sqrt{1 - 2\,\phi_j\,tanh\left(\frac{1}{2\phi_j}\right)}. \tag{3.5}$$

Equation (3.5) is plotted in figure (7).

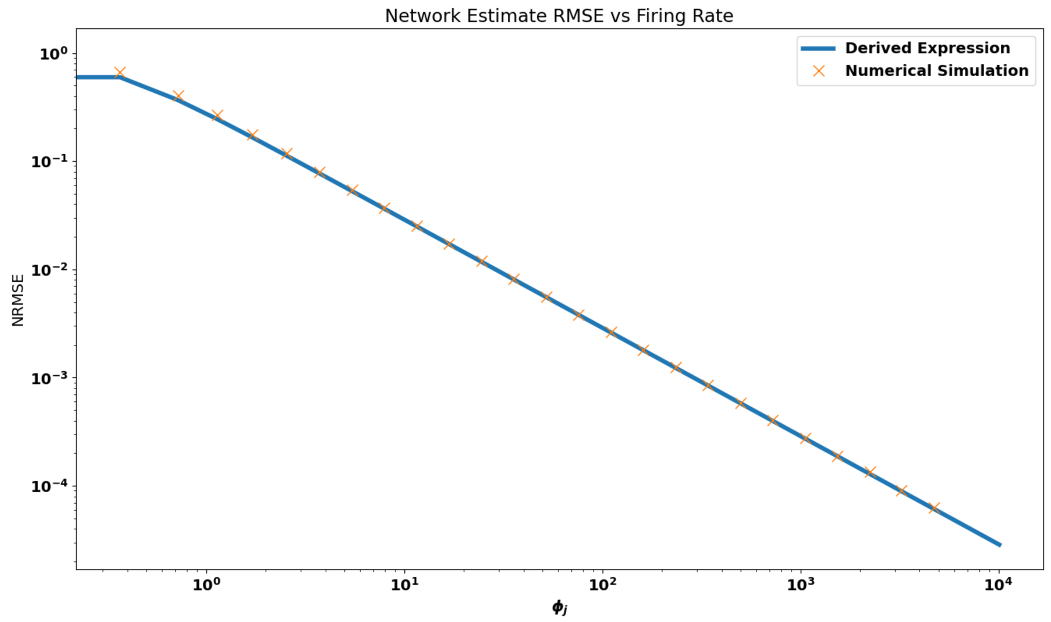


Figure 7: Log-log Plot of Equation (3.5). The RMSE was computed numerically by the discrete integral $RMSE = \sqrt{\frac{1}{\phi}\sum_i (y-\hat{y})^2 dt}$, where i sums over the data points in a spike. The integration is performed over $n = 100$ interspike intervals and averaged to form a data point. The time step was $d\xi = 10^{-4}$.

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

Here we derive the the predictive coding framework (PCF) as defined in Boerlin & Deneve, 2013. We highlight an assumption in this model which we later show worsens the network estimate. The correction of this assumption produces a third model that directly coupled membrane voltages. We term this a model the *gap-junction* (GJ) network.

4.1 Identical Initial Derivation for All Three Models (PCF, GJ, SC):

The PCF and GJ derivations are initially identical to the SC model in section (2). For all three models:

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

   $$\frac{dx}{d\xi} = Ax(\xi) + Bc(\xi). \tag{4.1}$$

   The neuron encoding directions are given by

   $$D = \begin{bmatrix} d_1 & \dots & d_N \end{bmatrix}.$$

   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

   $$\hat{x}(\xi) \triangleq Dr(\xi), \tag{4.2}$$

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

   $$\frac{dr}{d\xi} = -r + o(\xi). \tag{4.3}$$

   The network estimation error is

   $$e(\xi) \triangleq x(\xi) - \hat{x}(\xi). \tag{4.4}$$

2. Each network greedily minimizes the objective

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

   When neuron j spikes, the estimate becomes

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

If j does not spike the error is

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

Neuron j spikes when it decreases the objective, i.e.

$$\mathcal{L}_{sp} < \mathcal{L}_{ns},$$

which gives spiking condition

$$d_j^T e = \frac{||d_j||^2}{2}.$$

This leads us to define voltage as

$$v \triangleq D^T e.$$

3. 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.

4.2 PCF Derivation:

The voltage dynamics v_{pcf} are given by

$$\begin{aligned}\dot{v}_{pcf} &= D^T \dot{e} \\ &= D^T \left(\dot{x} - \dot{\hat{x}}\right) \\ &= D^T \left(Ax + Bc - Do - \hat{x}\right).\end{aligned}$$

The PCF argues that when the network functions, $x = \hat{x}$. We then have

$$\begin{aligned}\dot{v}_{pcf} &= D^T \left(A\hat{x} + Bc - Do - \hat{x}\right) \\ &= D^T \left(A - I\right) \hat{x} + D^T Bc - D^T Do.\end{aligned}$$

With $\hat{x} = Dr$ PCF has voltage dynamics

$$\dot{v}_{pcf} = D^T \left(A - I\right) Dr + D^T Bc - D^T Do. \tag{4.5}$$

Derive the spiking condition with an identical method to the SC network in section (2) to get PCF threshold voltages

$$v_{th} = \frac{1}{2} \begin{bmatrix} d_1^T d_1 \\ \vdots \\ d_N^T d_N \end{bmatrix}.$$

4.3 GJ Derivation:

The voltage dynamics of the GJ model are

$$\dot{v}_{GJ} = D^T \left(Ax + Bc - Do - \hat{x}\right).$$

The GJ model does not assume $x = \hat{x}$. Rather, it uses equations (4.4) and (**??**):

$$v_{gj} = D^T e$$

$$= D^T \left(x - \hat{x}\right)$$

$$\implies x = D^{T\dagger} v_{GJ} + \hat{x}.$$

Substitute this in the dynamics equation and simplify to get

$$\dot{v}_{GJ} = D^T A D^{T\dagger} v_{GJ} + D^T \left(A - I\right) Dr + D^T Bc - D^T Do. \tag{4.6}$$

The addition of the voltage coupling term $D^T A D^{T\dagger} v_{GJ}$ leads to the name Gap-Junction.

5 PCF and Gap-Junction Response to Constant Stimulus

We compute the response of the PCF and GJ models to a constant driving stimulus as we did for the SC model in section (3)

5.1 PCF Network Response to Constant Stimulus:

To compare between PCF and SC, we consider the same dynamical system as before, but using unrotated bases i.e.

$$\dot{x} = Ax + Bc, \quad x(0) = x_0$$

where,

$$A = \mathcal{U}\Lambda\mathcal{U}^T,$$

and the neuron encoding directions are

$$D = \mathcal{U}\begin{bmatrix} S & 0 \end{bmatrix} V^T = \begin{bmatrix} d_1 & \dots & d_N \end{bmatrix} \in \mathbf{R}^{d\times N}.$$

We choose c such that

$$x = k\frac{d_j}{||d_j||}$$

is a fixed point, i.e.

$$\dot{x} = 0$$

$$\implies c = -\frac{k}{||d_j||}B^{-1}Ad_j, \quad k \in \mathbf{R}.$$

The network error is $e = x - \hat{x}$ consequently grows parallel to d_j, ensuring only neuron j spikes periodically. The spike train o_j becomes a periodic sequence of impulses spaced in time by $\frac{1}{\phi_j}$. If the first spike occurs at $\xi_j^0 = 0$, then $\o_j(\xi) = \sum_{l=0}^{\infty}\delta\left(\xi - \frac{l}{\phi_j}\right)$. Since only neuron j spikes, the estimate is

$$\dot{\hat{x}}(\xi) = -\hat{x} + \sum_{l=0}^{\infty}\delta\left(\xi_j^k - \frac{l}{\phi_j}\right)d_j.$$

Using an identical inductive approach as before, the PCF network steady state estimate is

$$\hat{x}(\xi) = \frac{d_j}{1 - e^{-\frac{1}{\phi_j}}}e^{-(\xi) \mod \frac{1}{\phi_j}}, \tag{5.1}$$

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

We compute the RMSE of the error e by

$$RMSE = \sqrt{\phi_j\int_0^{\frac{1}{\phi_j}}||e(\tau)||^2 \, \mathrm{d}\tau}.$$

The integrand simplifies to

$$||e||^2 = (x - \hat{x})^2$$

$$= ||x||^2 - 2x^T\hat{x} + ||\hat{x}||^2$$

$$= k^2 - 2\frac{k}{1 - e^{-\frac{1}{\phi_j}}}||d_j||e^{-\tau} + \left(\frac{||d_j||}{1 - e^{-\frac{1}{\phi_j}}}\right)^2 e^{-2\tau}$$

This gives an RMSE of

$$RMSE(k, d_j, \phi_j) = \sqrt{k^2 - 2\phi_j\, k||d_j|| + \phi_j\, ||d_j||^2\frac{1 + e^{-\frac{1}{\phi_j}}}{1 - e^{-\frac{1}{\phi_j}}}}.$$

To simplify, note that immediately before a spike,

$$d_j^T e = d_j^T\left(k\frac{d_j}{||d_j||} - d_j\frac{e^{-\frac{1}{\phi_j}}}{1 - e^{-\frac{1}{\phi_j}}}\right)$$

$$= \frac{||d_j||^2}{2}$$

$$\implies \frac{||d_j||^2}{2} = d_j^T\left(k\frac{d_j}{||d_j||} - d_j\frac{e^{-\frac{1}{\phi_j}}}{1 - e^{-\frac{1}{\phi_j}}}\right)$$

$$\implies e^{\frac{1}{\phi_j}} - 1 = \frac{1}{\frac{k}{||d_j||} - \frac{1}{2}}$$

$$\implies \frac{1 + e^{-\frac{1}{\phi_j}}}{1 - e^{-\frac{1}{\phi_j}}} = \frac{2\,k}{||d_j||}.$$

Combine this with the RMSE expression to get

$$RMSE(\phi_j, k) = k\sqrt{1 - 2\phi_j tanh\left(\frac{1}{2\,\phi_j}\right)}.$$

Divide by driving strength k to get the dimensionless quantity that depends only on spike rate,

$$NRMSE(\phi_j) = \sqrt{1 - 2\phi_j tanh\left(\frac{1}{2\,\phi_j}\right)}. \tag{5.2}$$

Equation (5.3) is identical to the self-coupled network RMSE, equation (3.5) and is plotted against numerical simulations of a PCF network in figure (8)

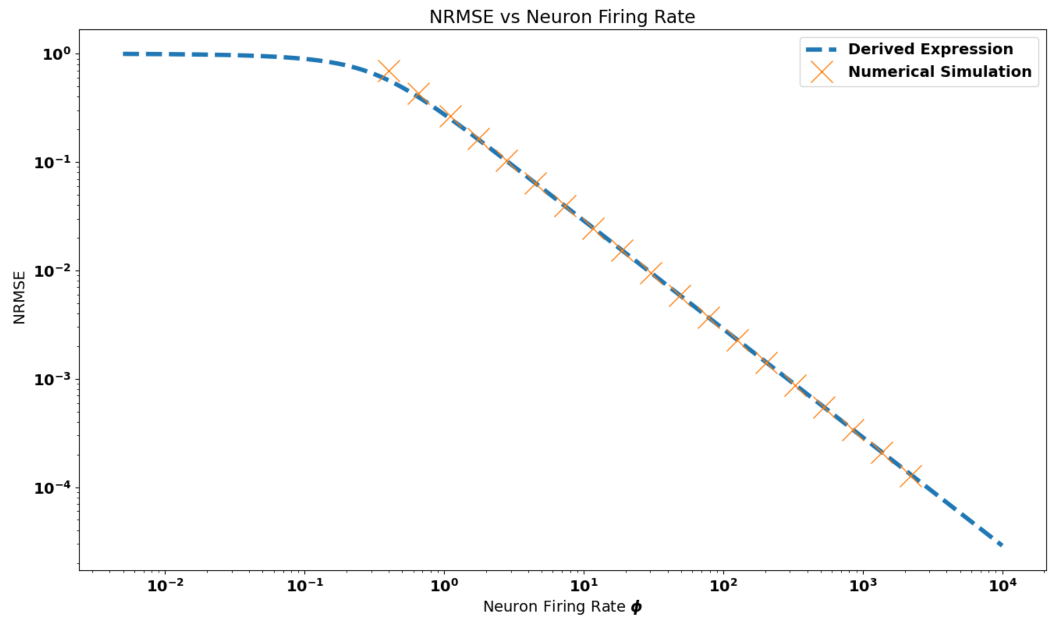


Figure 8: Log-log Plot of Equation (5.3). The RMSE was computed numerically by the discrete integral $RMSE = \sqrt{\frac{1}{\phi}\sum_i (x-\hat{x})^2 d\xi}$, where i sums over the data points in a spike. The integration is performed over $n = 100$ interspike intervals and averaged to form a data point. The time step was $d\xi = 10^{-4}$.

5.2 Gap-Junction Network Response to Constant Stimulus:

We now implement the same dynamical system as before with a GJ network. As with the PCF network, we drive the GJ network such that the fixed point is $x = k\frac{d_j}{||d_j||}$ parallel to neuron j,

$$\dot{x} = 0 \implies c = -\frac{k}{||d_j||}B^{-1}Ad_j.$$

This reduces the network to only neuron j spiking periodically.
The spike train o_j becomes a periodic sequence of impulses spaced in time by $\frac{1}{\phi_j}$. If the first spike occurs at $\xi_j^0 = 0$, then $ø_j(\xi) = \sum_{l=0}^{\infty} \delta\left(\xi - \frac{l}{\phi_j}\right)$. Since only neuron j spikes, the estimate is

$$\dot{\hat{x}}(\xi) = -\hat{x} + \sum_{l=0}^{\infty} \delta\left(\xi_j^k - \frac{l}{\phi_j}\right) d_j.$$

Note that this estimate is identical to the PCF estimate above. Following the same procedure, we arrive at the GJ NRMSE:

$$NRMSE(\phi_j) = \sqrt{1 - 2\phi_j tanh\left(\frac{1}{2\,\phi_j}\right)}. \tag{5.3}$$

Equation (5.3) is identical to the self-coupled network RMSE, equation (3.5) and is plotted against numerical simulations of a PCF network in figure (9)

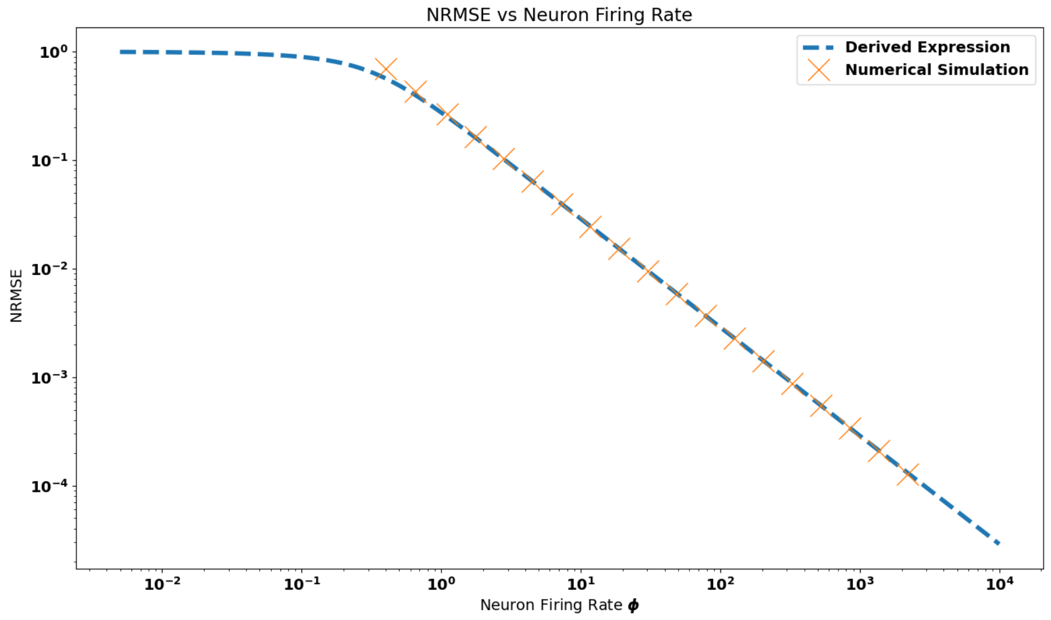


Figure 9: Log-log Plot of Equation (5.3). The RMSE was computed numerically by the discrete integral $RMSE = \sqrt{\frac{1}{\phi}\sum_i (x-\hat{x})^2 d\xi}$, where i sums over the data points in a spike. The integration is performed over $n = 100$ interspike intervals and averaged to form a data point. The time step was $d\xi = 10^{-4}$.

5.3 Comparison of Self-Coupled, Gap-Junction, and PCF Networks for a Constant Stimulus

We now compare all three models as they respond to a constant driving stimulus. Each is driven parallel to a single neuron j. As we showed, each results in an NRMSE given by

$$NRMSE(\phi_j) = \sqrt{1 - 2\phi_j tanh\left(\frac{1}{2\,\phi_j}\right)}.$$

To validate numerically, we simulate the SC, PCF, and GJ networks using the same network parameters. Next we compare each NRMSE as predicted by the equation above with numerical measurements. This is shown in figure (10). Note that while the relationship between firing rate and NRMSE is the same, the firing rate under a given set of parameters is not the same between networks.

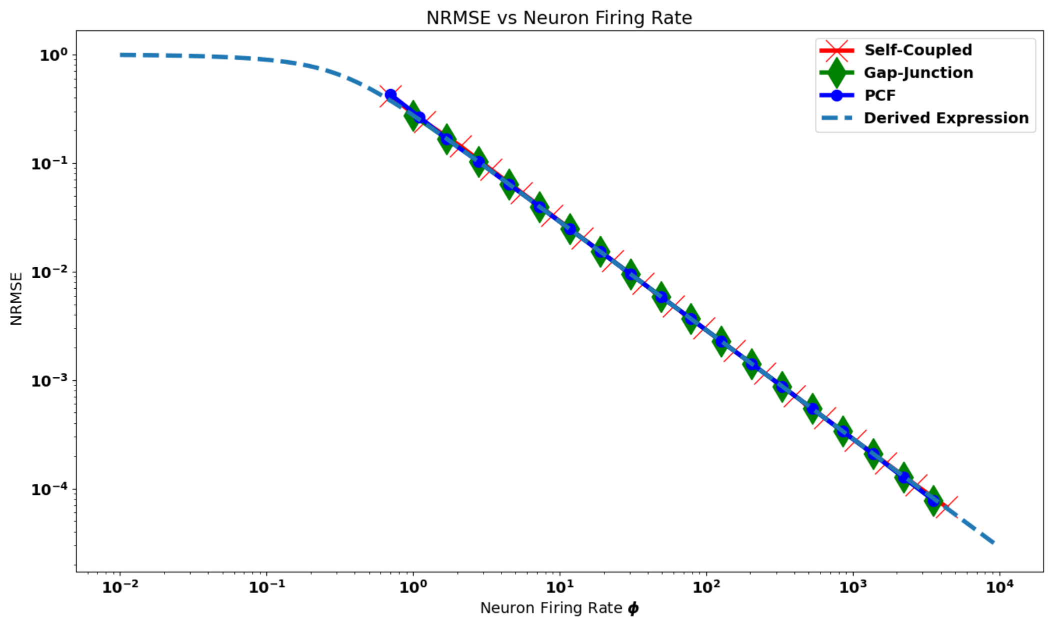


Figure 10: Simulated RMSE for self-coupled, gap-junction, and PCF networks. The dotted line is the derived expression for each model given by given above. Spike rates were estimated numerically by dividing the number of spikes by the simulation length. The RMSE was computed numerically by the discrete integral $R\hat{M}SE = \sqrt{\hat{\phi} \sum_{\tau \text{ between spikes}} \; e(\xi)^T e(\xi) \; d\xi}$. All computations used the numerically estimated spike rate.

6 Second Order Network for Oscillatory Dynamics

- In section (2) the basic model assumes that the dynamics matrix A is diagonalizable such that

$$A = \mathcal{U}\Lambda\mathcal{U}^T,$$

where Λ is real and diagonal. This decomposition does not exist in general as only a subset of matrices in $\mathbf{R}^{d\times d}$ are diagonalizable with real eigenvalues. Equivalently, the characteristic polynomial of a matrix A

$$P(A) = det(A - \Lambda I)$$

can have complex roots in Λ even when $A \in \mathbf{R}^{d\times d}$. Note that for $A = \mathcal{U}\Lambda\mathcal{U}^T$,

$$\Lambda \in \mathbf{C}^{d\times d} \implies \mathcal{U} \in \mathbf{C}^{d\times d}.$$

Consider the basic voltage equations of the self-coupled network with $d = N$:

$$\dot{v} = \Lambda v + S\left(\Lambda + I_2\right)\rho + \beta\tilde{c} - S^2\tilde{o},$$

$$\dot{\rho} = -\rho + \tilde{o},$$

$$\hat{y} = S\rho.$$

If $\Lambda \in \mathbf{C}^{d\times d}$, then $\dot{v}$ is a system of complex-valued differential equations of a real variable (time). The network estimation error is also complex:

$$\epsilon = \mathcal{U}^* e \in \mathbf{C}^d.$$

This network is deficient in that its estimate only minimizes real-valued errors, leaving imaginary components uncorrected. To see why, note that while $v \in \mathbf{C}^N$, the spikes are real-valued:

$$\tilde{o} \in \mathbf{R}^N,$$

as well as $S \in \mathbf{R}^{d\times d}$. Therefore a spike in neuron j will update the estimate by a real-valued vector:

$$\epsilon' = \epsilon + S,$$

and update the complex-valued voltage of neuron j by $s^2 \in \mathbf{R}$.

To avoid this deficiency, we restrict all quantities to real vector spaces $\mathbf{R}^d$, meaning A is no longer diagonalizable. To proceed, divide and conquer: Any real, square, full-rank matrix A can be rotated into a real orthonormal basis $\mathcal{U}$ such that it is block diagonal with the form:

$$\mathcal{U}^{-1}A\mathcal{U} = \begin{bmatrix} \Lambda_1 & & & & & \\ & \ddots & & & & \\ & & \Lambda_n & & & \\ & & & \mu_1 & & \\ & & & & \ddots & \\ & & & & & \mu_m \end{bmatrix},$$

where n and m are the number of distinct complex and real roots of $P(A)$ respectively. The blocks $\mu \in \mathbf{R}$ are scalars, while the blocks $\Lambda = a + ib$ have the form

$$\Lambda = \begin{bmatrix} a & -b \\ b & a \end{bmatrix}.$$

For the scalar blocks μ and eigenvectors $\mathcal{U}$, we can use the SC net already described with $N \geq 2m$. We need only focus on implementing the remaining blocks Λ. For simplicity, we handle just one 2×2 block by dropping the subscript j.

First we obtain the block and basis vectors from $A \in \mathbf{R}^{2\times 2}$. We have a complex eigenvector:

$$A(u_r + iu_i) = (a + ib)(u_r + iu_i),$$

where u_r and u_i are the real and imaginary parts of the eigenvector u. Both real and imaginary part of this equation hold, so

$$\begin{aligned} A \begin{bmatrix} u_r & u_i \end{bmatrix} &= \begin{bmatrix} au_r - bu_i & bu_r + au_i \end{bmatrix} \\ &= \begin{bmatrix} a & -b \\ b & a \end{bmatrix} \begin{bmatrix} u_r & u_i \end{bmatrix} \\ \implies \begin{bmatrix} u_r & u_i \end{bmatrix}^{-1} A \begin{bmatrix} u_r & u_i \end{bmatrix} &= \begin{bmatrix} a & -b \\ b & a \end{bmatrix}. \end{aligned}$$

Recognizing that $\begin{bmatrix} u_r & u_i \end{bmatrix}$ are an othornormal basis for $\mathbf{R}^2$, we have our desired block form of A.

The rotated dynamics matrix is no longer guaranteed to be diagonal, thus our network is no longer self-coupled. Rather, the network voltages may split into pairs of connected voltages with coupling Λ. This is physically unrealistic, since coupling between voltages is not symmetric as conductance-based models such as Hodgkin-Huxley suggest. From the uniqueness of the eigenvalues, this unrealistic outcome always occurs when rotating to an orthonormal basis while $P(A)$ has complex roots. Therefore our first order differential equations will always produce either a degenerate or unrealistic network. From first principles we've shown that the first order self coupled network is deficient for all but a small subset of dynamical systems, necessitating a second order approach.

- We seek a set of second order differential equations that capture the dynamics

  $$\dot{x} = Ax + Bc,$$

  and that permits a diagonalizable coupling matrix between neuron voltages. For simplicity, assume that A is already in real the block diagonal form above. We find a second order system that gives diagonal state transition matrices by exploiting the structure of the 2×2 block Λ:

  First we use the symmetric-skew symmetric decomposition of a square matrix:

  $$\Lambda = L + K,$$

  where

  $$L = \frac{1}{2}\left(\Lambda + \Lambda^T\right) = \begin{bmatrix} a & 0 \\ 0 & a \end{bmatrix} = a\,I,$$

and

$$K = \frac{1}{2}\left(\Lambda - \Lambda^T\right) = \begin{bmatrix} 0 & -b \\ b & 0 \end{bmatrix}.$$

From the second derivative of x, we find

$$\begin{aligned} \dot{x} &= (L+K)\,x + Bc \\ \implies \ddot{x} &= (L+K)\,\dot{x} + B\dot{c} \\ &= 2L\dot{x} + \left[K^2 - L^2 - \left(LK + (LK)^T\right)\right] x + B\dot{c} + (K-L)Bc. \end{aligned}$$

Recognizing that

$$\begin{aligned} \left[K^2 - L^2 - \left(LK + (LK)^T\right)\right] &= -\Lambda^T\Lambda \\ &= \begin{bmatrix} a & -b \\ b & a \end{bmatrix}^T \begin{bmatrix} a & -b \\ b & a \end{bmatrix} \\ &= (a^2+b^2)I \end{aligned}$$

we have

$$\ddot{x} = 2L\dot{x} - \Lambda^T\Lambda x + B\dot{c} + (K-L)Bc. \tag{6.1}$$

Equation (6.1)is a second order differential equation that gives both the target dynamics in the first order, and decouples the variables of state $(x, \dot{x})$ as desired.

- For the network implementation of the seconder order block in equation (6.1), we must compute

$$\ddot{e} = \ddot{x} - \ddot{\hat{x}}.$$

However to do so would give

$$\begin{aligned} \ddot{\hat{x}} &= (D\ddot{r}) \\ &= \frac{d}{d\xi} D\left[-r + o\right], \end{aligned}$$

where $D \in \mathbf{R}^{d\times d}$. We'd need the derivative of $o = \sum_k \delta(\xi - \xi^k)$. Since $\frac{d}{d\xi}\delta(\xi)$ is undefined, we must modify our definition of r so that its second derivative exists. We do this via cascading two leaky integrations together in a *second order synapse*. Let r now be the second order post-synaptic state described by

$$\dot{r} = -r + u,$$

where

$$\dot{u} = -u + o.$$

Since r and u are strictly nonnegative, we will again need to add a second set of anti-parallel neurons to ensure that the network estimate spans all of $\mathbf{R}^2$. The original encoding direction matrix is

$$D = \mathcal{U} S V^T,$$

where each of U, $S = sI$, and $V \in \mathbf{R}^{2\times 2}$. We replace this with

$$D = s \begin{bmatrix} \mathcal{U} & \\ & \mathcal{U} \end{bmatrix} \begin{bmatrix} V^T & \\ & -V^T \end{bmatrix},$$

to obtain an augmented $D \in \mathbf{R}^{4x4}$. With the doubled number neurons, we now have $r, o \in \mathbf{R}^4$, and the network estimate is:

$$\hat{x} = \begin{bmatrix} I_2 & -I_2 \end{bmatrix} Dr$$

$$\implies \ddot{\hat{x}} = \begin{bmatrix} I_2 & -I_2 \end{bmatrix} Dr - 2 \begin{bmatrix} I_2 & -I_2 \end{bmatrix} Du + \begin{bmatrix} I_2 & -I_2 \end{bmatrix} Do$$

$$\implies \dot{e} = (L + K)x + Bc + \begin{bmatrix} I_2 & -I_2 \end{bmatrix} Dr - \begin{bmatrix} I_2 & -I_2 \end{bmatrix} Du$$

$$\implies \ddot{e} = 2L\dot{e} + (I_2 - \Lambda^T\Lambda - 2L)\left(\begin{bmatrix} I_2 & -I_2 \end{bmatrix} Dr\right) + 2(L + I_2)\begin{bmatrix} I_2 & -I_2 \end{bmatrix} Du - \begin{bmatrix} I_2 & -I_2 \end{bmatrix} Do + B\dot{c} + (K - L)Bc.$$

The first order network greedily minimized

$$\mathcal{L}(\xi) = ||e(\xi)||.$$

A spike of neuron k at time ξ updated the estimate by

$$e(\xi + d\xi) = e(\xi) - d_k \quad \text{(First Order Network)},$$

where d_k was the k^{th} column of D. With the second order network, the estimate does not change over the interval $d\xi$, i.e

$$e(\xi + d\xi) \simeq e(\xi) \quad \text{(Second Order Network)}.$$

Thus a greedy optimization of e over the interval $d\xi$ will perform poorly, since each possible choice of spike time and neuron leads to no change in the network estimate. However, minimizing the derivative $||\dot{e}||$ works similarly to minimizing $||e||$ in the first order case: Let the network minimize

$$\mathcal{L}(\xi) = ||\dot{e}||$$

When neuron k spikes, the k_{th} column of the augmented D, $d_k \in \mathbf{R}^4$ is premultiplied by $\begin{bmatrix} I_2 & I_2 \end{bmatrix}$ then added to the network estimate:

$$\mathcal{L}_{sp} = ||\dot{x} - \left(\dot{\hat{x}} + \begin{bmatrix} I_2 & -I \end{bmatrix} d_k\right)||$$

$$= \mathcal{L}_{ns} - 2\dot{e}^T \left(\begin{bmatrix} I_2 & -I \end{bmatrix} d_k\right) + d_k^T \begin{bmatrix} I_2 & -I_2 \\ -I_2 & I_2 \end{bmatrix} d_k$$

The spiking condition $\mathcal{L}_{sp} < \mathcal{L}_{ns}$ gives

$$d_k^T \begin{bmatrix} \dot{e} \\ -\dot{e} \end{bmatrix} > \frac{1}{2} d_k \begin{bmatrix} I_2 & -I_2 \\ -I_2 & I_2 \end{bmatrix} d_k$$

$$\implies v_k > \frac{1}{2} d_k \begin{bmatrix} I_2 & -I_2 \\ -I_2 & I_2 \end{bmatrix} d_k,$$

where

$$v_k = d_k^T \begin{bmatrix} \dot{e} \\ -\dot{e} \end{bmatrix} \qquad k \in [1, \ldots, 4]$$

$$\implies \dot{v} = D^T \begin{bmatrix} \ddot{e} \\ -\ddot{e} \end{bmatrix},$$

where $v \in \mathbf{R}^4, e \in \mathbf{R}^2$.

Using the expression for $\ddot{e}$ above, we arrive at the second order voltage equations for a given 2×2 block j:

$$\dot{v} = 2 \begin{bmatrix} L & \\ & L \end{bmatrix} v - \begin{bmatrix} \Lambda^T\Lambda & \\ & \Lambda^T\Lambda \end{bmatrix} \int v(\tau) d\tau + D^T \begin{bmatrix} I_2 - \Lambda^T\Lambda - 2L & \\ & I_2 - \Lambda^T\Lambda - 2L \end{bmatrix} \begin{bmatrix} I_2 & -I_2 \\ -I_2 & I_2 \end{bmatrix} Dr +$$

$$2D^T \begin{bmatrix} I + L & \\ & I + L \end{bmatrix} \begin{bmatrix} I_2 & -I_2 \\ -I_2 & I_2 \end{bmatrix} Du - D^T \begin{bmatrix} I_2 & -I_2 \\ -I_2 & I_2 \end{bmatrix} Do + D^T B\dot{c} + D^T (K - L) Bc$$

Because we've assumed A was already in block diagonal form, we can get the self-coupled network voltage equations by simple substitution of the rotated quantities ρ, ϵ, $\tilde{o}$, $S = sI$, and now $\tilde{u}$ for u:

$$\dot{v} = 2 \begin{bmatrix} L & \\ & L \end{bmatrix} v - \begin{bmatrix} \Lambda^T\Lambda & \\ & \Lambda^T\Lambda \end{bmatrix} \int v(\tau) d\tau + s^2 \begin{bmatrix} I_2 - \Lambda^T\Lambda - 2L & \\ & I_2 - \Lambda^T\Lambda - 2L \end{bmatrix} \begin{bmatrix} I_2 & -I_2 \\ -I_2 & I_2 \end{bmatrix} r +$$

$$2s^2 \begin{bmatrix} I + L & \\ & I + L \end{bmatrix} \begin{bmatrix} I_2 & -I_2 \\ -I_2 & I_2 \end{bmatrix} u - s^2 \begin{bmatrix} I_2 & -I_2 \\ -I_2 & I_2 \end{bmatrix} o + s\beta\dot{\tilde{c}} + s(K - L)\beta\tilde{c}$$

Note $v \in \mathbf{R}^4$ is the voltage of the four neurons associated with the j^{th} block of A's normal form. The integral $\int v d\tau$ physically describes the Calcium concentration of the four neurons.