

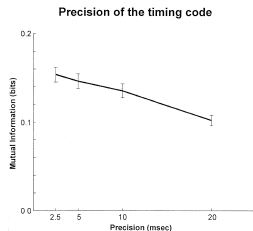
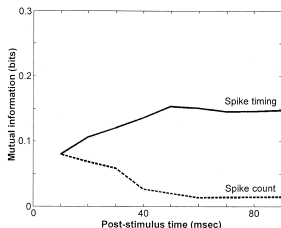
# Biologically plausible solutions for spiking networks with efficient coding

Veronika Koren, Stefano Panzeri (advisor)  
Department of Excellence for Neural Information Processing  
Center for Molecular Neurobiology  
University Medical Center Hamburg-Eppendorf, Hamburg, Germany



# A biologically plausible model of spiking neural dynamics developed from first principles

- Evolutionary pressure enforces efficient implementations of biological functions that are necessary for survival.
- Neural networks are very likely subjected to such pressure.
- Neural function stems from neural dynamics, with action potentials / spikes the elementary signals that underlie neural information processing.
- Methods of information theory suggest that information is transmitted with a time-dependent neural code [1-3].



[1] Panzeri et al., *Neuron* (2001), [2] Petersen et al., *Neuron* (2001) [3] Kayser, Logothetis, Panzeri, *PNAS* (2010)

Generalized leaky integrate-and-fire networks [1,2] with adaptation, refractoriness or dynamic threshold [3] accurately describe spiking dynamics of biological neural networks [4,5], at least with parameters fitted for a particular brain state.

- [1] Brunel, *J. Comp. Neurosci* (2000) [2] Renart et al., *Science* (2010) [3] Brette & Gerstner, *J. Neurophys.* (2005)  
[4] Jolivet, Lewis, Gerstner, *J. Neurophys.* (2004); [5] Jolivet et al., *J. Neuroscience* (2008)

Generalized leaky integrate-and-fire networks [1,2] with adaptation, refractoriness or dynamic threshold [3] accurately describe spiking dynamics of biological neural networks [4,5], at least with parameters fitted for a particular brain state.

[1] Brunel, *J. Comp. Neurosci* (2000) [2] Renart et al., *Science* (2010) [3] Brette & Gerstner, *J. Neurophys.* (2005)  
[4] Jolivet, Lewis, Gerstner, *J. Neurophys.* (2004); [5] Jolivet et al., *J. Neuroscience* (2008)

However,

- the neural function in these networks is not defined
- typically, unstructured connectivity is assumed, while in the brain, recent analyses of neural data suggest structured connectivity [6-10]
- unclear functional meaning of network parameters

[6] Ko et al., *Science* (2011, 2013) [7] Song et al., (2005) [8] Chettih and Harvey *Nat. Neurosci.* (2019) [9] Koren, Andrei, Hu, Dragoi, Obermayer *Cell reports* (2020)

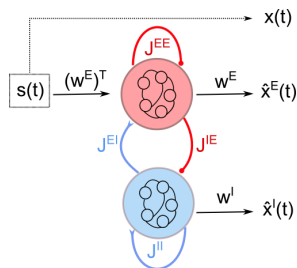
# Efficient coding (with spikes)

- Efficient coding: accurate representations of sensory stimuli with limited neural resources [1-2].
- This theory has been successful in describing classical and non-classical receptive fields in the primary visual cortex [3], among others.
- Recently, efficient coding theory has been extended to dynamical systems [4-5] and to spiking neural networks [5-9].
- However, previous implementations lack biological plausibility: Dale's law, E-I architecture, local currents, realistic time constants, state-dependent activity, etc...
- Our aim is to
  - **extend, generalize, adapt** the efficient coding theory so that it is fully consistent with biological networks
  - see to what extent we can **explain information processing** in biological networks

[1] Barlow [2] Bialek, Rieke, van Steveninck, Warland, *Advances in Neural Information Processing* (1989) [3] Olshausen and Field, *Nature* (1996) [4] Zhu & Rozell, *PLOS Comp. Bio.* (2013) [5] Boerlin, Machens, Denève, *PLOS Comp. Bio.* (2013) [6] Chalk, Gutkin, Deneve, *eLife* (2016) [7] Koren & Denève, *PLOS Comp. Bio.* (2017) [8] Buxo and Pillow, *PLOS Comp. Bio.* (2020) [9] Timcheck, Kadmon, Boahen, Ganguli, *PLOS Comp. Bio.* (2021)

## Build-in properties of the model (assumptions)

- 1 distributed (population) code
- 2 mixed selectivity of single neurons
- 3 efficient coding
- 4 Dale's law



Let us define the following variables

- high-dimensional time-dependent stimulus  $\vec{s}(t)$
- target representation  $\frac{d}{dt} \vec{x}(t) = A\vec{x}(t) + \vec{s}(t)$   
 $A$ : linear transformation between the stimulus and the target representation
- linear readout of spiking activity  $\vec{\hat{x}}_E(t)$  and  $\vec{\hat{x}}_I(t)$

# Build-in properties of the model: distributed code and mixed selectivity of single neurons

1) Distributed code is build-in by defining the readout as a sum of activity across neurons [1-2]:

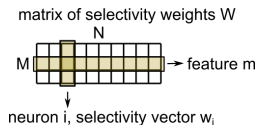
$$\frac{d\hat{x}_m^E(t)}{dt} = -\frac{1}{\tau_E}\hat{x}_m^E(t) + \sum_{i=1}^{N_E} w_{mi}^E f_i^E(t)$$

$$\frac{d\hat{x}_m^I(t)}{dt} = -\frac{1}{\tau_I}\hat{x}_m^I(t) + \sum_{i=1}^{N_I} w_{mi}^I f_i^I(t)$$

where  $f_i^y(t) = \sum_{\alpha} \delta(t - t_{i,\alpha}^y)$  is the spike train of neuron  $i$  of type  $y \in \{E, I\}$ .

2) Mixed selectivity of single neurons [3] is build-in by assigning to each neuron a selectivity vector

$$\vec{w}_i^y = [w_{1i}^y, \dots, w_{Mi}^y]^T$$



- [1] Boerlin, Machens, Deneve, *PLoS Comp. Bio.* 2013 [2] Koren & Panzeri, *Advances in Neural Information Processing Systems* (2022) [3] Fusi et al. *Curr. Opin. Neurobiol.* (2016) [4] Kasfahan et al. *Nat. Comm* (2021) [5] Kira, ..., Panzeri, Harvey et al. *Nat. Comm.* (2023)

# Build-in properties of the model: efficient coding with spikes

Efficient = **Accurate** and **with limited number of spikes**:

$$L^E(t) = \sum_{m=1}^M (x_m(t) - \hat{x}_m^E(t))^2 + \beta^E \sum_{i=1}^{N_E} (r_i^E(t))^2$$

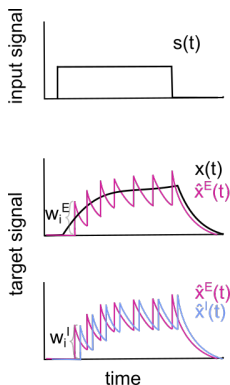
$$L^I(t) = \sum_{m=1}^M (\hat{x}_m^E(t) - \hat{x}_m^I(t))^2 + \beta^I \sum_{i=1}^{N_I} (r_i^I(t))^2$$

$$\frac{d}{dt} r_i^y(t) = -\frac{1}{\tau_r^y} r_i^y(t) + f_i^y(t)$$

We assume there will be a spike of a specific neuron only if this decreases the loss function.

$$L_y(t^+ | [f_i^y(t^+) = 1] + \eta_i^y(t^+)) < L_y(t^- | [f_i^y(t^-) = 0]),$$

Error-corrective spiking:



[1] Koren & Schwalger, *CoSyNe* (2020) [2] Koren & Schwalger, *OCNS talk* (2020) [3] Koren & Panzeri, *Advances in Neural Information Processing Systems* (2022)



# Analytically derived model: generalized leaky integrate-and-fire

Subthreshold dynamics of single neurons:

$$\tau_E \dot{V}_i^E(t) = -V_i^E(t) + I_i^{\text{ff}}(t) + I_i^{EE}(t) + I_i^{EI}(t) + I_i^{\text{local } E}(t) + I_i^h(t),$$

$$\tau_I \dot{V}_i^I(t) = -V_i^I(t) + I_i^{IE}(t) + I_i^{II}(t) + I_i^{\text{local } I}(t),$$

with fire-and-reset rule:

$$\text{if } V_i^y(t^-) \geq \vartheta_i^y(t^-) \rightarrow V_i^y(t^+) = V_i^{\text{reset } y},$$

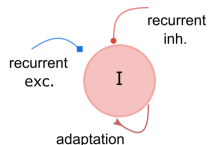
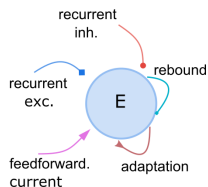
firing threshold:

$$\vartheta_i^y(t) = \frac{1}{2}(\mu_y + \|\vec{w}_i^y\|_2^2) + \sigma_i^y \xi_i^y(t), \quad y \in \{E, I\},$$

and reset potential:

$$V_i^{\text{reset } E} = -\frac{1}{2}(\beta^E - \|\vec{w}_i^E\|_2^2)$$

$$V_i^{\text{reset } I} = -\frac{1}{2}(\beta^I + \|\vec{w}_i^I\|_2^2).$$



[1] Koren & Panzeri, *Advances in Neural Information Processing Systems* (2022) [2] Koren & Panzeri, *DGKN kongress* (2023)

# Feedforward and synaptic currents

Feedforward current:

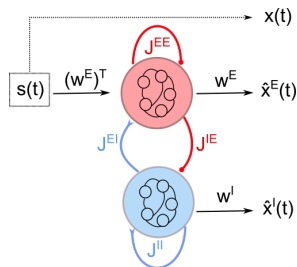
$$I_i^{\text{ff}}(t) = \tau_E \sum_{m=1}^M w_{mi}^E s_m(t).$$

Assuming network computation is leaky integration of the stimulus,  
 $\frac{d}{dt} \vec{x}(t) = -\frac{1}{\tau_E} \vec{x}(t) + \vec{s}(t)$  we get [E-to-I, I-to-I, I-to-E] synaptic currents (no E-E connections):

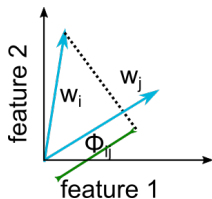
$$I_i^{IE}(t) = -\tau_I \sum_{j=1}^{N_E} J_{ij}^{IE} f_j^E(t),$$

$$I_i^{II}(t) = -\tau_I \sum_{\substack{j=1 \\ j \neq i}}^{N_I} J_{ij}^{II} f_j^I(t),$$

$$I_i^{EI}(t) = -\tau_E \sum_{j=1}^{N_I} J_{ij}^{EI} f_j^I(t),$$



# Analytically derived properties of the model: structured connectivity



Similarity of vectors:

From analytical derivation of the loss functions, we get that the connectivity is determined by the similarity of selectivity vectors:

$$J_{ij}^{\text{post pre}} = (\vec{w}_i^{\text{pre}})^T \vec{w}_j^{\text{post}}$$

We use random weights  $w_{mi}^y \sim \mathcal{N}(0, \sigma_w^y)$  and enforce Dale's law by removing connections between neurons with different selectivity, justified also by empirical studies [1-2]:

$$J_{ij}^{\text{post pre}} = \begin{cases} (\vec{w}_i^{\text{pre}})^T \vec{w}_j^{\text{post}}, & \text{if } (\vec{w}_i^{\text{pre}})^T \vec{w}_j^{\text{post}} > 0 \\ 0 & \text{otherwise} \end{cases}$$

[1] Ko et al. *Nature* (2011), [2] Koren, Andrei, Hu, Dragoi, Obermayer, *Cell reports* (2020)

## Structural property of the model: spike-triggered local current (not build-in)

- Spike-triggered adaptation [1] arises if we assume that the time constant of the population readout  $\vec{x}_E(t)$  ( $\vec{x}_I(t)$ ) is faster than the single neuron readout  $r_i^E(t)$  ( $r_i^I(t)$ )
- If the opposite is true, we get spike-triggered facilitation

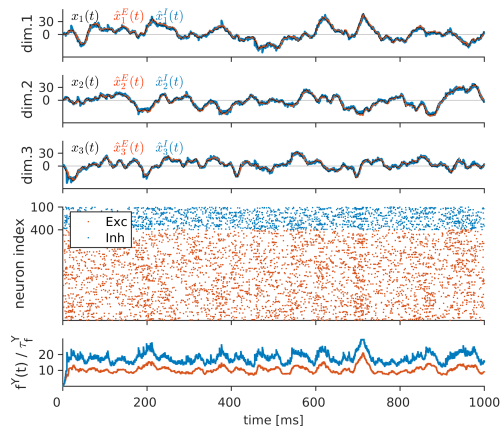
$$I_i^{\text{local } y}(t) = -\beta^y \left( 1 - \frac{\tau_y}{\tau_i^{r,y}} \right) r_i^y(t), \quad y \in \{E, I\},$$

- The theory also predicts this biologically plausible relation of membrane time constants:  $\tau^E \geq \tau^I$

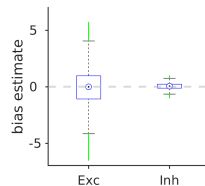
[1] Mensi et al., *J. Neurophys.* (2012)

# Coding property of the leaky integrator: unbiased estimator

Simulation of 400 E and 100 I neurons encoding 3 input variables, with every  $s_m(t)$  an Ornstein-Uhlenbeck processes, independent across dimensions.



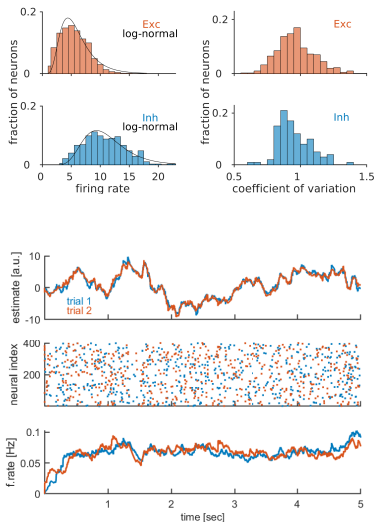
Distribution of time-dependent bias between target signal and estimate:



# Dynamical property of the leaky integrator: firing rates and variability

- firing rates are in physiological ranges
- log-normal distribution of firing rates across neurons [1]
- coefficient of variation (single neuron variability) around 1

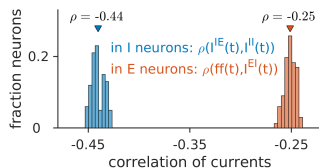
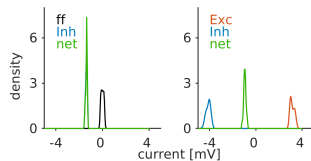
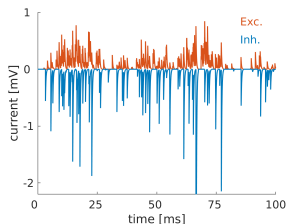
Strong trial-to-trial variability of single neurons, but nearly identical population readout across trials [2] → stable perception.



[1] Koren, Blanco-Malerba, Panzeri, Schwalger, *in prep.* [2] Koren and Denève, *PLOS Comp. Bio.* (2017)

# Dynamical property of the leaky integrator: E-I balance

- average E-I balance
- time-dependent E-I balance



# State-dependent activity of the leaky integrator

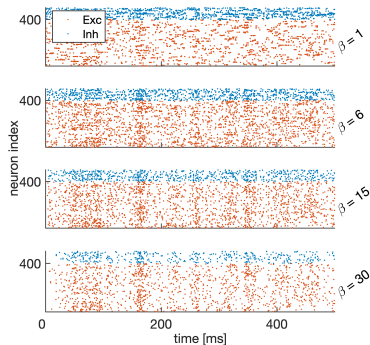
## The model

- displays state-dependent activity as a function of the metabolic constant  $\beta^y$
- but does not go into regimes with unphysiological firing rates as in previous works on efficient coding [1-2]

## Loss functions:

$$L^E(t) = \sum_{m=1}^M (x_m(t) - \hat{x}_m^E(t))^2 + \beta^E \sum_{i=1}^{N_E} (r_i^E(t))^2$$

$$L^I(t) = \sum_{m=1}^M (\hat{x}_m^E(t) - \hat{x}_m^I(t))^2 + \beta^I \sum_{i=1}^{N_I} (r_i^I(t))^2$$



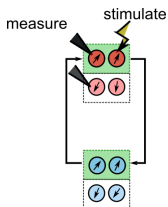
[1] Boerlin, Machens, Denève, *PLOS Comp.Bio.* (2013) [2] Koren & Denève, *PLOS Comp.Bio.* (2017)



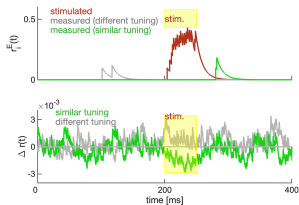
# Dynamical consequence of structured E-I connectivity: Lateral inhibition between E neurons with similar selectivity.

In a network without feedforward input,

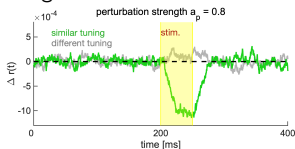
- stimulate a single E neuron
- measure the change in firing rate in other (E) neurons [1].



Effect of perturbation in single trial:



averaged across trials:



[1] Chettih & Harvey *Nat. Neurosci* (2019) [perturbation study in V1]

## Assuming a general linear transformation defines E-E connectivity

We now assume a general linear transformation between the stimulus and target representation:

$$\frac{d}{dt} \vec{x}(t) = A\vec{x}(t) + \vec{s}(t).$$

We write the matrix  $A$  as:

$$A = B - \tau_E^{-1} \mathbf{I}^{M \times M}$$

and  $\tau_E^{-1} \mathbf{I}^{M \times M}$  defines the leak current in E neurons, while  $B$  defines recurrent E-E connectivity:

$$J_{ij}^{EE} = \begin{cases} (\vec{w}_i^E)^\top B \vec{w}_j^E, & \text{if } (\vec{w}_i^E)^\top \vec{w}_j^E > 0, \\ 0, & \text{otherwise.} \end{cases} \quad B \text{ positive semi-def.,}$$

[1] Koren & Panzeri, *Advances in Neural Information Processing Systems* (2022)

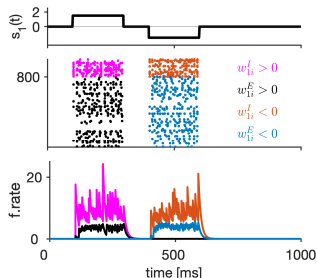
# The matrix B and the E-E connectivity

To observe the property of positive semi-definiteness, we write  $B$  as follows:

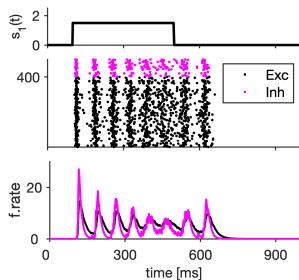
$$B = a\Gamma\Gamma^T, \quad \Gamma = [\vec{b}_1, \dots, \vec{b}_{M'}], \quad a > 0, \quad M' \leq M$$

- To have  $\text{rank}(B) = 1$ ;  $\Gamma = \vec{b}_1$ ,  $B = ab_1\vec{b}_1^T$
- To have  $1 < \text{rank}(B) \leq M$ ,  $\Gamma = [\vec{b}_1, \dots, \vec{b}_{M'}]$ ;  $\vec{b}_1, \vec{b}_2, \dots, \vec{b}_{M'}$  linearly independent

$A = \tau_E^{-1} \mathbf{I}^{M \times M}$ ,  $B = 0$   
 (no E-E connections, feedforward-driven):

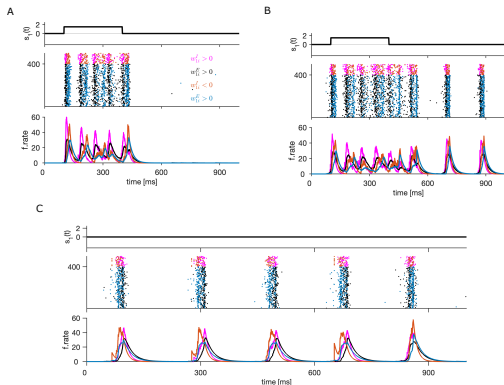


$\text{rank}(B) = 1$ :



## Assuming more complex computations: $\text{rank}(B) > 1$

...distributes the representation across all neurons in the network: also neurons that are not driven by the feedforward current participate in network's response.



**A.** Network simulation with weak noise at spike generation. **B.** Network simulation with stronger noise at spike generation. **C.** Same as in **B**, but without the external stimulus. Network shows spontaneous Up and Down states.

- Optimal solution of a quadratic loss between low-dimensional target and estimated signals with quadratic metabolic cost is a generalized leaky integrate and fire model.
- Lateral inhibition is the core mechanism of efficient coding, implemented through structured connectivity between E and I populations.
- Network's computation is reflected in the structure of the connectivity.
- The model shows a number of structural, dynamical and coding properties of biological networks.

# Summary

- Optimal solution of a quadratic loss between low-dimensional target and estimated signals with quadratic metabolic cost is a generalized leaky integrate and fire model.
- Lateral inhibition is the core mechanism of efficient coding, implemented through structured connectivity between E and I populations.
- Network's computation is reflected in the structure of the connectivity.
- The model shows a number of structural, dynamical and coding properties of biological networks.

## Coding properties:

- efficient coding
- distributed population code
- mixed selectivity of single neurons
- encoding of high-dimensional stimuli

## Structural properties:

- local current (adaptation)
- structured recurrent connectivity
- network's computation determines the complexity of E-E synaptic interactions

## Dynamical properties:

- firing rates in physiological ranges
- strong trial-to-trial variability
- average and time-dependent E-I balance
- state-dependent dynamics; Up and Down states

# Thank you for your attention.

Big thanks to Stefano Panzeri and Sophie Denève!

- collaborators
  - Alan J. Emanuel (Emory University)
  - Tilo Schwalger (Technische Universität Berlin)
- providing extensive feedback / discussion
  - Tatiana Engel (Princeton)
  - Nicolas Brunel
  - Benjamin Lindner (Humboldt University, Berlin)
  - Klaus Obermayer (Technische Universität Berlin)

For more details, please see

Koren & Panzeri, Biologically plausible solutions for spiking networks with efficient coding, *Advances in Neural Information Processing Systems* (2022)

Koren, Bondanelli, Panzeri, Computational methods to study information processing in neural circuits, *Computational and Structural Biology Journal* (2023)