Nengo Summerschool 2019

Biologically Detailed Networks and Neuron Models

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OUTLINE

I *Motivation & Background*
Why care about biological detail?

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II *Conductance-based n-LIF neurons* ← Andreas
How to computationally exploit nonlinear dendritic interaction

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How to integrate detailed neuron models into the NEF

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How to integrate detailed neuron models into the NEF

IV *`nengo-bio` hands-on* ← Andreas
Build networks adhering to Dale's principle and exploit dendritic computation

PART I

Motivation & Background

Motivation — *Levels of Analysis*

mechanistic functional

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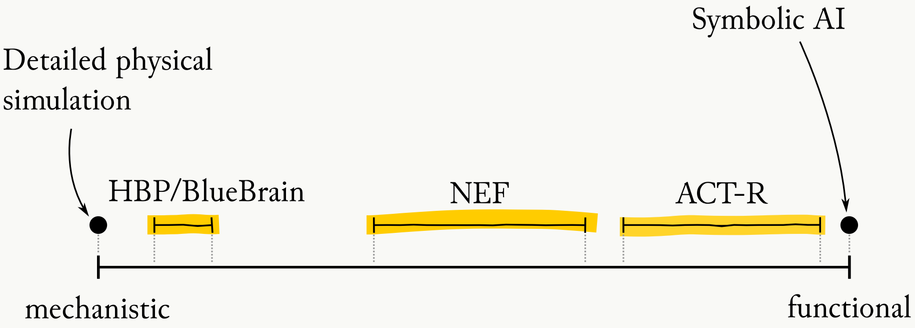

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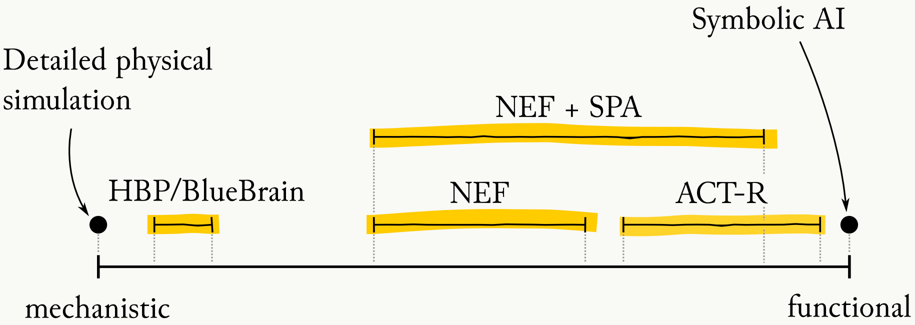

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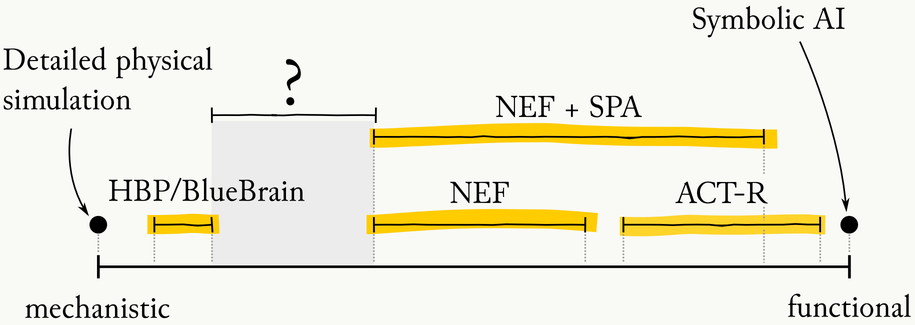
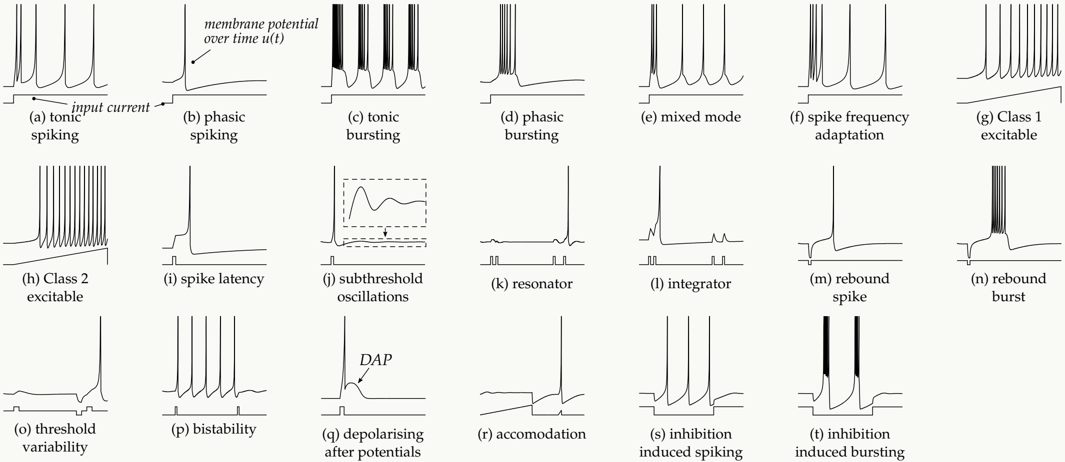


Motivation — *Computational Power of Biological Neurons*



Adapted from Izhikevich (2004), *Which Model to Use for Cortical Spiking Neurons?*

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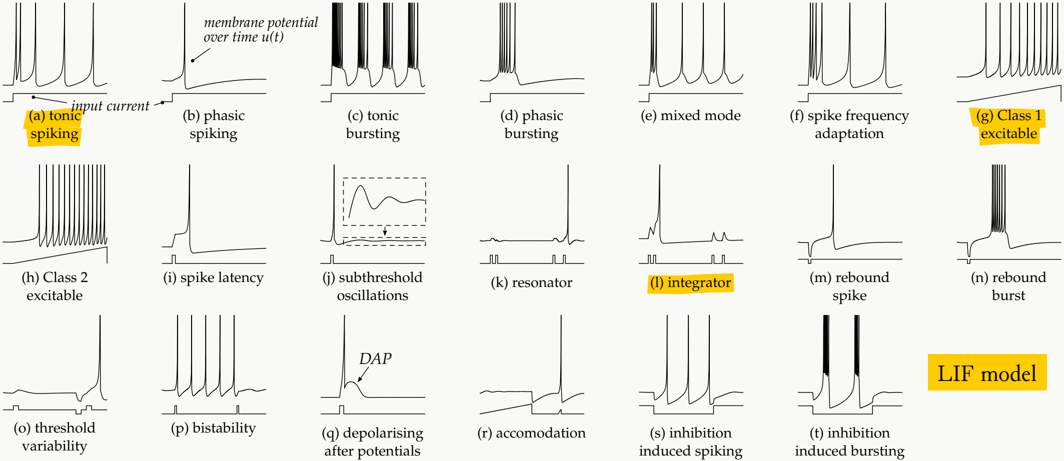

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$\rightsquigarrow$ Can we exploit this nonlinearity systematically?

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① Study Perturbations

- Drugs
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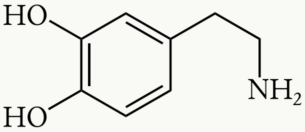

DOPAMINE

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1 Study Perturbations

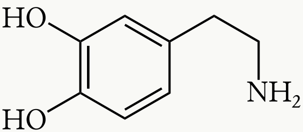
- Drugs
- Neurological/mental disorders

2 Neuromodulation

- Model additional pathways for information processing/learning

3 Constrain Models

- Constrain models to available biophysical data



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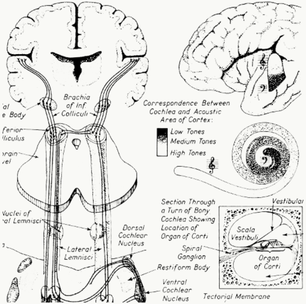
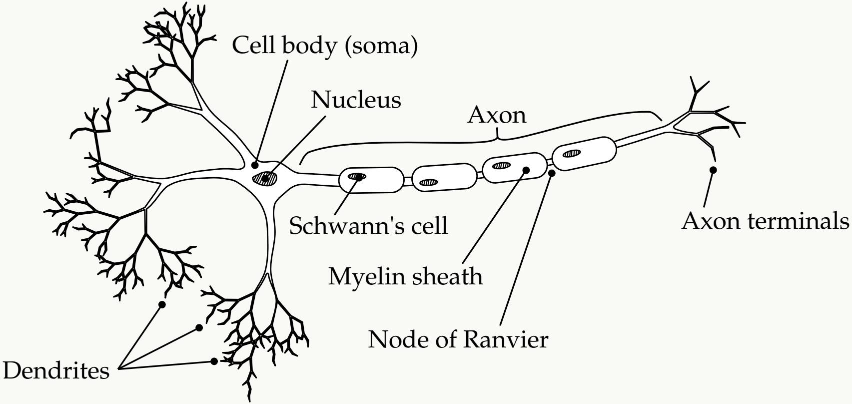


Neurobiology — *Idealized "Textbook" Neuron*



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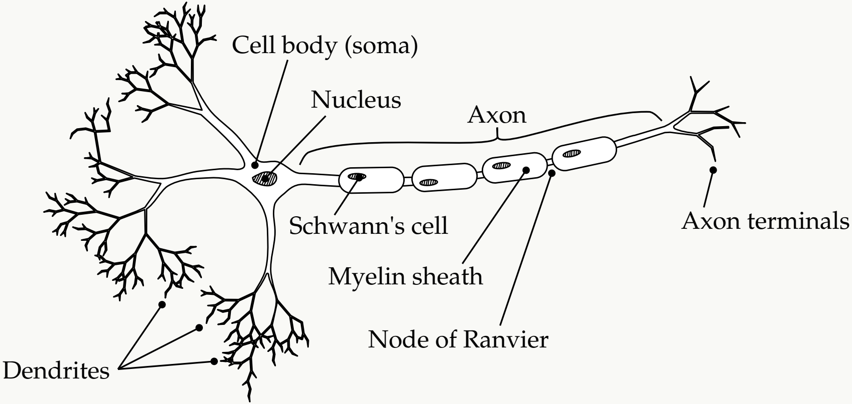
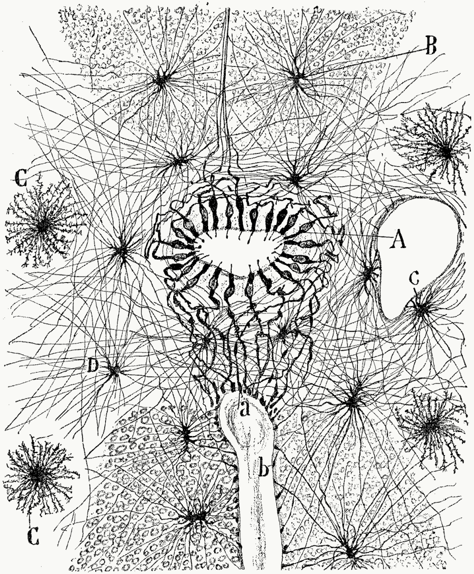
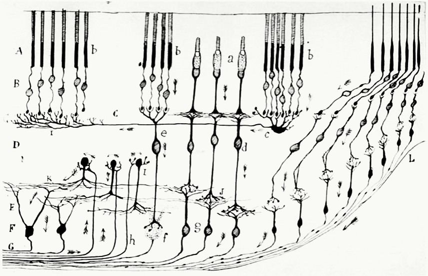
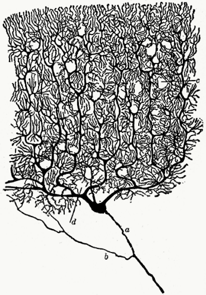


❶ Dendrites collect input ⟶ ❷ Integrated in soma ⟶ ❸ Output spikes travel along axon

Neurobiology — *Neural Heterogeneity*







Drawings by
Santiago Ramón y Cajal

Comparing LIF and Biology

Complexity			NEF compatibility		
	LIF	*BIO*		*LIF*	*BIO*
Geometry	point	compartmental	**Tuning curve**	$A = f(\mathbf{x})$	$A = f(\mathbf{x}, t)$
Synapse	current	conductance	**Inputs**	linear filter	synaptic nonlinearity
Dynamics	integrate, leak	ion channels	**Dynamics**	synapse dominates	neuron dominates
	voltage reset	cable equation	**Decoders**	static	time-dependent
Simulation	fast	slow	**Estimates**	$\sum_j a_i(t) * \mathbf{d}_i^f$	?

PART II

Conductance-based n-LIF neurons

Reversal potentials

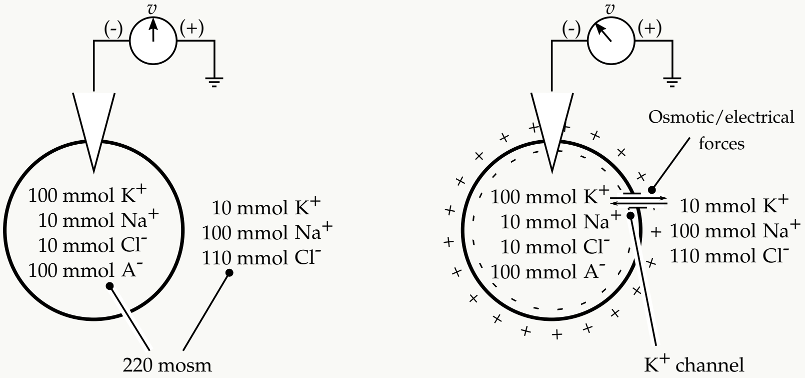
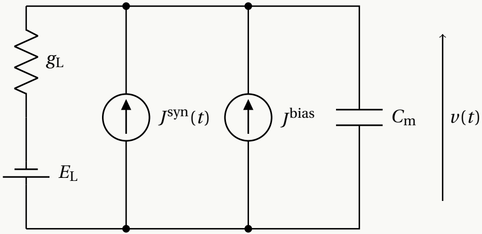


Illustration adapted from Reichert, 2000, Neurobiology.

Ion channels possess a specific *reversal potential* corresponding to the combination of *ion species* they are permeable for.

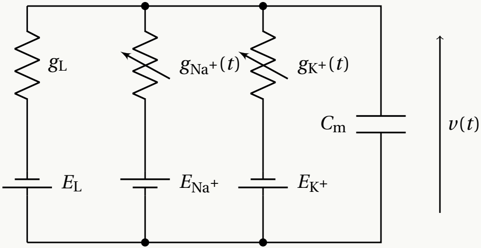
Current vs. Conductance-Based LIF

Current-based LIF



$$
\begin{aligned}
C_m \dot{u}(t) = J^{\text{bias}} \\
+ \alpha J^{\text{syn}}(t) \\
+ g_L(E_L - u(t))
\end{aligned}
$$

Conductance-based LIF



$$
\begin{aligned}
C_m \dot{u}(t) &= g_E(t)(E_E - u(t)) \\
&+ \ g_I(t)(E_I - u(t)) \\
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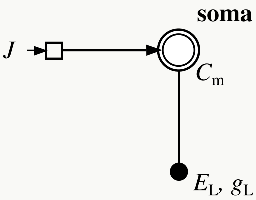

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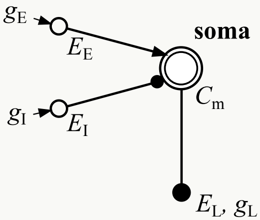

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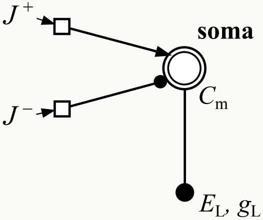

$$
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C_\mathrm{m}\dot{u}(t) = J^\mathrm{bias} & \\
&+ \alpha\big(J^+(t) - J^-(t)\big) \\
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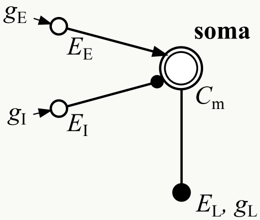

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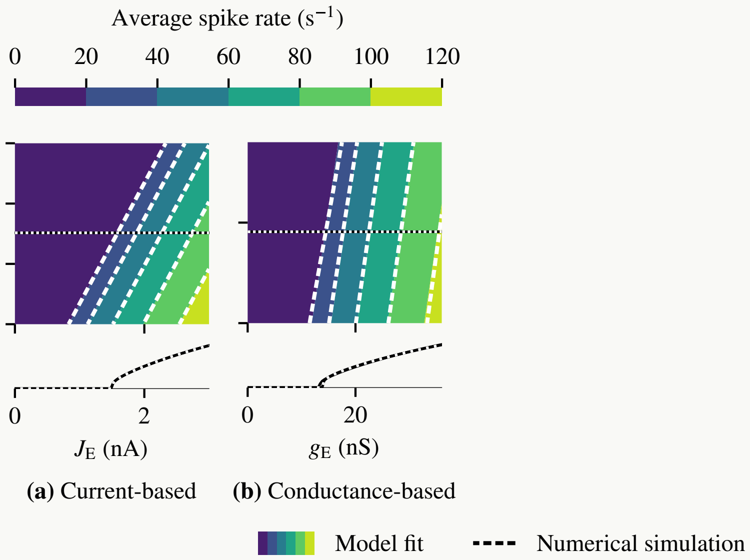
Current vs. Conductance-Based LIF Tuning Curves



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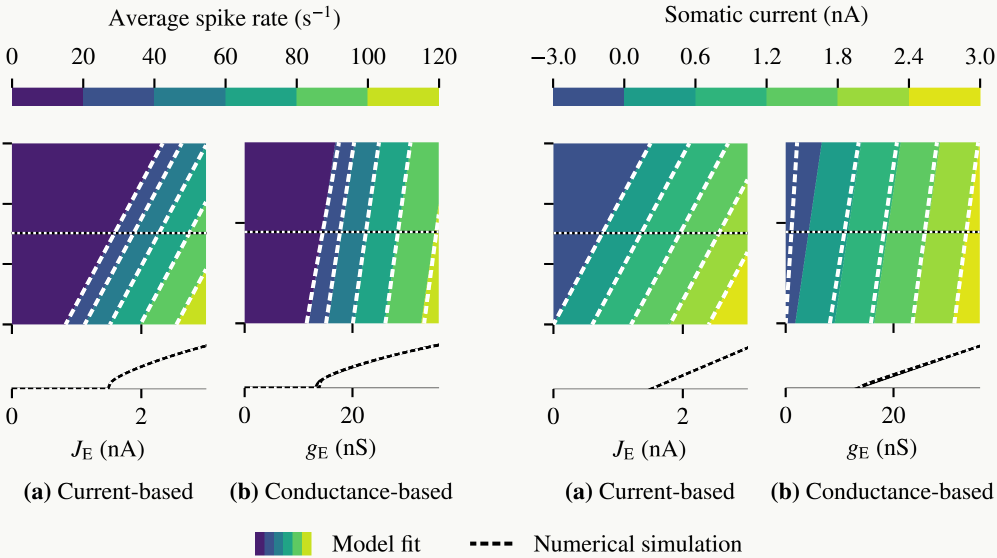

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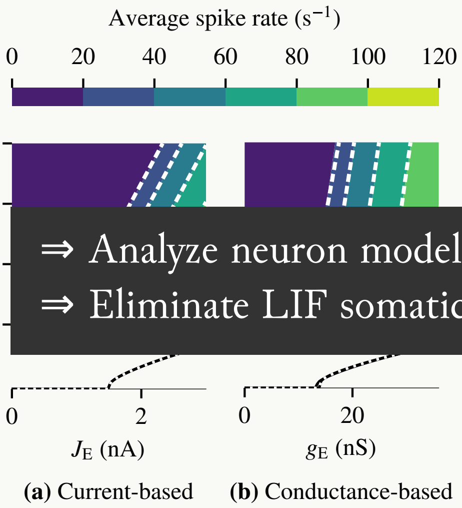
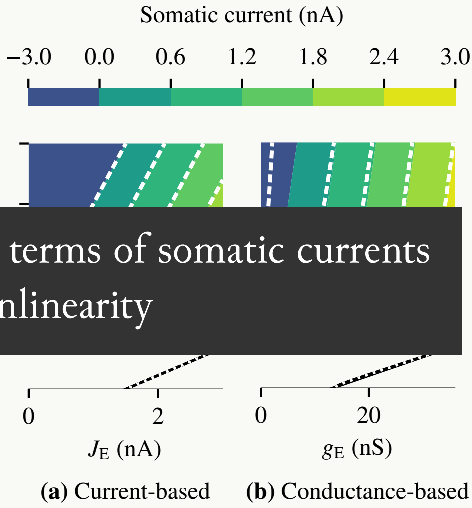




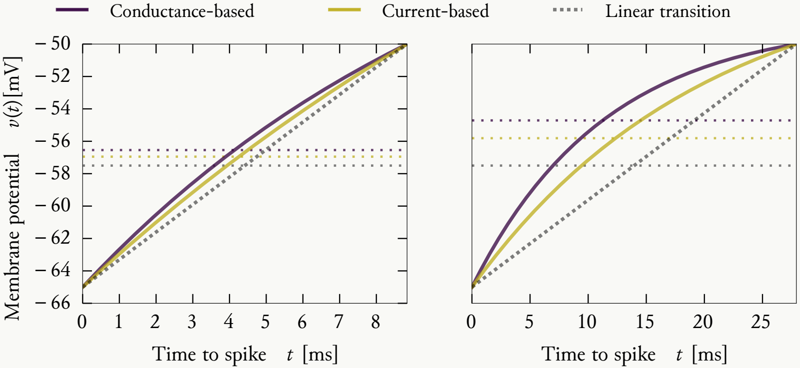
⇒ Analyze neuron models in terms of somatic currents

⇒ Eliminate LIF somatic nonlinearity

Model fit   Numerical simulation

Single-compartment conductance-based LIF

- For firing rates $\gg 0$, conductance-based LIF is boring



- Can assume average membrane potential $\bar{u}$

$$C_\mathrm{m}\dot{u}(t) = g_\mathrm{E}(t)(E_\mathrm{E} - u(t)) + g_\mathrm{I}(t)(E_\mathrm{I} - u(t)) + g_\mathrm{L}(E_\mathrm{L} - u(t))$$

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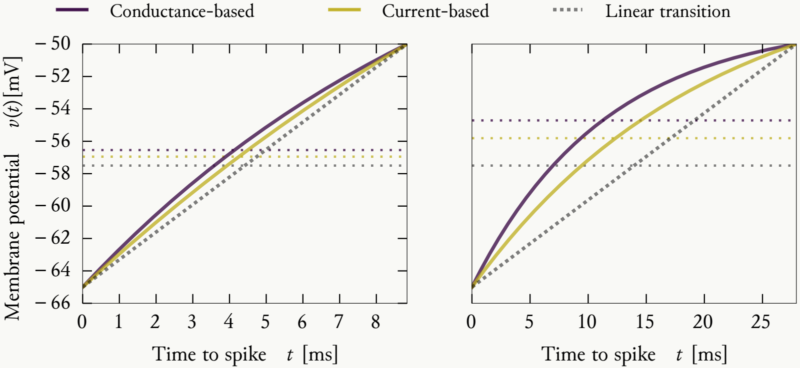

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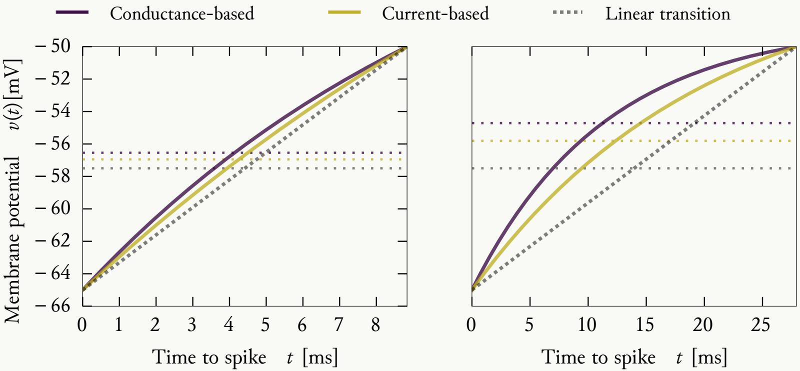

- Can assume average membrane potential $\bar{u} \Rightarrow$ just a skewed current-based LIF!

$$C_{\mathrm{m}}\dot{u}(t) = g_{\mathrm{E}}(t)\alpha_{\mathrm{E}} + g_{\mathrm{I}}(t)\alpha_{\mathrm{I}} + g_{\mathrm{L}}(E_{\mathrm{L}} - u(t))$$

Challenges and Extending the NEF

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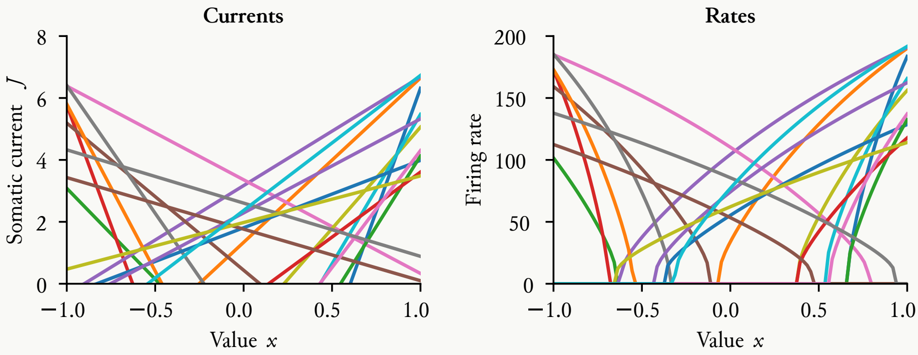
  4. Take *dendritic non-linearity* into account

❶ Eliminating the Bias Current



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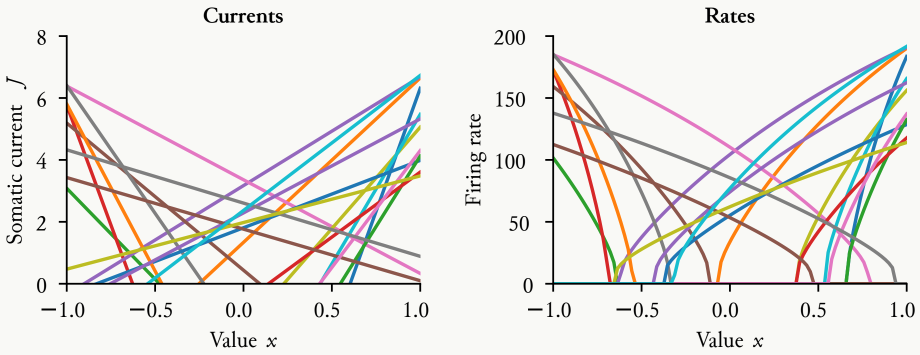

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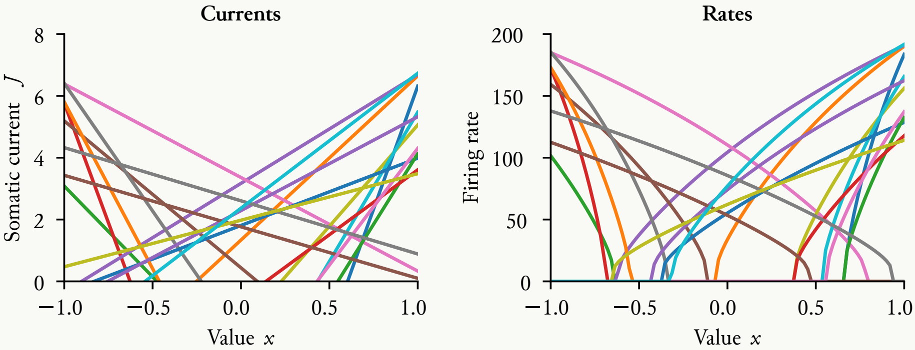

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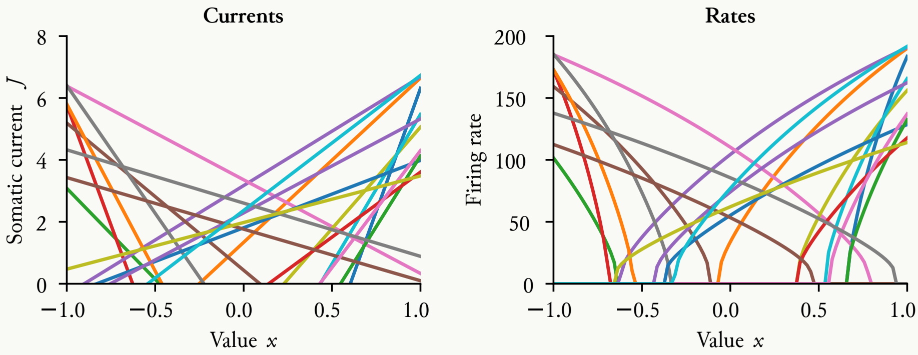

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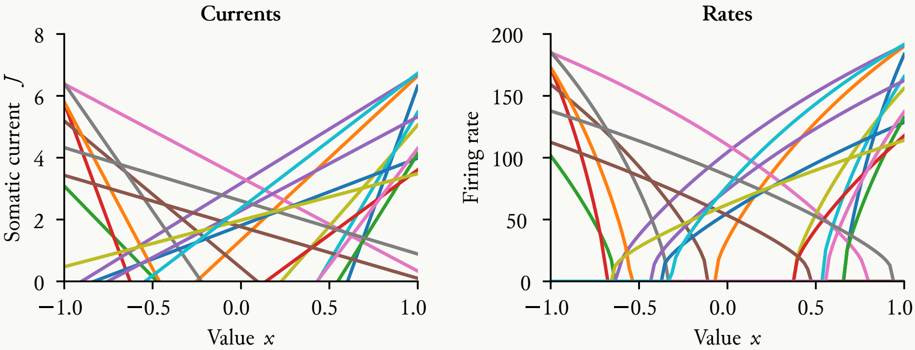

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- Firing rates correspond to a current J: “We *want* a current J if the neuron represents x”

$\Rightarrow$ Find a current-decoder for **each individual post-neuron** (instead of population-wise)

❷ Nonnegative Weight Optimization

- Assume a post-neuron receives both excitatory and inhibitory input from each pre-neuron i ⇒ weight vectors $\vec{w}_i^+$, $\vec{w}_i^-$.

$$\min_{\vec{w}_i^+, \vec{w}_i^-} \quad \frac{1}{2} \sum_{k=1}^{N} \left\| \vec{w}_i^+ \vec{a}_k^+ - \vec{w}_i^- \vec{a}_k^- - J\big(\langle \vec{e}_i, f(\vec{x}_k) \rangle\big) \right\|_2^2$$

$$= \frac{1}{2} \left\| \vec{w}_i' A' - \vec{j} \right\|_2^2 \quad \text{where } \vec{w}_i' = (\vec{w}_i^+, \vec{w}_i^-),\ A' = (A^+, -A^-)^T,$$

$$\text{and } (\vec{j})_k = J\big(\langle \vec{e}_i, f(\vec{x}_k) \rangle\big)\,,$$

subject to $\vec{w}_i^+ \geq 0, \vec{w}_i^- \geq 0$

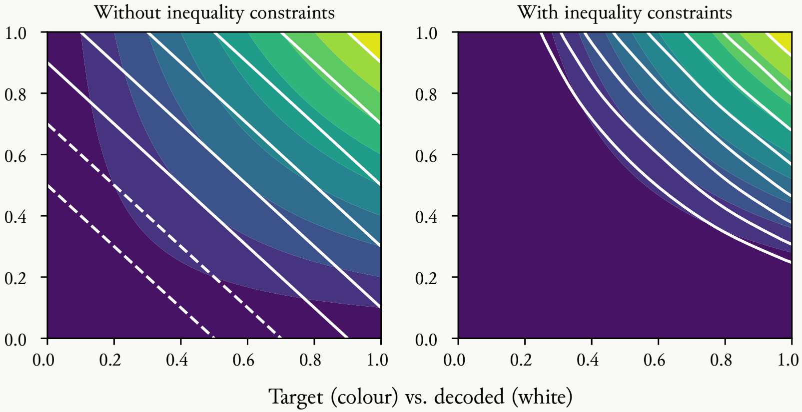
- Can remove rows/columns from A' and $\vec{w}_i$ to account for Dale's principle (e.g. only 20% of pre-neurons are inhibitory, 80% are excitatory)

③ Account for sub-threshold currents

- Tuning curves are not injective (one-to-one): multiple x map onto a zero output rate

$\Rightarrow$ If the target rate is zero, we do not care about the current, as long as the rate is zero

$\Rightarrow$ Turn zero-rates into inequality instead of equality constraints (quadratic programming)



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- Generalise dendritic interaction between excitation and inhibition
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- **Example:**
  Current-based model: $H(J^+, J^-) = J^+ - J^-$

$$\min_{\vec{w}_i^+, \vec{w}_i^-} \quad \frac{1}{2} \sum_{k=1}^{N} \left\| H(\vec{w}_i^+ \vec{a}_k^+, \vec{w}_i^- \vec{a}_k^-) - J\big(\langle \vec{e}_i, f(\vec{x}_k) \rangle\big) \right\|_2^2$$

subject to $\vec{w}_i^+ \geq 0, \vec{w}_i^- \geq 0$

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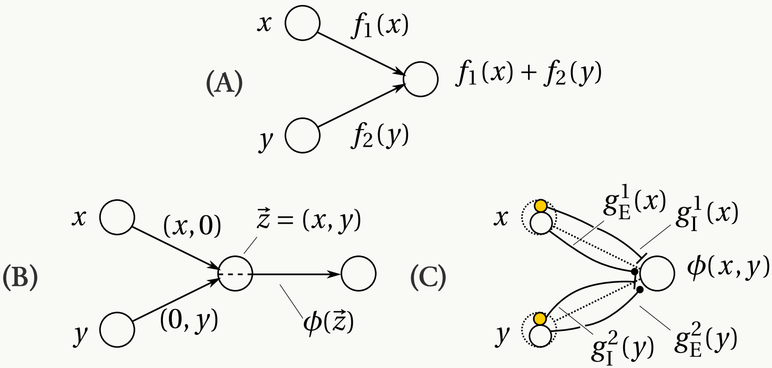
$$\text{subject to } \vec{w}_i^+ \geq 0, \vec{w}_i^- \geq 0$$

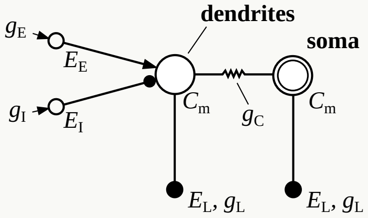
- **Questions:**
  - Can we find more interesting H?
  - Can we exploit H as a computational resource?
  - Under which conditions can we efficiently solve the optimization problem?

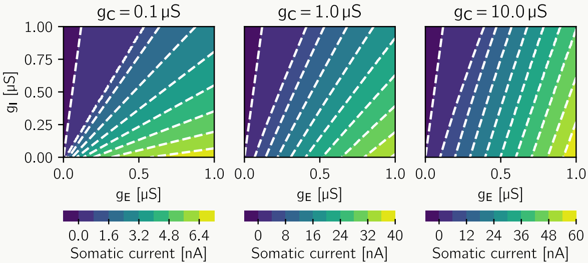
Computing Multivariate Nonlinear Functions



Example: Multiplication, compute $\phi(\vec{z}) = \phi(x, y) = x \cdot y$

Two-compartment LIF neuron

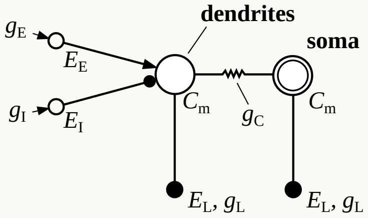


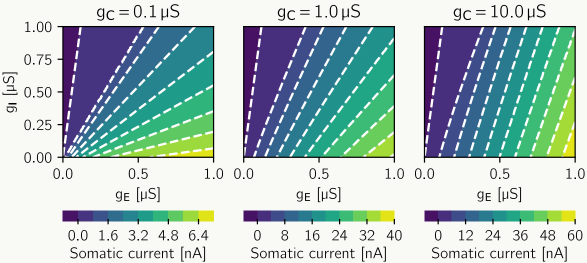


- Dendritic nonlinearity:

$$H(g_E, g_I) = \frac{b_1 + b_2 g_E + b_3 g_I}{a_1 + a_2 g_E + a_3 g_I}$$

Two-compartment LIF neuron



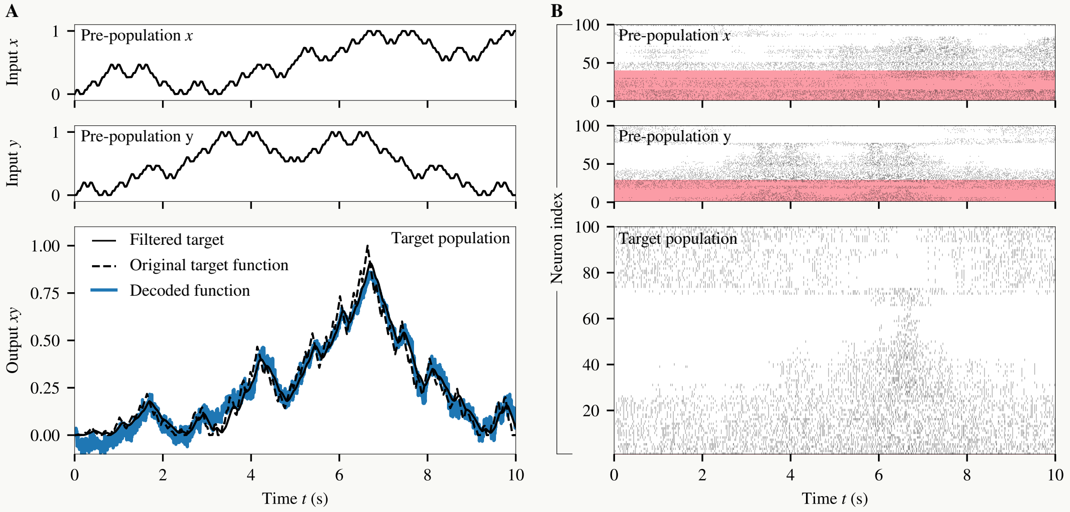


- Dendritic nonlinearity:

$$H(g_E, g_I) = \frac{b_1 + b_2 g_E + b_3 g_I}{a_1 + a_2 g_E + a_3 g_I}$$

- Can still formalize weight-optimization as convex quadratic programming problem, guaranteed to find global optimum

Results – *Dendritic computation* (I)

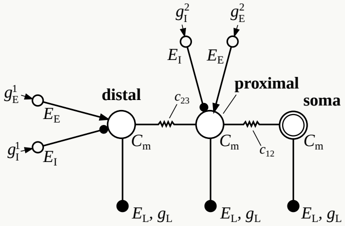


Results – *Dendritic computation* (II)

	Experiment setup						
	Standard LIF			Two comp. LIF $g_C = 50\,\mathrm{nS}$		Two comp. LIF $g_C = 100\,\mathrm{nS}$	
Target	no relaxation	A standard	B two-layer	C standard	noise model	standard	noise model
$x + y$	$5.1 \pm 0.6\%$	$5.5 \pm 1.1\%$	$11.0 \pm 1.3\%$	$\mathbf{3.2 \pm 1.1\%}$	$9.1 \pm 1.2\%$	$5.1 \pm 1.2\%$	$11.5 \pm 1.3\%$
$x \times y$	$26.2 \pm 0.4\%$	$21.5 \pm 6.6\%$	$15.4 \pm 4.0\%$	$13.9 \pm 2.9\%$	$\mathbf{11.9 \pm 1.8\%}$	$18.2 \pm 4.0\%$	$14.3 \pm 2.1\%$
$\sqrt{x \times y}$	$14.1 \pm 0.4\%$	$19.7 \pm 6.1\%$	$16.3 \pm 3.0\%$	$9.7 \pm 2.6\%$	$\mathbf{7.1 \pm 1.0\%}$	$13.3 \pm 4.2\%$	$8.9 \pm 1.7\%$
$(x \times y)^2$	$44.5 \pm 0.6\%$	$33.0 \pm 6.6\%$	$\mathbf{18.7 \pm 6.7\%}$	$27.7 \pm 4.1\%$	$27.4 \pm 4.1\%$	$34.3 \pm 5.3\%$	$30.3 \pm 4.3\%$
$x/(1 + y)$	$6.0 \pm 0.4\%$	$5.2 \pm 0.7\%$	$9.5 \pm 0.8\%$	$\mathbf{3.4 \pm 1.0\%}$	$10.0 \pm 1.6\%$	$5.3 \pm 1.3\%$	$14.0 \pm 1.9\%$
$\|(x, y)\|$	$8.0 \pm 0.4\%$	$5.7 \pm 1.1\%$	$10.5 \pm 1.0\%$	$\mathbf{3.1 \pm 1.3\%}$	$8.9 \pm 1.2\%$	$4.3 \pm 1.8\%$	$12.3 \pm 1.8\%$
$\mathrm{atan}(x, y)$	$10.3 \pm 0.3\%$	$8.6 \pm 1.0\%$	$13.4 \pm 1.1\%$	$\mathbf{5.8 \pm 1.3\%}$	$8.4 \pm 1.0\%$	$7.0 \pm 1.2\%$	$12.7 \pm 1.6\%$
$\max(x, y)$	$14.9 \pm 0.3\%$	$10.0 \pm 0.9\%$	$11.3 \pm 1.4\%$	$\mathbf{5.5 \pm 0.9\%}$	$7.7 \pm 0.9\%$	$7.3 \pm 0.9\%$	$9.7 \pm 1.0\%$

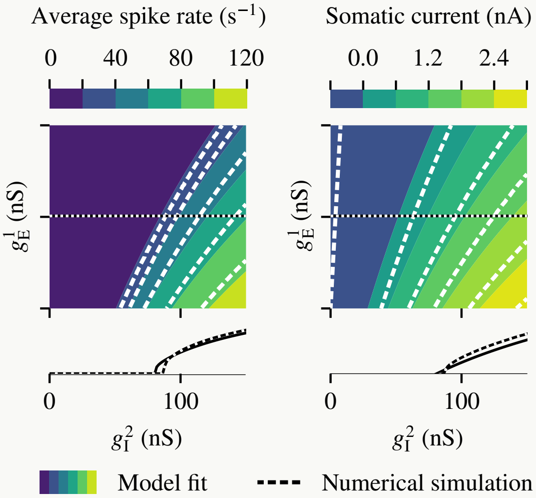
`http://arxiv.org/abs/1904.11713`

Three-compartment LIF neuron

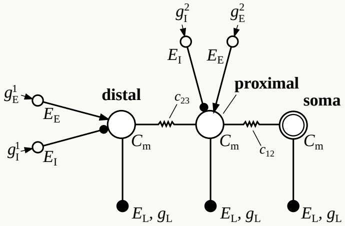


- Dendritic nonlinearity:

$$\left(\frac{b_1^1 + b_2^1 g_E + b_3^1 g_I}{a_1^1 + a_2^1 g_E + a_3^1 g_I}\right) \cdot \left(\frac{b_1^2 + b_2^2 g_E + b_3^2 g_I}{a_1^2 + a_2^2 g_E + a_3^2 g_I}\right)$$



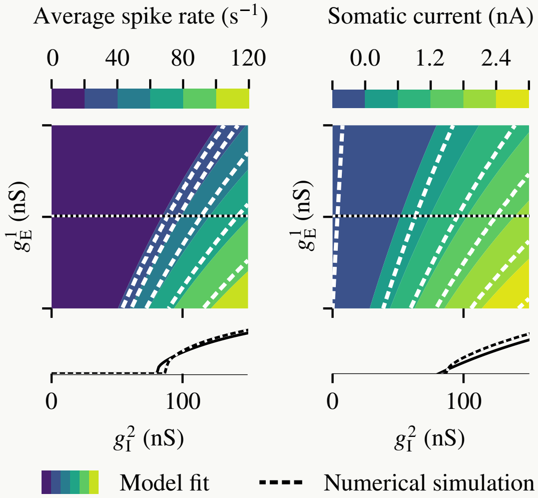
Three-compartment LIF neuron



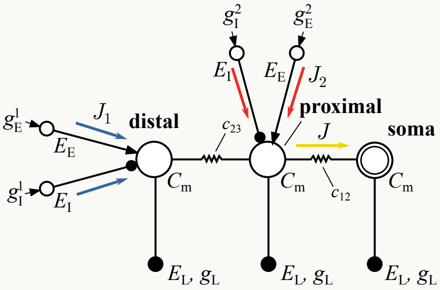
- Dendritic nonlinearity:

$$\left(\frac{b_1^1 + b_2^1 g_\mathrm{E} + b_3^1 g_\mathrm{I}}{a_1^1 + a_2^1 g_\mathrm{E} + a_3^1 g_\mathrm{I}}\right) \cdot \left(\frac{b_1^2 + b_2^2 g_\mathrm{E} + b_3^2 g_\mathrm{I}}{a_1^2 + a_2^2 g_\mathrm{E} + a_3^2 g_\mathrm{I}}\right)$$

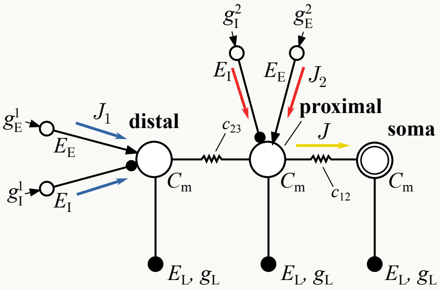
- For n-LIF, $n \geq 3$: can formalize weight-optimization as iterative trust-region-based optimization problem; *not* guaranteed to find global optimum

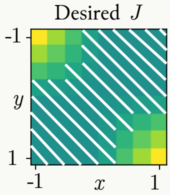


Three-compartment LIF neuron – *Example*

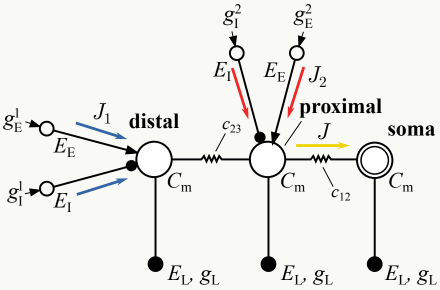


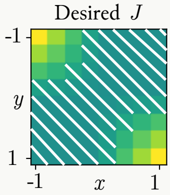
Three-compartment LIF neuron – *Example*

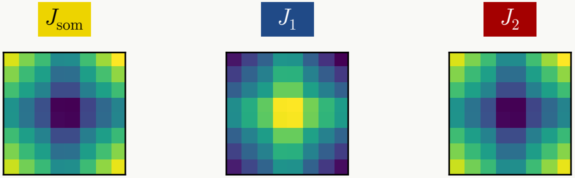




Three-compartment LIF neuron – *Example*

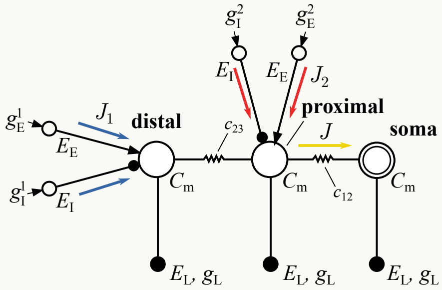


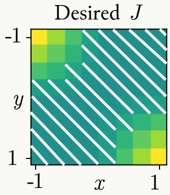




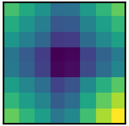
ITERATION 0

Three-compartment LIF neuron – *Example*

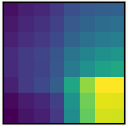




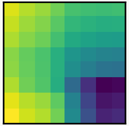
J_som



J_1

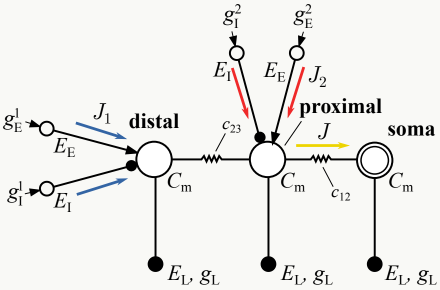


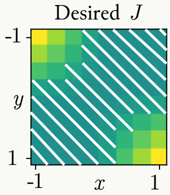
J_2

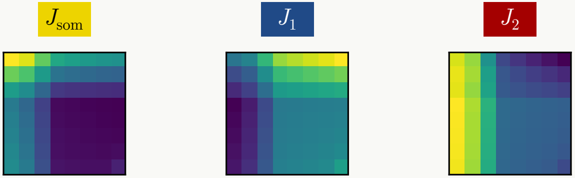


ITERATION 1

Three-compartment LIF neuron – *Example*

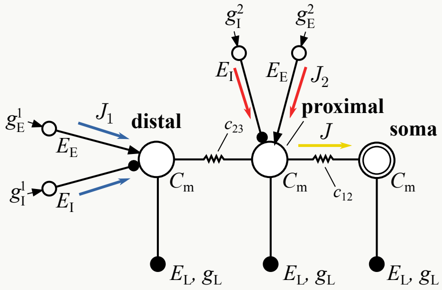


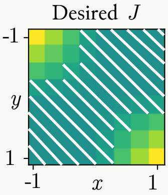


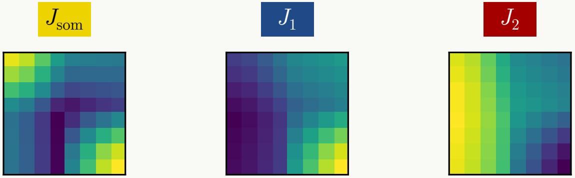


ITERATION 2

Three-compartment LIF neuron – *Example*

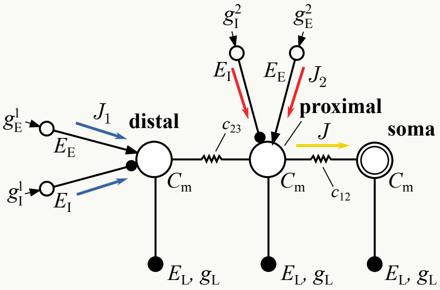


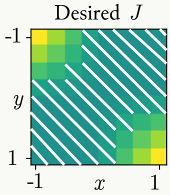


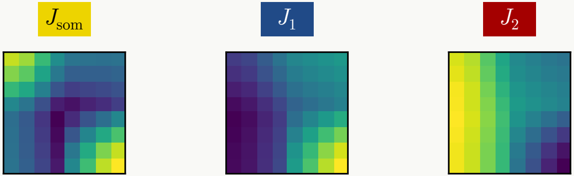


ITERATION 3

Three-compartment LIF neuron – *Example*

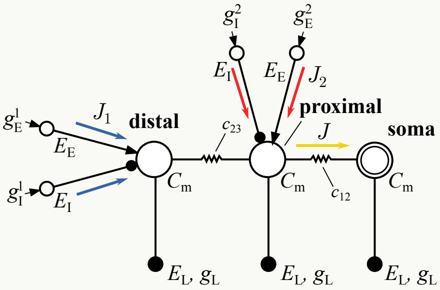


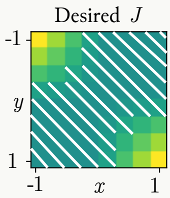


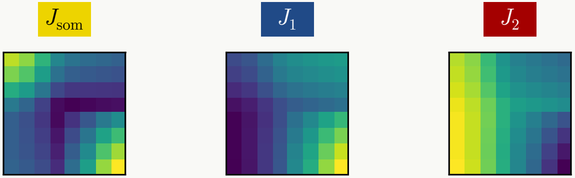


ITERATION 4

Three-compartment LIF neuron – *Example*

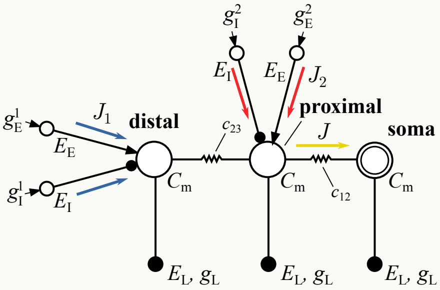


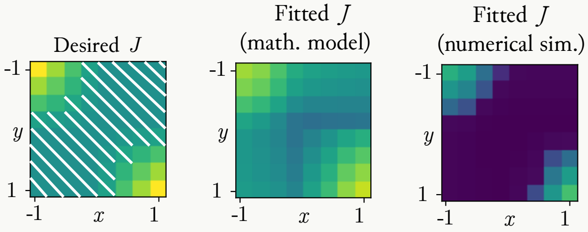


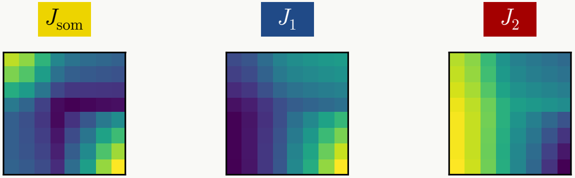


ITERATION 5

Three-compartment LIF neuron – *Example*







ITERATION 5

PART III

Detailed Neuron Models and the NEF

Neural Engineering Framework

state space $\mathbf{x}$ $\Longleftrightarrow$ neuron space A

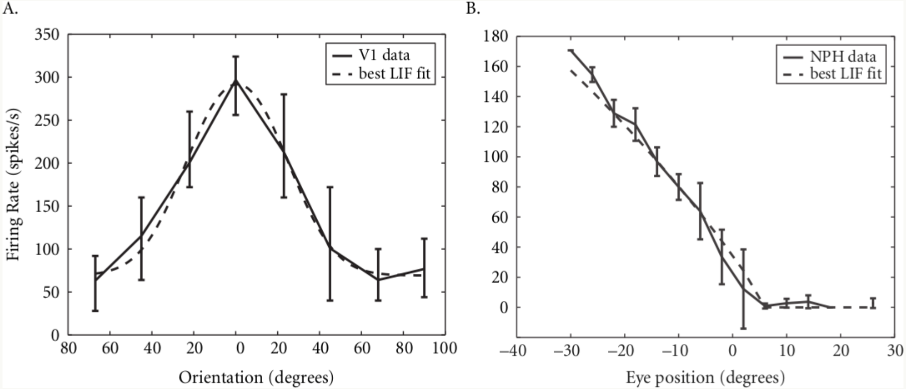


Figure: Tuning curves from monkey visual cortex (A) and human NPH (B)

Problem Statement

Tuning-curve-based methods assume non-adaptive neurons:

$$a_i = f(\mathbf{x})$$

For adaptive neurons, activity depends on signal history

$$a_i = f(\mathbf{x}, t)$$

Goal: Extend NEF methods to account for cellular dynamics

Approach

Assume neuron model is a “black box”

Use time-varying signals $\mathbf{x}(t)$ to train neural connection parameters

- Encoding: iterative optimization of gain, bias
- Decoding: least squares optimization of decoders, synapses

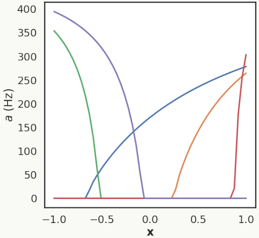
Considerations:

- $\mathbf{x}(t)$ spans state space and activates appropriate dynamics
- $\mathbf{x}(t)$ passes through preliminary filters (spikes, dendrites, etc.)

Static Encoding

Find `gain` and `bias` that achieve desired `max_rates` and `intercepts`

1. Find $J^{\text{test}}(x)$ for $\mathbf{x} \in [-1, 1]$ assuming $\alpha = 1$, $\beta = 0$
2. Calculate $a(J^{\text{test}})$ using rate-approximation
3. Interpolate $a = G(J(\mathbf{x}))$
4. Use G^{-1} to solve for α and β



Temporal Encoding

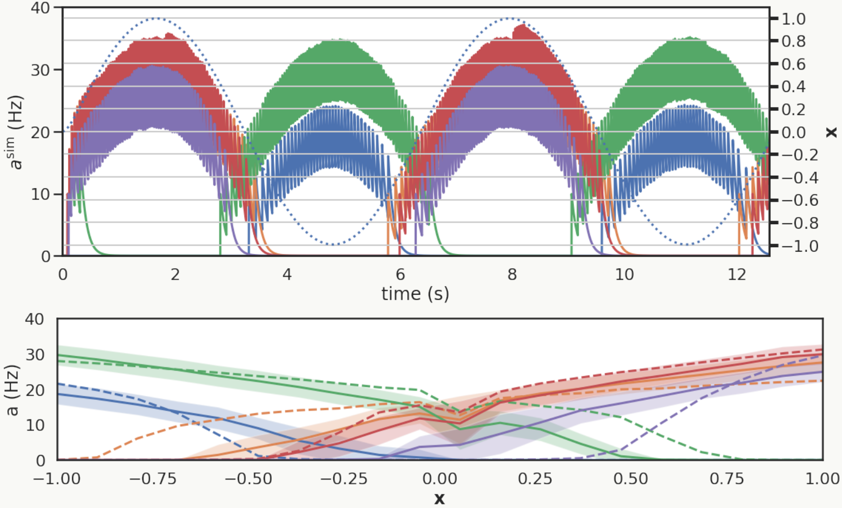


Figure: Find `gain` and `bias` that achieve desired `max_rates` and `intercepts`

Static Decoding

Minimizes state-space error over $\mathbf{x}$

$$E = \frac{1}{2} \int_{-1}^{1} (\mathbf{x} - \hat{\mathbf{x}})^2 dx$$

$$\hat{\mathbf{x}} = \sum_i a_i \, \mathbf{d}_i$$

Solve using least-squares

$$A \, \mathbf{d} = \mathbf{x}$$
$$\mathbf{d} = (A^T A + \sigma^2)^{-1} A^T \mathbf{x}$$

Static Decoding

Minimizes state-space error over $\mathbf{x}$

$$E = \frac{1}{2}\int_{-1}^{1}(\mathbf{x}-\hat{\mathbf{x}})^2 dx$$

$$\hat{\mathbf{x}} = \sum_i a_i\,\mathbf{d}_i$$

Solve using least-squares

$$A\,\mathbf{d} = \mathbf{x}$$
$$\mathbf{d} = (A^T A + \sigma^2)^{-1} A^T \mathbf{x}$$

Activity matrix calculated by static encoding

$$A = \begin{bmatrix} a_1(\mathbf{x}=-1) & \dots & a_n(\mathbf{x}=-1) \\ \vdots & \ddots & \vdots \\ a_1(\mathbf{x}=1) & \dots & a_n(\mathbf{x}=1) \end{bmatrix}$$

$$a_i(\mathbf{x}) = G_i(\mathbf{x}, \alpha_i, \beta_i)$$

Temporal Decoding

Minimize state-space error over t

$$E = \frac{1}{2} \int_0^{t'} (\mathbf{x}(t) - \hat{\mathbf{x}}(t))^2 dt$$

$$\hat{\mathbf{x}}(t) = \sum_i a_i(t)\ \mathbf{d}_i$$

Solve using least-squares

$$A\ \mathbf{d} = \mathbf{x}(t)$$
$$\mathbf{d} = (A^T A)^{-1} A^T \mathbf{x}(t)$$

Temporal Decoding

Minimize state-space error over t

$$E = \frac{1}{2} \int_0^{t'} (\mathbf{x}(t) - \hat{\mathbf{x}}(t))^2 dt$$

$$\hat{\mathbf{x}}(t) = \sum_i a_i(t)\ \mathbf{d}_i$$

Solve using least-squares

$$A\ \mathbf{d} = \mathbf{x}(t)$$
$$\mathbf{d} = (A^T A)^{-1} A^T \mathbf{x}(t)$$

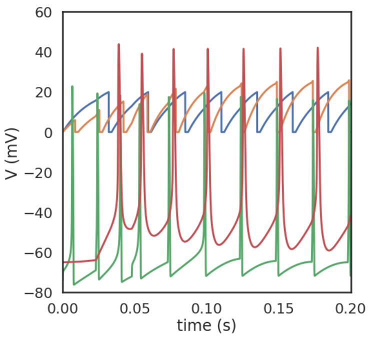
Activity matrix collected by simulating over time

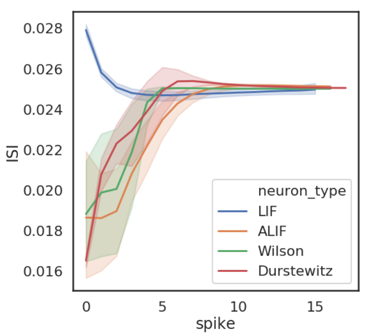
$$A = \begin{bmatrix} a_1(t=0) & \dots & a_n(t=0) \\ \vdots & \ddots & \vdots \\ a_1(t=t') & \dots & a_n(t=t') \end{bmatrix}$$

$$\mathbf{x}(t) = [\text{computed directly}]$$

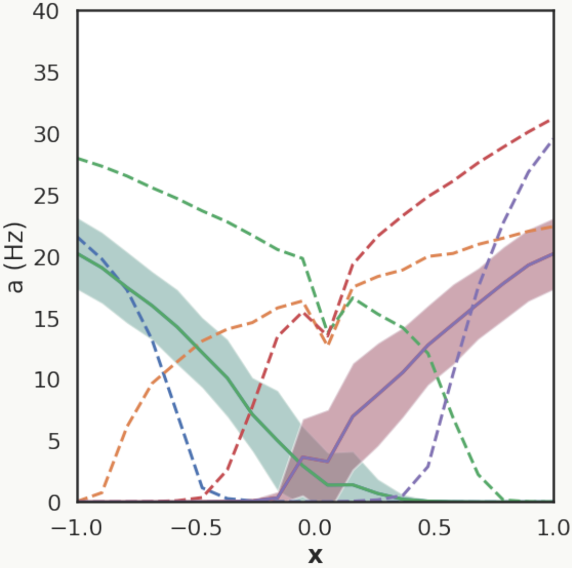
Neuron Models

Adaptive LIF	**Wilson**	**Durstewitz**
- spikes increase V^{thr} - divisive effect on J	- mamalian neocortex - 3 coupled ODEs for V, R, C	- Layer-V PC - conductance syn. - 4 geo. compartments - 6 HH ion channels

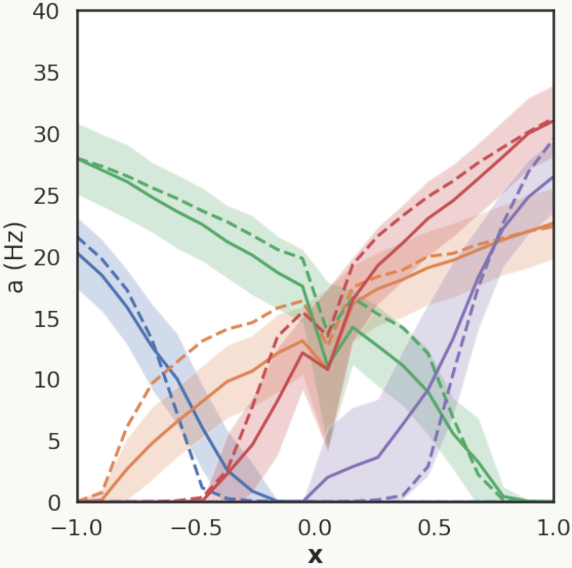




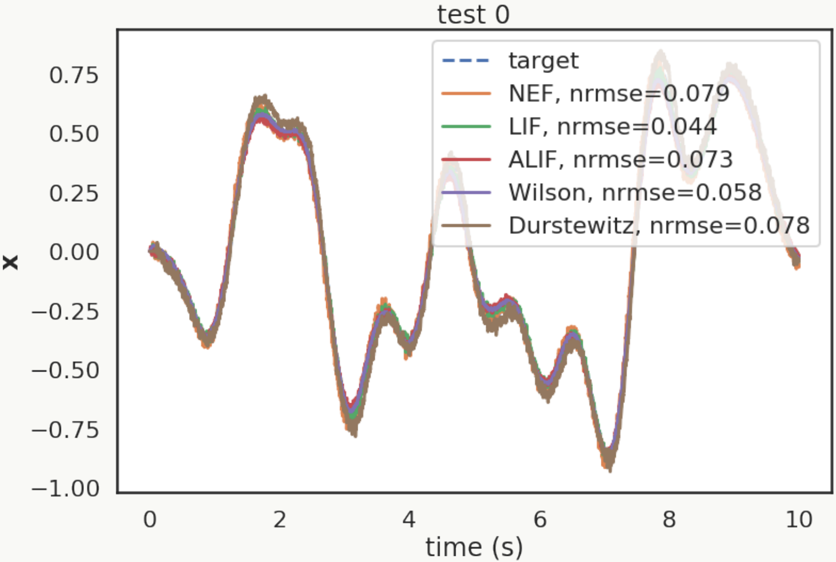
Encoding: Training α and β



Encoding: Training α and β



Decoding: $f(x) = x$



Decoding: $f(x) = x$

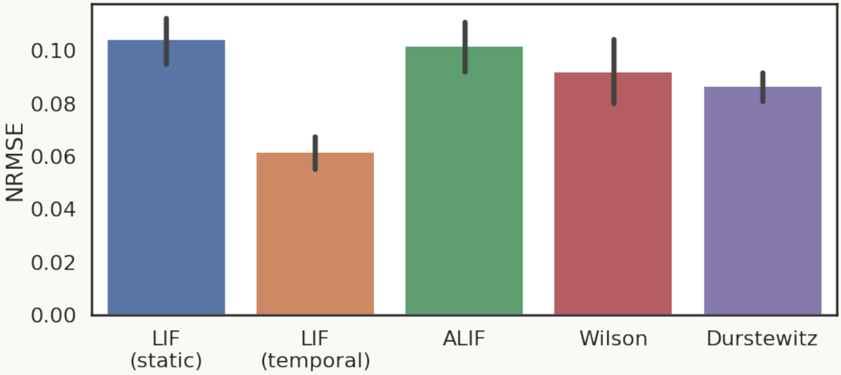
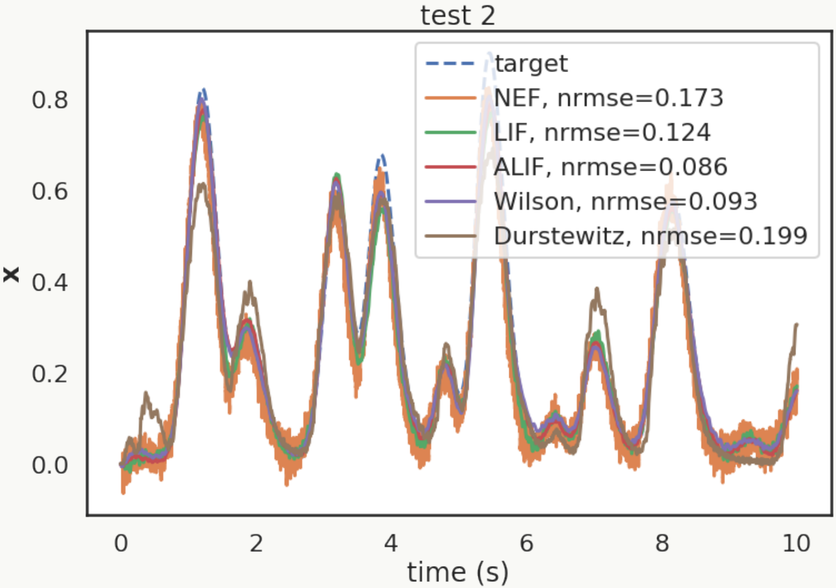


Figure: Average performance across neuron models

Decoding: $f(x) = x^2$



Decoding: $f(x) = x^2$

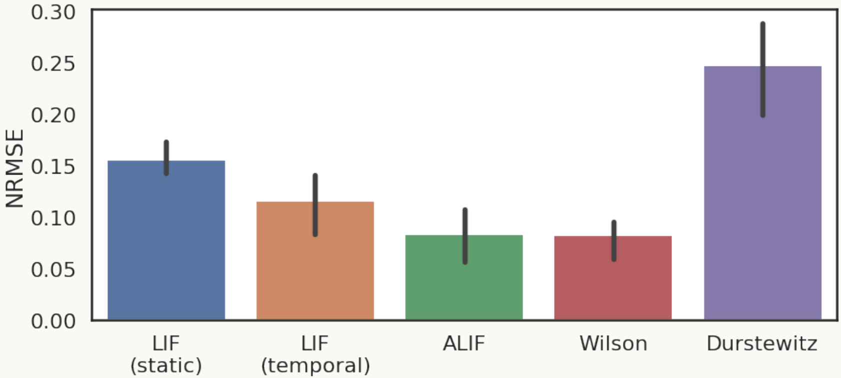


Figure: Average performance across neuron models

Dynamical System: 2D Oscillator

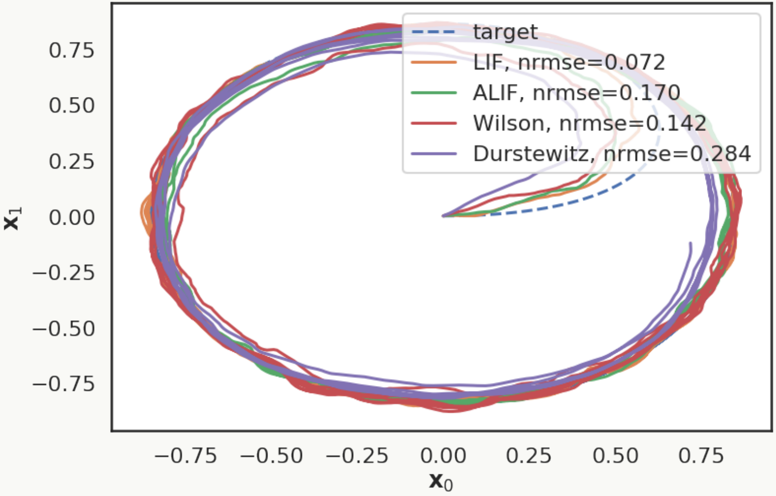


Figure: Implementing a two-dimensional oscillator using 200 recurrently-connected neurons

Dynamical System: Lorenz Attractor

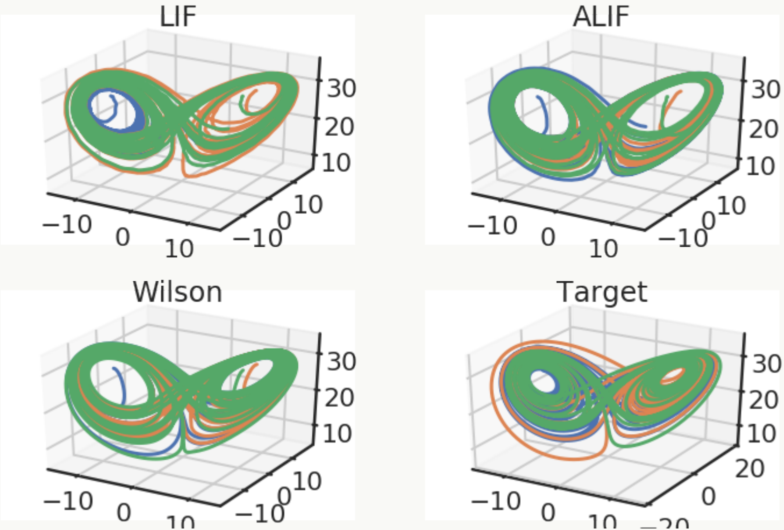


Figure: Implementing a three-dimensional chaotic attractor using 2000 recurrently-connected neurons

Future Work

Nengo Integration

- Online learning

Applications

- Harder dynamics
- Cognitive models
- Drug effects

Extensions

- Dale's principle
- Functional neuromodulation

Summary

Training α, β using $\mathbf{x}(t)$ distributes tuning curves of complex neurons

Training $\mathbf{d}$ using $\mathbf{x}(t)$ decodes activities of adaptive neurons

Training $h(t)$ using $\mathbf{x}(t)$ controls for cell dynamics in recurrent networks

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Thanks to

Aaron Voelker Terry Stewart Andreas Stöckel Chris Eliasmith

PART IV

`nengo-bio` hands-on