An Efficient Multilayer Spiking Network as a Model of Ascending Pathways

Veronika Koren[1], Alan J. Emanuel[2], Stefano Panzeri [1]

[1]University Medical Center Hamburg-Eppendorf (UKE), Germany; [2]Emory University School of Medicine, Atlanta, USA

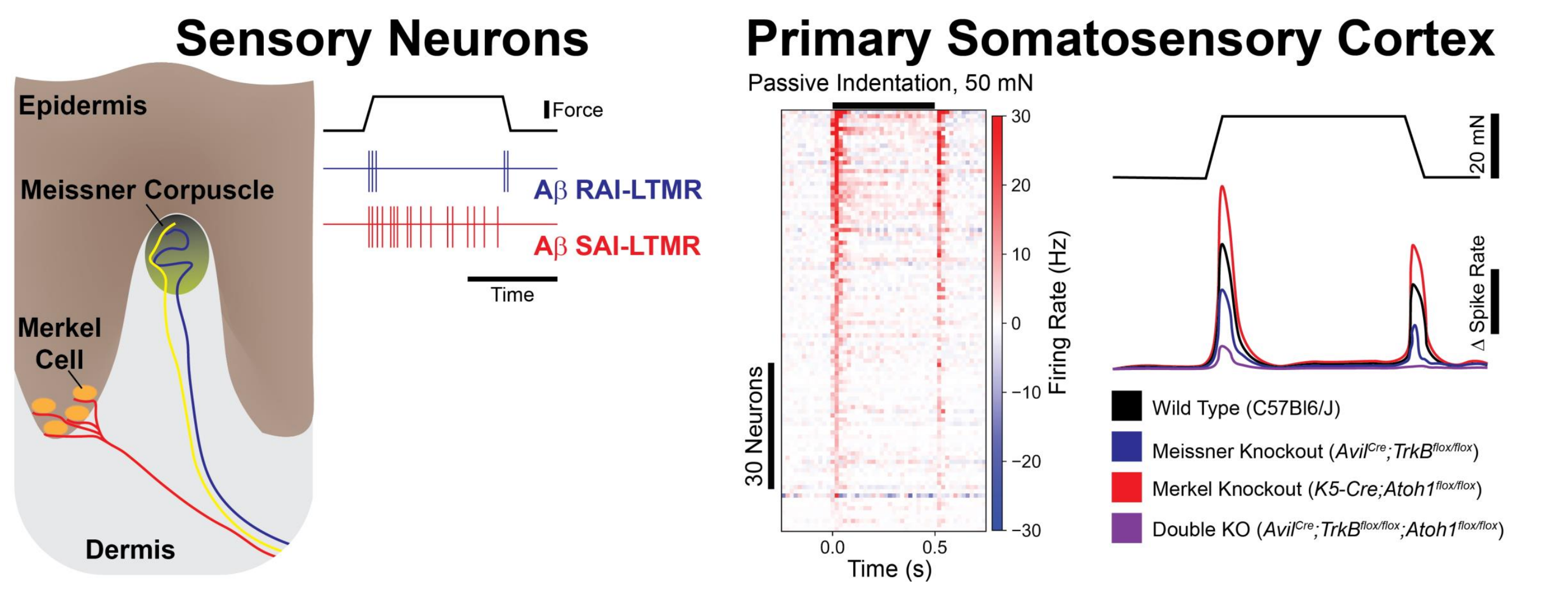
Introduction

A large part of mammalian brains is dedicated to sensory processing. Sensory receptors extract distinct but partly correlated features of the environment that vary at different timescales [1], and then transmit them through subcortical structures and a succession of recurrently connected cortical areas. **A general theory on how sensory pathways encode, propagate, and transform sensory features is still missing.**

Objectives:

- Extend efficient coding theory [2-4] to capture an ascending sensory pathway.
- Computational objectives: formulate efficient encoding, transformation and transmission of sensory features across brain areas.
- Modelling objectives: reproduce empirically observed properties of the somatosensory (SOM) system of the mouse in response to simple stimuli.

Empirical observations in the SOM system of the mouse:



Theoretical assumptions

We conceptualize brain areas as processing layers.

- Layer n=(0) [sensory receptors]: efficiency objective for each neuron i of type m is:

$$\mathrm{E}_{mi}^{(0)}(t) = \left(x_m^{(0)}(t) - \hat{x}_{mi}^{(0)}(t)\right)^2 + \beta_m^{(0)}\left(r_{mi}^{(0)}(t)\right)^2, \qquad m = 1,\dots,M,\ M \geq 2, \tag{1}$$

with $\hat{x}_{mi}$ the linear readout of neuron's activity, r_{mi} the neuron's low-pass filtered spike train and $x_m(t)$ the target for all neurons of type m, integrating the stimulus feature s_m:

$$\frac{d}{dt}x_m^{(0)} = -\frac{1}{\tau_m^{(0)}}x_m^{(0)} + s_m(t). \tag{2}$$

- Layers n=(1),(2),…,(n): efficiency objective for the population y:

$$\mathrm{E}_y^{(n)}(t) = \left\|\boldsymbol{x}^{(n)}(t) - \hat{\boldsymbol{x}}_y^{(n)}(t)\right\|^2 + \beta_y^{(n)}\sum_{i=1}^{N_y^{(n)}}(r_{yi}^{(n)}(t))^2, \qquad y \in \{E, I\},\ \beta_y^{(n)} > 0, \tag{3}$$

with $\boldsymbol{x}(t)$ the target, $\hat{\boldsymbol{x}}_y$ the linear readout of population y and r_{yi} the low-pas filtered spike train of neuron i.

- Target in subcortical areas is:

$$\frac{d}{dt}\boldsymbol{x}^{(n)}(t) = -\Lambda^{(n)}\boldsymbol{x}^{(n)}(t) + \hat{\boldsymbol{x}}_E^{(n-1)}(t), \tag{4}$$

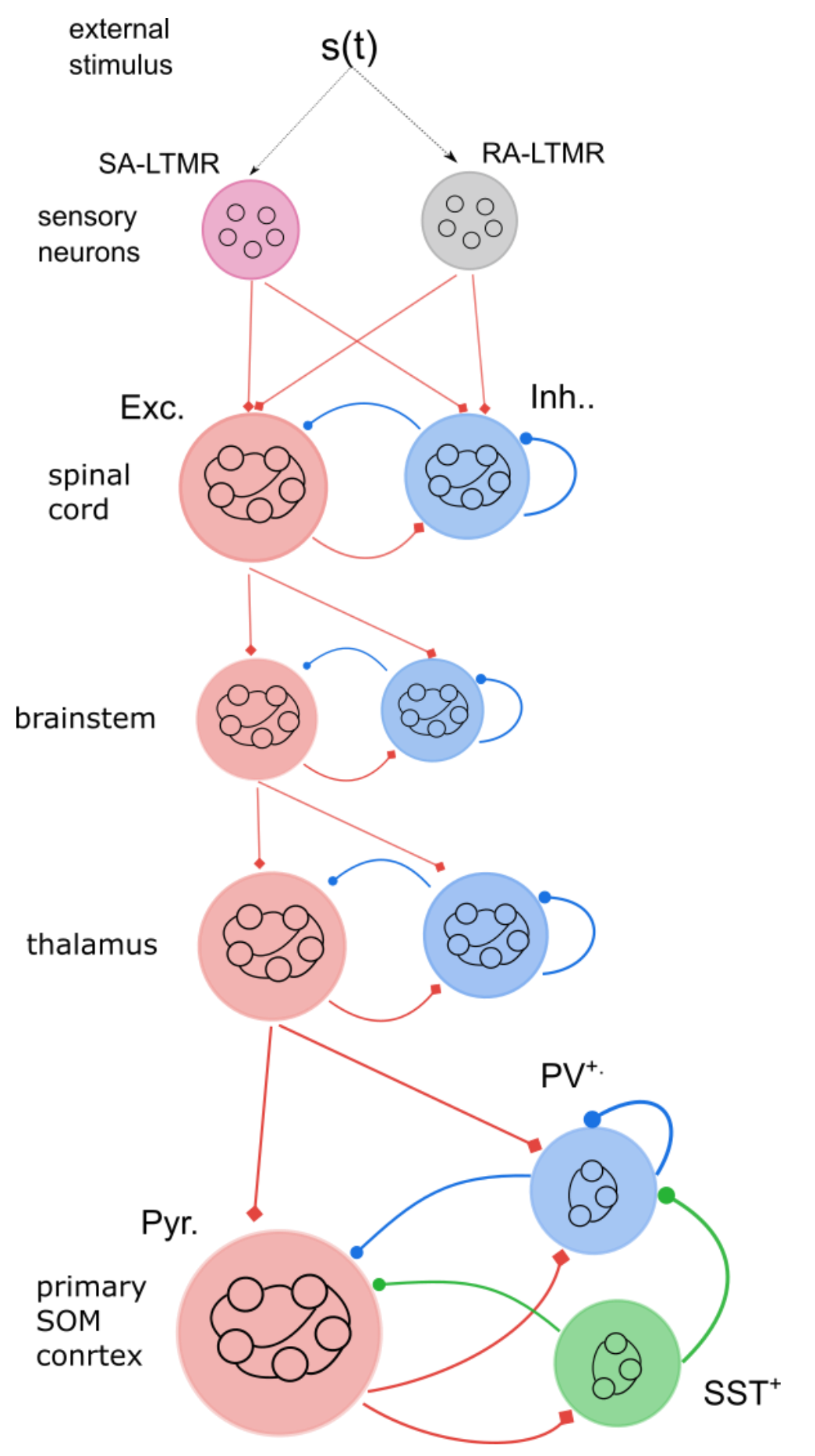
with Λ a diagonal M-by-M matrix with diagonal elements $\Lambda_{ii} = \tau^{-1}$.

- Target in the primary somatosensory cortex (S1) is:

$$\frac{d}{dt}\boldsymbol{x}^{(n)}(t) = A^{(n)}\boldsymbol{x}^{(n)}(t) + \hat{\boldsymbol{x}}_E^{(n-1)}(t), \tag{5}$$

with $A = -\Lambda + A^{\mathrm{INT}}$ an M-by-M matrix and where A^{INT} determines the interaction across features.

Theoretical results: spiking network models



- Layer 0: feedforward networks of unconnected spiking neurons

$$\frac{d}{dt}V_{mi}^{(0)} = -\frac{1}{\tau_m^{(0)}}V_{mi}^{(0)} + \omega_{mi}^{(0)}s_m^{(0)}(t) - \beta_m^{(0)}\left(\frac{1}{\tau_m^{(0)}} - \frac{1}{\tau_r^{(0)}}\right)r_{mi}^{(0)}(t) + \sigma_m^{(0)}\eta_{mi}^{(0)}(t), \qquad \tau_r^{(0)} > \tau_m^{(0)}, \tag{6}$$

with fire-and-reset rule: $V_{mi}^{(0)}(t^-) \geq \vartheta_{mi}^{(0)}(t^-) \rightarrow V_{mi}^{(0)}(t^+) = V_{mi}^{\mathrm{reset}}$.

- All other layers: recurrently connected E-I spiking networks

$$\frac{d}{dt}V_{yi}^{(n)}(t) = -\frac{1}{\tau_y^{(n)}}V_{yi}^{(n)} + \frac{1}{C_m}\left(I_{yi}^{\mathrm{FF},(n)}(t) + I_{yi}^{\mathrm{REC},(n)}(t) + I_{yi}^{\mathrm{ad},(n)}(t)\right) + \sigma_y^{(n)}\eta_{yi}^{(n)}(t), \tag{7}$$

with C_m the capacitance of the neural membrane and with a fire-and-reset rule as in sensory neurons.

- Feedforward and most recurrent connectivity is like-to-like:

$$J_{ij}^{yx} = \begin{cases}(\mathbf{d}_i^y)^\top\mathbf{d}_j^x & \text{if } (\mathbf{d}_i^y)^\top\mathbf{d}_j^x > 0\\ 0 & \text{otherwise}\end{cases} \tag{8a}$$

with $\mathbf{d}_i^y$ a vector of decoding weights of neuron i of type y.

- Inh. connection from PV onto Pyr. in S1 contains feature interaction:

$$J_{ij}^{\mathrm{Pyr\ PV}} = \left[(\mathbf{d}_i^{\mathrm{Pyr}})^\top A^{\mathrm{INT}}\mathbf{d}_j^{\mathrm{PV}}\right]_+, \tag{8b}$$

with $[a]_+ \equiv \max(0, a)$ a rectified linear function, required to enforce Dale's law.

- Inhibitory connection from SST onto Pyr. in S1 is like-antilike:

$$J_{ij}^{\mathrm{Pyr\ SST}} = \begin{cases}\left|(\mathbf{d}_i^{\mathrm{Pyr}})^\top\mathbf{d}_j^{\mathrm{SST}}\right| & \text{if } (\mathbf{d}_i^{\mathrm{Pyr}})^\top\mathbf{d}_j^{\mathrm{SST}} < 0\\ 0 & \text{otherwise.}\end{cases} \tag{8c}$$

Model of the SOM system in the mouse

1) We simulate all brain areas involved in processing of fine touch in the mouse SOM system.
   - Two types of sensory neurons: slowly-adapting and rapidly adapting low threshold mechanoreceptors (SA-LTMRs and RA-LTMRs)
   - Dorsal Horn of the spinal cord
   - Cuneate Nucleus of the Brainstem
   - Sensory Thalamus
   - Primary Somatosensory Cortex (S1)
2) Model includes presynaptic inhibition, direct and indirect pathway and feedback connections from S1 onto thalamus as observed empirically [1].
3) We use efficient neuron model as in Eqs. 6-7.
4) Connectivity is constructed following Eqs. 8.
5) Other parameters are taken from the empirical literature [1,5,6].

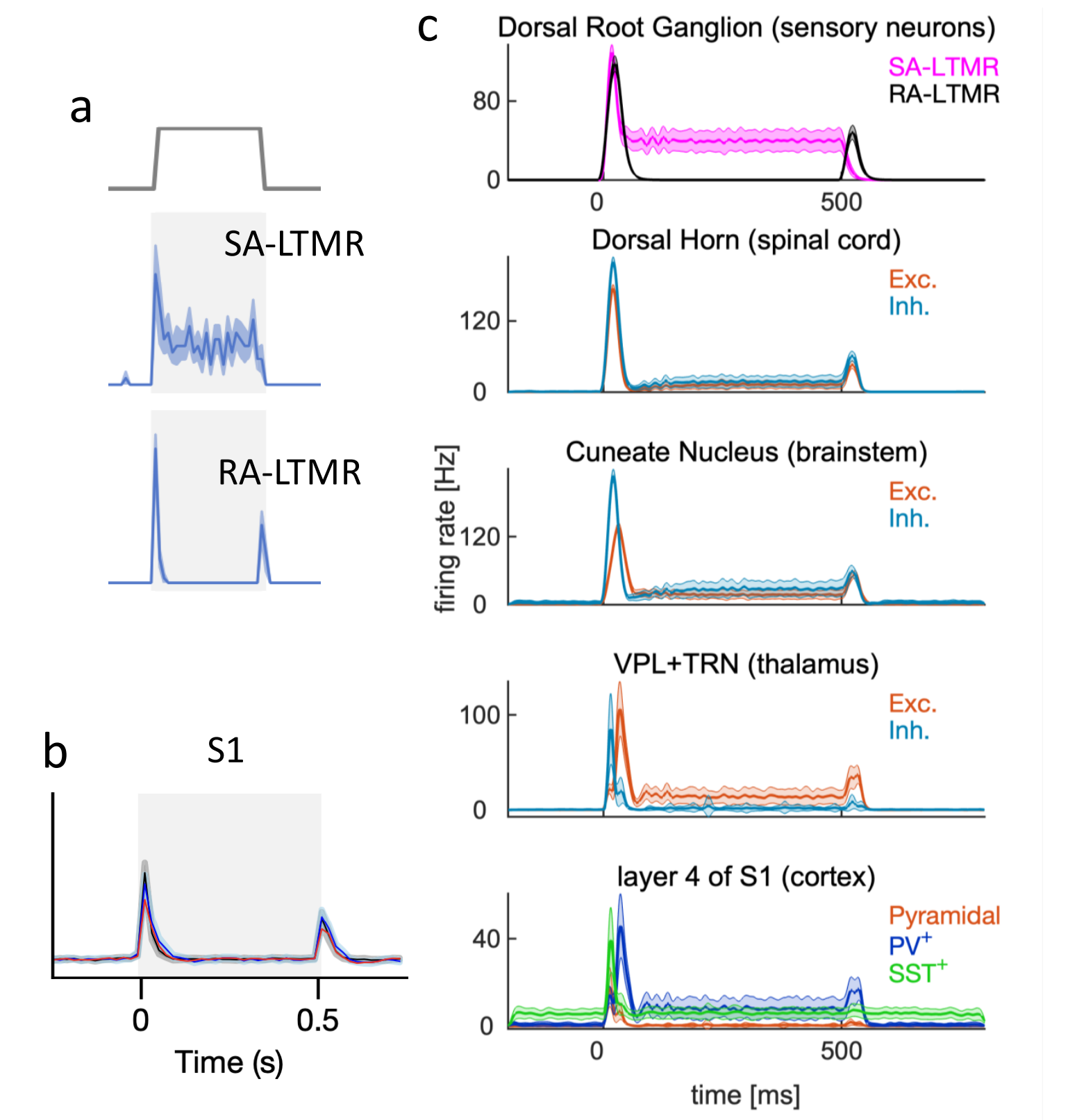


Figure 1 a-b) Empirically observed response of sensory neurons (a) and Pyr. neurons in S1 (b) to the step stimulus, from[5]. c) Trial-averaged model activity capturing the SOM pathway in response to a step stimulus. We used 30 simulation trials.

Propagation of minimal perturbation across the pathway

- To assess the propagation of weak signals across the pathway, we measure the number of spikes evoked by a single spike of a sensory neuron in downstream areas.
- Between sensory periphery and S1, neural signals are amplified, as observed empirically [5], because of efficient transmission of spikes together with the increase in network sizes.

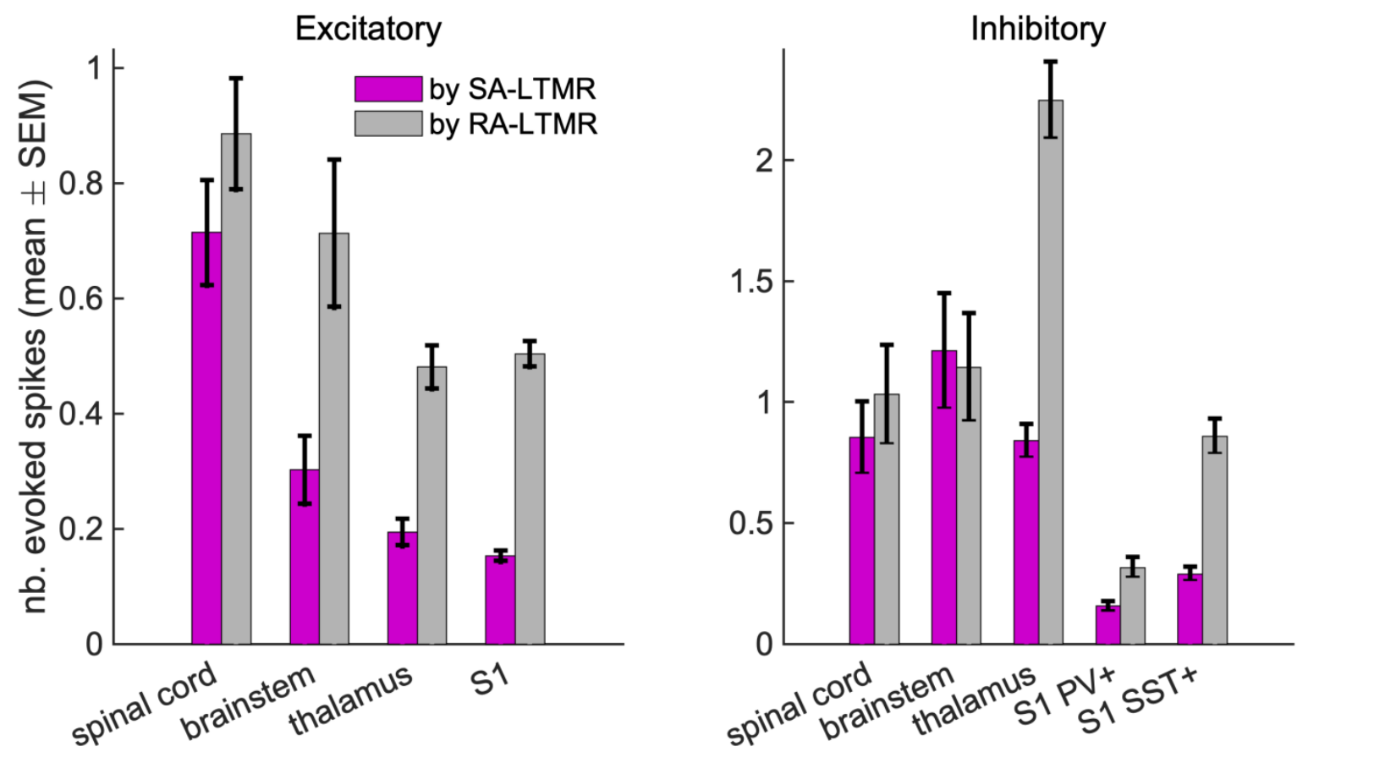


Figure 2 Number of evoked spikes **per neuron** in response to one spike of a sensory neuron for each brain area along the SOM pathway. We used 100 simulation trials. Bars indicate the mean and errorbars indicate S.E.M.

Activity profiles with knock-out of mechanoreceptors

- In Pyramidal neurons of S1, knock-out of SA-LTMRs provokes an increase in sensitivity, while the knock-out of RA-LTMRs provokes a decrease [5].
- Reproduced (Fig. 3) if model's computation is an **asymmetric negative interaction across features**.
- We found that, while Pyramidal and SST neurons increase the sensitivity with the knock-out of SA-LTMRs, PV neurons always decrease the sensitivity.

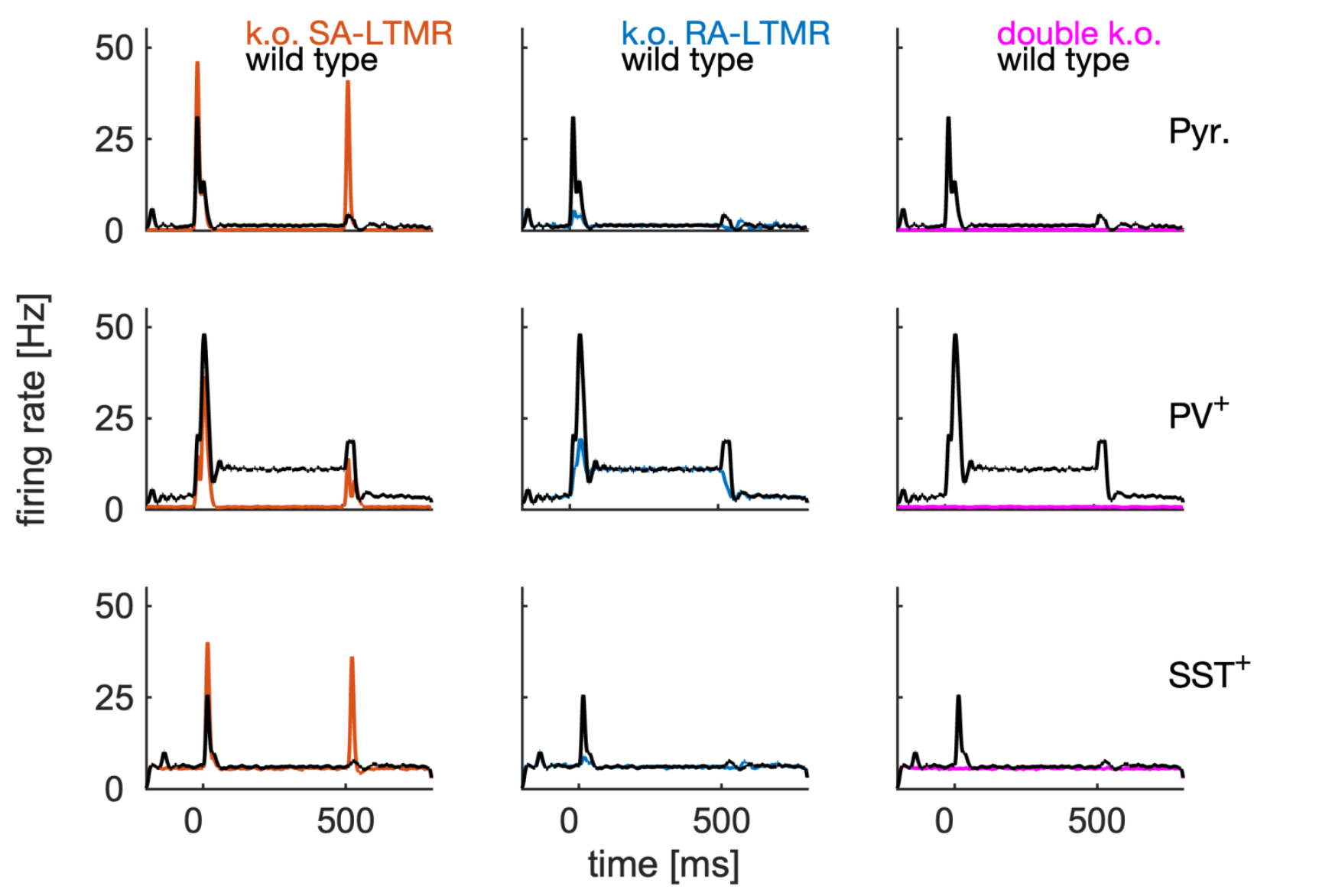


Figure 3 Activity profiles of Pyramidal (top), PV⁺ (middle) and SST⁺ (bottom) neurons comparing the knock-out of the SA-LTMRs (red), RA-LTMRs (bue) and double knock-out (magenta) with the response in the wild type (black). We used 50 simulation trials.

Mechanism of sensitivity alterations with knock-out

Reproducing differential sensitivity changes as on Fig. 3 required: sufficiently strong and dense PV-driven inhibition, sufficiently weak SST-driven inhibition, synaptic delay Pyramidal-PV of about 1.5 ms and connection probability of feedforward synapses to Pyramidal and PV neurons of about 0.5 (all Fig. 4).

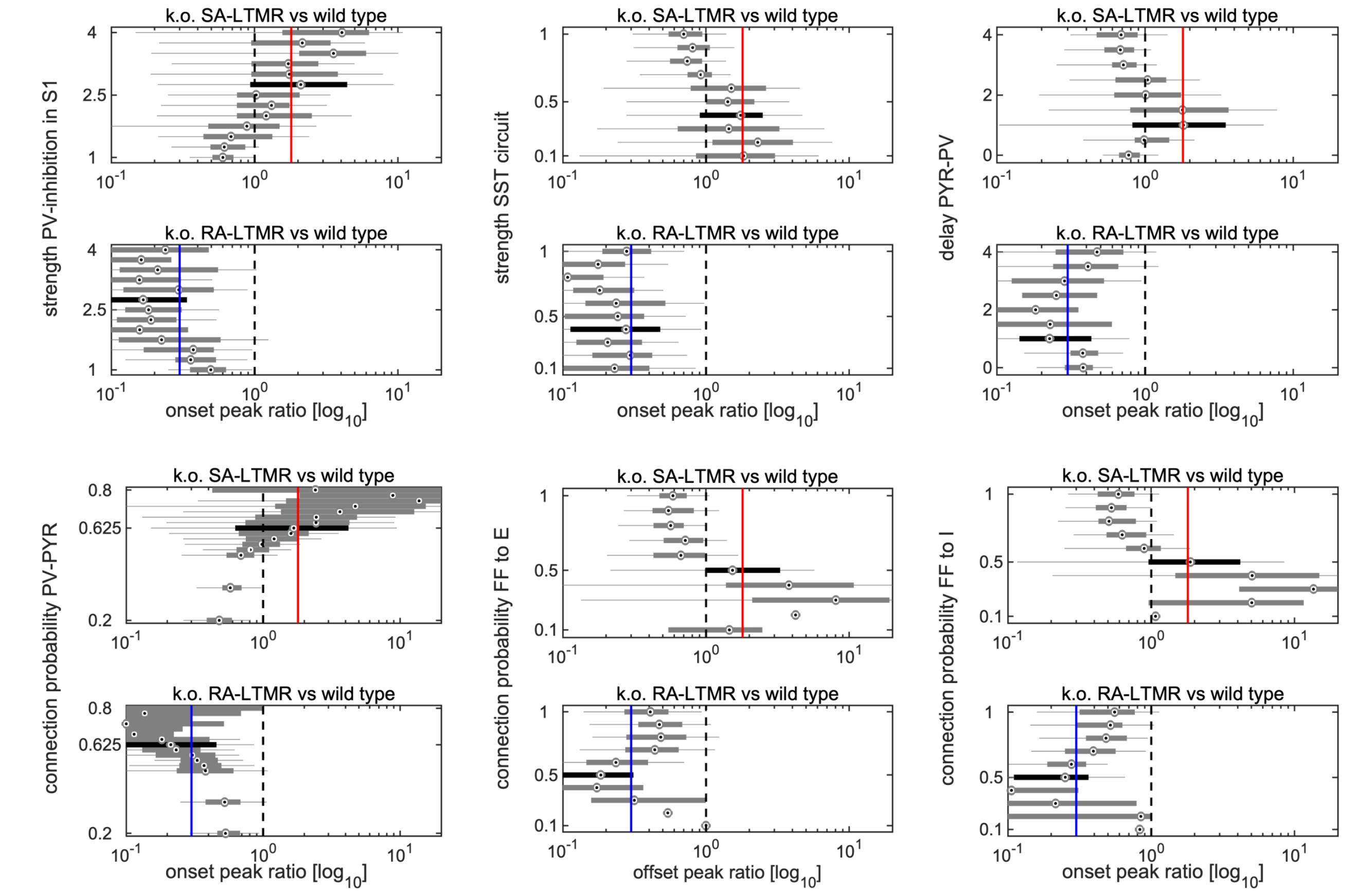


Figure 4 Ratio of the onset peak comparing the knock-out with the wild type, as a function of relevant model parameters. The peak ratio is on the logarithmic scale while the parameter grid is on a linear scale. All results are computed using 50 simulation trials for each tested parameter. Red and blue line mark the observed peak ratios [5] with the knock-out of SA- and RA-LTMRs, respectively.

Conclusions

- Empirically observed properties of the somatosensory system can be reproduced with a model of efficient processing of sensory features.
- A computation relevant to the SOM system is a negative feature interaction, creating a temporal contrast across features (prediction).
- A plausible implementation thereof is a strong inhibition of SA-LTMR driven feature by the RA-LTMR driven feature in PV-Pyr connectivity in S1 (prediction).

References: [1] Abraira & Ginty (2013), *Neuron* [2] Deneve & Machens (2016), *Nat. Neurosci.* [3] Koren & Panzeri (2022), *NeurIPS* [4] Koren, Blanco Malerba, Schwalger, Panzeri (2024), *eLife* [5] Emanuel, Lehnert, Panzeri, Harvey, Ginty (2021), *Nature* [6] Tureck, Lehnert, Ginty (2022), *Nature* [7] Koren, Emanuel, Panzeri (2024), *Biorxiv*