



ETH AI CENTER  
INSTITUTE OF NEUROINFORMATICS

NEURAL LEARNING AND INTELLIGENT SYSTEMS LAB

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# Spiking Neural Network model of cortical Layer 5

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**Author:**  
Incicau Daniel Cosmin

**Supervisor:**  
Prof. Dr. Benjamin Grewe  
Anh Duong Vo

29 January 2023

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# 1 Introduction

The neocortex is the largest and most highly developed part of the brain. It is responsible for many of the highest cognitive functions in mammals, including perception, cognition, and consciousness. In humans, the neocortex is responsible for many advanced abilities such as speech, abstract thinking, and problem-solving. It is structured into six horizontal layers, numbered 1 – 6 from the outermost to the innermost. Each of the layers has specific functions and connections with other areas of the brain. Additionally, the neocortex is also divided into functional regions, such as the motor cortex, somatosensory cortex, visual cortex, and auditory cortex.

Selectivity of neurons is an important mechanism through which the nervous system processes and interprets sensory information and selectively filters out irrelevant information. In the scope of this project, I have explored the selectivity of the visual cortex and how different types of connections affect it. Niell and Stryker 2008 has shown that the mouse visual cortex neurons are highly selective and that they respond preferentially to specific types of stimuli. Building upon that, Kim et al. 2015 has revealed there are three types of neurons in Layer 5 of the visual cortex of mice, each of which plays distinct roles.

Here I propose a microcircuit model of Layer 5 of the primary visual cortex. I used a spiking neural network based on experimentally measured connectivity (Campagnola et al. 2022). The model, which is summarized in Figure 1, consists of four neuron populations with different connection patterns. On the one hand there are excitatory pyramidal cells: Cortico-Cortical (CC) and Cortico-Subcortical (CS) neurons. On the other hand there are inhibitory cells: Somatostatin-expressing (SST) and Parvalbumin-expressing (PV) interneurons. I proceeded to analyse relevant metrics obtained from simulation runs of the network. Because I am basing my model on the available literature, I expected to reproduce the orientation and direction selectivity results of previous experimental work (Kim et al. 2015). This served as a validation step for a well-implemented model. Furthermore, I investigated the influence of specific neuronal connection patterns on orientation and direction selectivity.

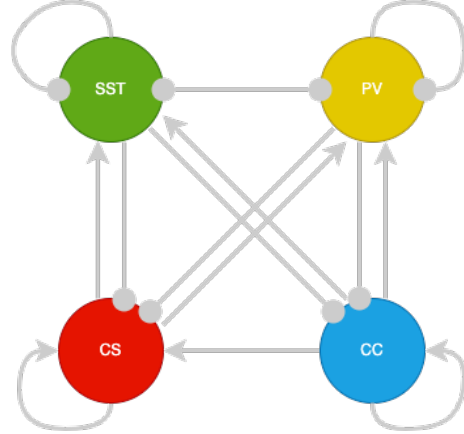
Overall, I developed a maintainable and robust codebase which can be used as a starting point for running various simulations. The model has multiple modes of operation along with a diverse range of parameters that allow customization. Moreover, it can easily be extended to adapt to future research questions.

## 2 Methods

### 2.1 Network

The network consisted of a total of 400 neurons grouped into 4 subpopulations of different types of excitatory or inhibitory neurons. Each simulation has 34 SST interneurons, 46 PV interneurons, 275 CC pyramidal cells and 45 CS pyramidal cells.

**Model.** Neurons were modelled as conductance-based spiking leaky-integrate and fire neurons. Governing equations of neurons are taken from Naud and Sprekeler 2018 with minor adjustments. Pyramidal cells (CC and CS) were modelled as having two compartments: somatic and dendritic.



**Figure 1:** Network model.

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(1) The somatic  $s$  compartment of pyramidal cells (CC and CS) is modeled as:

$$\begin{aligned} \frac{\partial}{\partial t} v_i^{(s)} &= \frac{E_L - v_i^{(s)}}{\tau_s} + \frac{g_s * f(v_i^{(d)}) + I_i^{(s)}}{C_s} \\ \frac{\partial}{\partial t} g_i^{E(s)} &= -\frac{g_i^{E(s)}}{\tau_E} & \frac{\partial}{\partial t} g_i^{I(s)} &= -\frac{g_i^{I(s)}}{\tau_I} \\ I_i^{(s)} &= g_i^{E(s)} * (E_E - v_i^{(s)}) + g_i^{I(s)} * (E_I - v_i^{(s)}) \end{aligned} \quad (1)$$

(2) The dendritic  $d$  compartment of pyramidal cells (CC and CS) is modeled as:

$$\begin{aligned} \frac{\partial}{\partial t} v_i^{(d)} &= \frac{E_L - v_i^{(d)}}{\tau_d} + \frac{g_d * f(v_i^{(d)}) + c_d * K(t - \hat{t}_i^{(s)}) + I_i^{(d)}}{C_d} \\ \frac{\partial}{\partial t} g_i^{E(d)} &= -\frac{g_i^{E(d)}}{\tau_E} & \frac{\partial}{\partial t} g_i^{I(d)} &= -\frac{g_i^{I(d)}}{\tau_I} \\ I_i^{(d)} &= g_i^{E(d)} * (E_E - v_i^{(d)}) + g_i^{I(d)} * (E_I - v_i^{(d)}) \end{aligned} \quad (2)$$

In equations (1) and (2), the active coupling between soma and dendrite is encapsulated by the terms  $g_s$  (propagates dendritic regenerative activity to the soma) and  $c_d$  (back-propagates somatic spikes to the dendrites) which communicate supra-threshold activity between compartments. Passive coupling (sub-threshold fluctuations) was assumed negligible. The regenerative dendritic activity is modeled by a nonlinear term controlled by  $g_d$ . The nonlinearity exists in both the soma and dendritic compartment and is modeled via a sigmoidal function  $f(x) = 1/(1 + \exp(-(x - E_d)/D_d))$  where  $E_d = -38mV$  controls the position of the threshold and  $D_d = 6mV$  the sharpness of the threshold. Additionally, backpropagating action potential is modeled by term  $K$  from equation (2), representing a simple rectangular kernel of amplitude one, which is delayed by  $0.5ms$  and lasts  $2ms$ .

All subsequent analysis was conducted using the two-compartment model, although the codebase also allows for simulations using only the soma compartment by switching simulation modes. More details about simulation modes can be found in Appendix C.

(3) Interneurons (SST and PV) are modelled as having only one compartment:

$$\begin{aligned} \frac{\partial}{\partial t} v_i^{(x)} &= \frac{E_L - v_i^{(x)}}{\tau_x} + \frac{I_i}{C_x} \\ \frac{\partial}{\partial t} g_i^E &= -\frac{g_i^E}{\tau_E} & \frac{\partial}{\partial t} g_i^I &= -\frac{g_i^I}{\tau_I} \\ I_i &= g_i^E * (E_E - v_i) + g_i^I * (E_I - v_i) \end{aligned} \quad (3)$$

The following variables are present in the above equations:  $v_i$  membrane potential of neuron  $i$ ,  $E_L$  leak reversal potential,  $E_E$  and  $E_I$  are the excitatory and inhibitory reversal potentials,  $C_x$  membrane capacitance,  $\tau$  time constant,  $I_i$  is the synaptic current received by each neuron  $i$ ,  $g_i^E$  and  $g_i^I$  are the leak excitatory and inhibitory conductances received by each neuron  $i$ . All curated model parameters can be found in Appendix A.

**Connectivity.** Neurons of different types  $N = (CC, CS, SST, PV)$  are connected via chemical synapses.

Connection probability  $P_{IJ}$  from population  $I$  to  $J$  where  $I, J \in N$  was chosen based on experimental findings from Campagnola et al. 2022.

The synaptic weights  $W_{IJ}$  were similarly chosen according to experimental findings from Campagnola et al. 2022. The weights determine how much the synaptic conductances  $g_j^E$  and  $g_j^I$  of neuron  $j$  increase or decrease upon a spike in neuron  $i$ .

All curated connection probabilities and synaptic weights can be found in Appendix A.

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**Inputs.** Each neuron received an independent Poisson distributed input with a rate of  $10Hz$  and a custom weight, applied to its associated excitatory neuron conductance, similar to receiving a synapse impulse. The custom weight was specific to each neuron and was characterizing a time-dependent visual stimulus.

The stimulus represents a moving bar described by a counter-phase sinusoidal grating, taken from the *Visual Stimuli* Chapter of *Theoretical Neuroscience* (Dayan and Abbott 2005). Stimulus is generated for different amplitudes of neuron subpopulations using an orientation degree. Later, in Subsection 2.2, I'll describe how selectivity is calculated by taking aggregating results from multiple simulations having inputs of different orientation degrees.

**Simulation.** All spiking simulations were done using the Brian 2 (v2.5.1) simulator (Stimberg et al. 2019), using a time step of  $0.1ms$ . Each simulation was run for  $10seconds$  before proceeding to analyse the results.

## 2.2 Metrics

Various metrics and concepts are used for the statistical description of neuronal spike trains. In this section. I'll briefly explain what each of them means and for more in details explanations, consult *Theoretical Neuroscience* (Dayan and Abbott 2005).

**Firing rate  $r$ .** For a neuron, the spike count rate is used to determine the firing rate. This is equal to counting the number of spikes  $n$  during a trial and dividing it by the duration of the trial  $\Delta T$ . It is measured in  $Hz$ . For a population of neurons, the average firing rate was calculated.

$$r = \frac{n}{\Delta T}$$

**Interspike intervals  $ISI$ .** Represents the time between subsequent spikes of a neuron or a group of neurons. ISIs are used to characterize the spiking patterns of neurons. The distribution for a homogenous Poisson spike train follows an exponential decay curve. Hence, the most likely interspike intervals are short and the longer ones have a probability that is exponentially lower for their duration.

**Spike autocorrelation function  $acf$ .** Represents the probability of finding a spike at time  $t + \Delta t$  knowing that there was a spike a time  $t$ . It is computed from the interspike intervals which are sorted by duration and grouped into bins. An example of an autocorrelation function can be seen in Figure 8.

**Burst train.** Represents a series of consecutive spikes of a specific neuron which have short interspike intervals between them. Different bursts are separated by a long interspike interval. The threshold between a short and a long interspike interval is determined by the minimum of the autocorrelation function.

**Burst length.** Represents the number of spikes in a burst train. Calculated by simply counting the spikes that are known to be in a burst train.

**Classic selectivity.** Quantifies the response preference (maximum response) of a neuron given two different stimuli. The response of a neuron is described by its firing rate.

$$Selectivity = \frac{|r(input1) - r(input2)|}{r(input1) + r(input2)}$$

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**Orientation selectivity.** Quantifies the response preference of a neuron to stimuli of a particular orientation but not to the orthogonal orientation. Simulations were conducted using inputs resembling a moving bar with different orientation angles ( $0$ ,  $90$ ,  $180$  and  $270$  degrees). The preferred input was the one in the direction provoking the highest firing rate. The preferred and orthogonal orientations were determined based on that, taking into account both directions of an orientation angle. Finally, the neuron response provoked by the stimuli was compared using the classic selectivity formula.

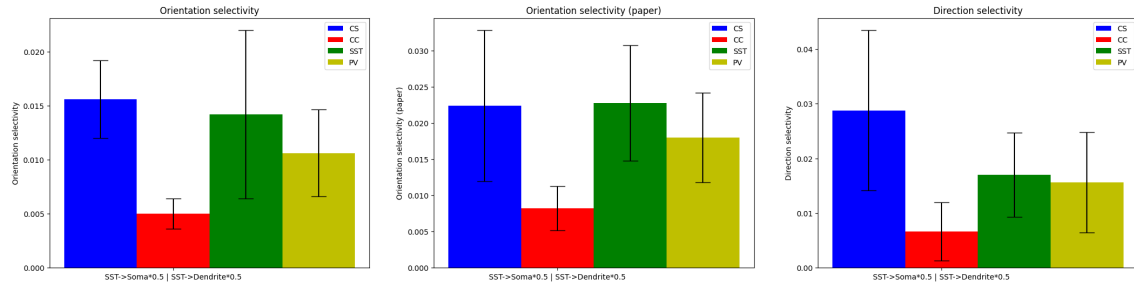
**Orientation selectivity (paper).** Quantifies the response preference of a neuron to stimuli of a particular orientation but not to the orthogonal orientation. Similar to orientation selectivity, instead of defining the preferred orientation as the stimuli in both directions of a preferred stimulus angle (e.g.  $0$  &  $180$  or  $90$  &  $270$ ), it is defined as just the stimulus in the preferred direction.

**Direction selectivity.** Quantifies the response preference of a neuron to stimuli of a particular direction but not to the opposite direction. Simulations were conducted using inputs resembling a moving bar with different orientation angles ( $0$ ,  $90$ ,  $180$  and  $270$  degrees). The preferred input was the one in the direction provoking the highest firing rate. The opposite stimulus was the one in the opposite direction. Finally, the neuron response provoked by the stimuli was compared using the classic selectivity formula.

### 3 Results

#### 3.1 Orientation and direction selectivity

A moving bar input stimuli of different orientations were applied as input to the neurons as described in the *Inputs* section of 2.1. With a weighted SST  $\rightarrow$  Soma/Dendrite connection of 0.5 (meaning that the connection probability from SST to CC or CS neurons was split half-half to their soma and dendrite) simulations were run to determine the orientation and direction selectivities of the four neuron populations.



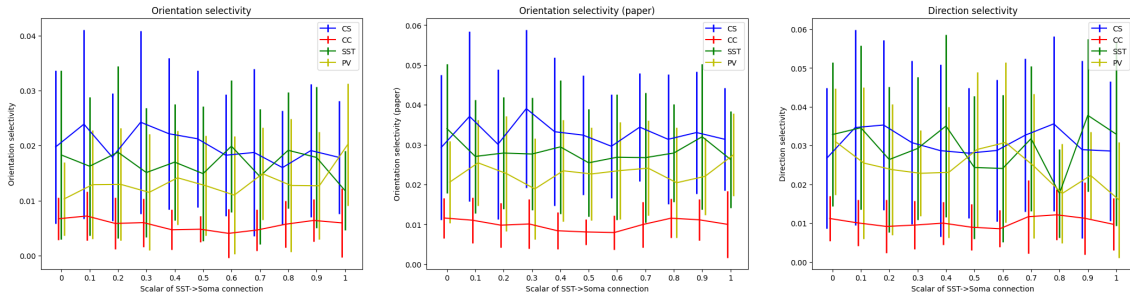
**Figure 2:** CS neurons are more direction selective.

Cortico-subcortical cells (CS) have been found to be more direction-selective than Cortico-Cortical cells (CC). This is in accordance with the experimental results from Kim et al. 2015. Although I have expected CC neurons to be more orientation selective, there were no results statistically significant to support it.

### 3.2 Connection patterns affect selectivity

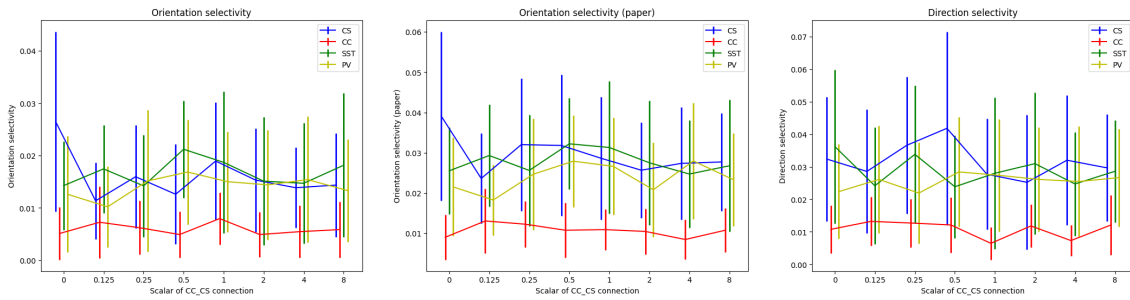
Connection patterns were found to affect the selectivity relations between neuron populations. I have explored two important connection patterns by running simulations with weighted connection probabilities.

**SST  $\rightarrow$  (CC/CS) Soma connection** The synaptic connection from the Somatostatin-expressing interneuron (SST) to the CC or CS neuron can be formed against either the Soma or the Dendrites of the pyramidal cells. The connection probability to the Soma was weighted with a scalar incrementally from 0 to 1, using increments of 0.1. The connection probability to the Dendrite was set to be complementary to the one for the Soma. Figure 3 shows the evolution of selectivity metrics for different populations of cells by adjusting this connection probability. A trend can be observed by increasing connection probability to the Soma compared to the Dendrite: both orientation and direction selectivities are increasing for the CS neurons, while they are decreasing for the CC neurons. Unfortunately, the relevance of the trends observed is diminished by high error rates in successive trials.



**Figure 3:** Selectivity of SST  $\rightarrow$  (CC/CS) Soma connection

**CC  $\rightarrow$  CS connection** The topology of the network in Layer 5 has a particularity: there are only connections from CC neurons to CS neurons and not the other way around. Adjusting the probability of the existing connection using a weight results in the scalar plot observed in Figure 4. Similarly, some trends can be observed, like the increase in direction selectivity for the CS neurons given an increase in the scalar. The trends are not conclusive due to the high error rates in successive trials.



**Figure 4:** Selectivity of CC  $\rightarrow$  CS connection



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## 4 Discussion

*How do connection patterns influence selectivity of neurons in cortical Layer 5?* This is the main objective I set when I started working on this project. To test that, I implemented a spiking neural network model based on the works of Naud and Sprekeler 2018 which I used to generate data for my further analysis.

Excitatory pyramidal cells present in the primary visual cortex integrate inputs from a variety of sources, process the stimuli, and distribute information to other areas of the brain. They play a crucial role in visual processing and are known to have different specializations (Kim et al. 2015). Cortical Layer 5 hosts pyramidal cells known to be involved in visual perception. A detailed map of connectivity patterns in Layer 5 from a recent study (Campagnola et al. 2022) allowed me to computationally simulate the behaviour of this region of the cortex.

I managed to partly recreate the experimentally found behaviour of pyramidal cells: CS neurons I found to be more direction-selective than CC neurons. High error rates still leave room for doubt, although with some further refinement of the model, errors can be corrected. Nonetheless, selectivity is just one metric through which I analysed the activity of neurons. Additionally, I examined interspike intervals and burst dynamics from simulation results.

A side output of my project is the codebase for the simulations. The modular design and documentation make it easy for future developers to understand and contribute. Further research questions can be easily asked and answered by building upon this codebase, as it provides a solid foundation for exploring new simulation scenarios.

Finally, I recognize that further refinement is needed for the network to become more stable. By tuning the hyperparameters used to generate the input stimulus, one can achieve desired relations between orientation and direction selectivity. On the implementation side, the project requires some parallelization of trials for multi-simulation runs to speed them up.

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# Appendix

## A Parameters

	$CC$	$CS$	$SST$	$PV$
$N_x$	275	45	34	46

**Table 1:** Neuron population size (Taken from Anh Duong Vo’s work<sup>1</sup>)

	$CC$	$CS$	$SST$	$PV$
$CC$	0.06	0.09	0.26	0.22
$CS$	0	0.16	0.23	0.18
$SST$	0.13	0.52	0.10	0.29
$PV$	0.38	0.43	0.14	0.50

**Table 2:** Connection probabilities  $P_{IJ}$  (Campagnola et al. 2022)

	$CC$	$CS$	$SST$	$PV$
$CC$	0.24	0.19	0.09	0.48
$CS$	0	0.27	0.05	1.01
$SST$	-0.11	-0.19	-0.19	-0.18
$PV$	-0.52	-0.32	-0.44	-0.47

**Table 3:** Connection weights  $W_{IJ}$  ( $nS$ ) (Campagnola et al. 2022)

	$CC$	$CS$	$SST$	$PV$	
$A_x^{(0)}$	0	0	0	0	Stimulus steady-state
$A_x$	200	100	50	50	Stimulus amplitude
$\lambda_x$	10Hz	10Hz	10Hz	10Hz	Poisson input rate

**Table 4:** Stimulus characteristics (Chosen by me)

	<i>Excitatory E</i>	<i>Inhibitory I</i>	
$\tau_x$	1ms	5ms	Synaptic time constant
$E_x$	0mV	-70mV	Synaptic reversal potential

**Table 5:** Synaptic properties (Naud and Sprekeler 2018)

	<i>Soma</i>	<i>Dendrite</i>	$SST$	$PV$	
$\tau_x$	16ms	7ms	20ms	10ms	Time constant
$C_x$	370pF	170pF	100pF	100pF	Membrane capacitance
$E_L$	-70mV	-70mV	-70mV	-70mV	Leak reversal potential
$V_T$	-50mV	—	-50mV	-50mV	Spiking threshold
$c_x$	—	2600pA	—	—	Backpropagation term for somatic spikes
$g_x$	1300pA	1200pA	—	—	Propagation term for dendritic activity

**Table 6:** Neuron compartment dynamics (Naud and Sprekeler 2018)

<sup>1</sup>Rate Model Selectivity - [https://github.com/AnhDuongVo/rate\\_model\\_selectivity](https://github.com/AnhDuongVo/rate_model_selectivity)

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<i>File</i>	<i>Function</i>	<i>Figure</i>
<i>plotting.py</i>	<i>plot_raster</i>	<i>Figure 5: Spike raster plot</i>
<i>plotting.py</i>	<i>plot_states</i>	<i>Figure 6: Neuron state plot</i>
<i>plotting.py</i>	<i>plot_firing_rate_histograms</i>	<i>Figure 7: Firing rate hist</i>
<i>plotting.py</i>	<i>plot_isi_histograms</i>	<i>Figure 8: Interspike intervals hist</i>
<i>plotting.py</i>	<i>plot_neuron_connectivity</i>	<i>Figure 9: Connectivity plot</i>
<i>plotting.py</i>	<i>plot_selectivity_comparison</i>	<i>Figure 10: Selectivity comparison</i>
<i>layer5_CC_CS_connection.ipynb</i>	–	<i>Figure 11: CC → CS selectivity</i>
<i>layer5_SST_Soma_selectivity.ipynb</i>	–	<i>Figure 12: SST → Soma selectivity</i>

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**Table 7:** Where plots are generated

## B Data & Code availability

All data analysed is generated by the simulation code. All simulation code used for this paper is available on GitHub ([https://github.com/DanInci/snn\\_visual\\_cortex](https://github.com/DanInci/snn_visual_cortex))

## C Simulation modes

**Complete simulation.** It can be run from *run\_complete\_simulation.py* file. The simulation takes as input a set of parameters which can be customized. The default parameters describing the network are contained in *parameters.py* file. They are collected from literature or are hypertuned by me in order to satisfy experimental findings such as observed firing rates of different populations.

In addition to the parameters, a simulation run can be adjusted using 2 flags:

- *use\_synaptic\_probabilities* - If true, then synapses between neuron populations are formed in a probabilistic manner according to Table 2. If false, then synapses strictly respect the network topology (i.e. probability is 1).
- *use\_dendrite\_model* - Cortico-Cortical cells (CC) and Cortico-Subcortical cells (CS) can be modelled by having either 1 compartment, the soma, or 2 compartments, the soma and the dendrite. If true, then the pyramidal cells are modelled using 2 compartments. If false, they have just the soma compartment.

**Input amplitude hypertuning.** It can be run from *run\_amplitude\_hypertuning.py* file. The script runs multiple simulations using different input amplitudes for the external stimuli, analyses each one of them and outputs results about neuron firing rate and selectivity relations in *./data* directory.

**Jupyter notebooks: connection scalars.** There are 2 important Jupyter notebooks in the codebase: *layer5\_CC\_CS\_connection.ipynb* and *layer5\_SST\_Soma\_selectivity.ipynb*. They have similar structure, but they are analysing the effect on selectivity of two different connection patterns. The results are aggregated from multiple simulation runs (trials).

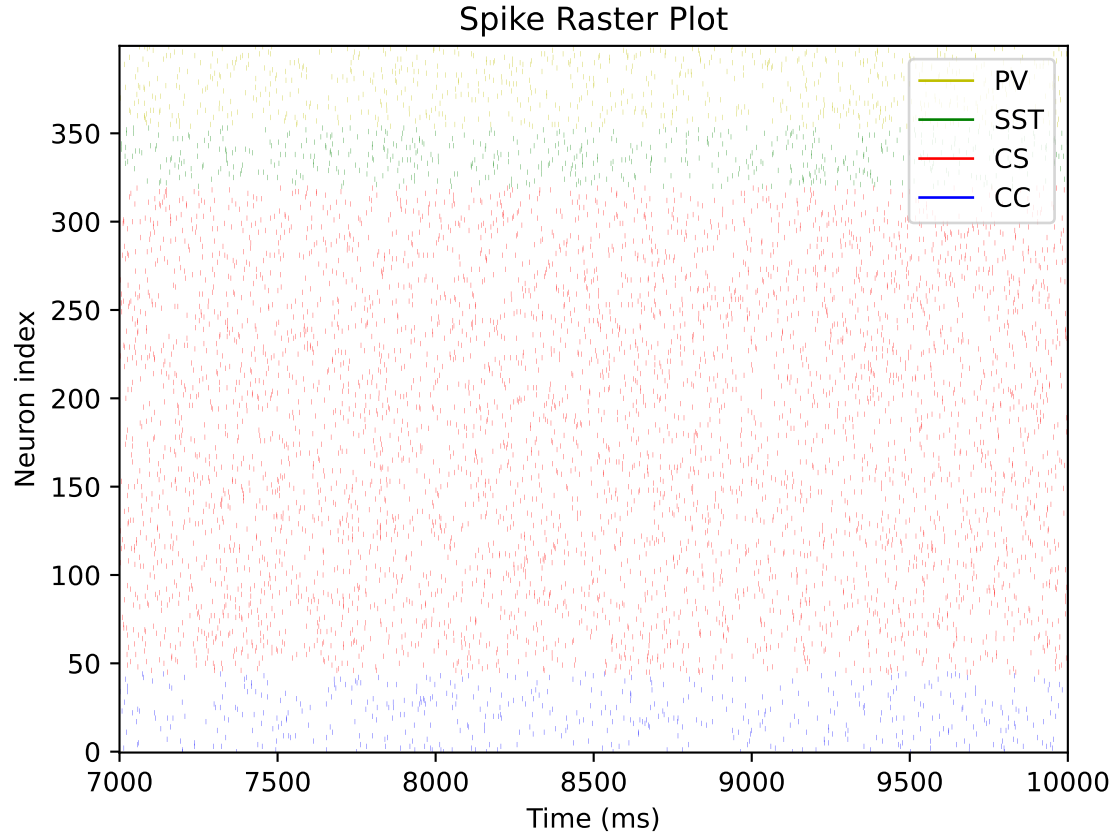
- *layer5\_CC\_CS\_connection.ipynb* - Addresses the connection between CC → CS neurons. Multiplies the connection probability with a spectrum of scalars.
- *layer5\_SST\_Soma\_selectivity.ipynb* - Addresses the connection between SST → Soma of both CC and CS neurons. Multiplies the connection probability with a spectrum of scalars. Implicitly, the SST → Dendrite connection is also changed (as it is the complement of the SST → Soma connection).

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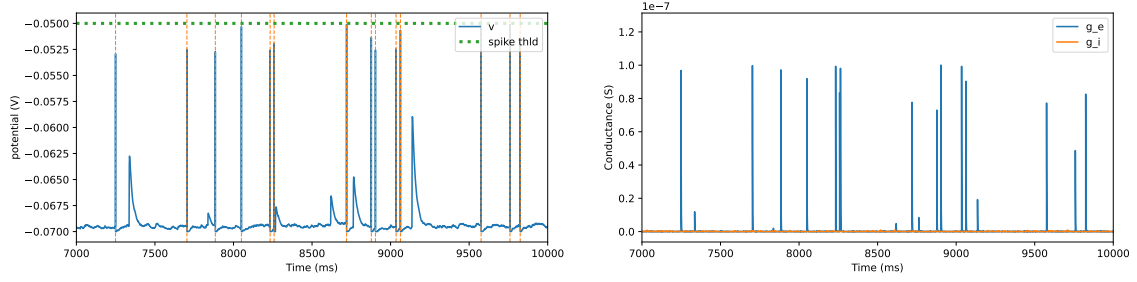
## D Plots

### Individual simulation plots

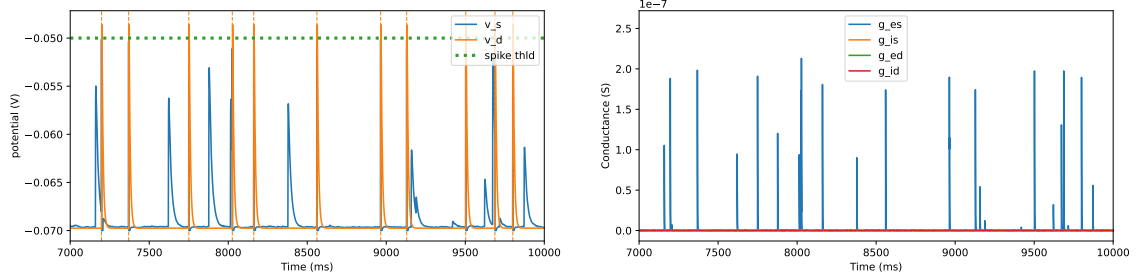
In this subsection plots resulting from a single simulation run are described.



**Figure 5: Spike raster plot.** It marks the neural activity (spikes) through time at a specific neuron position

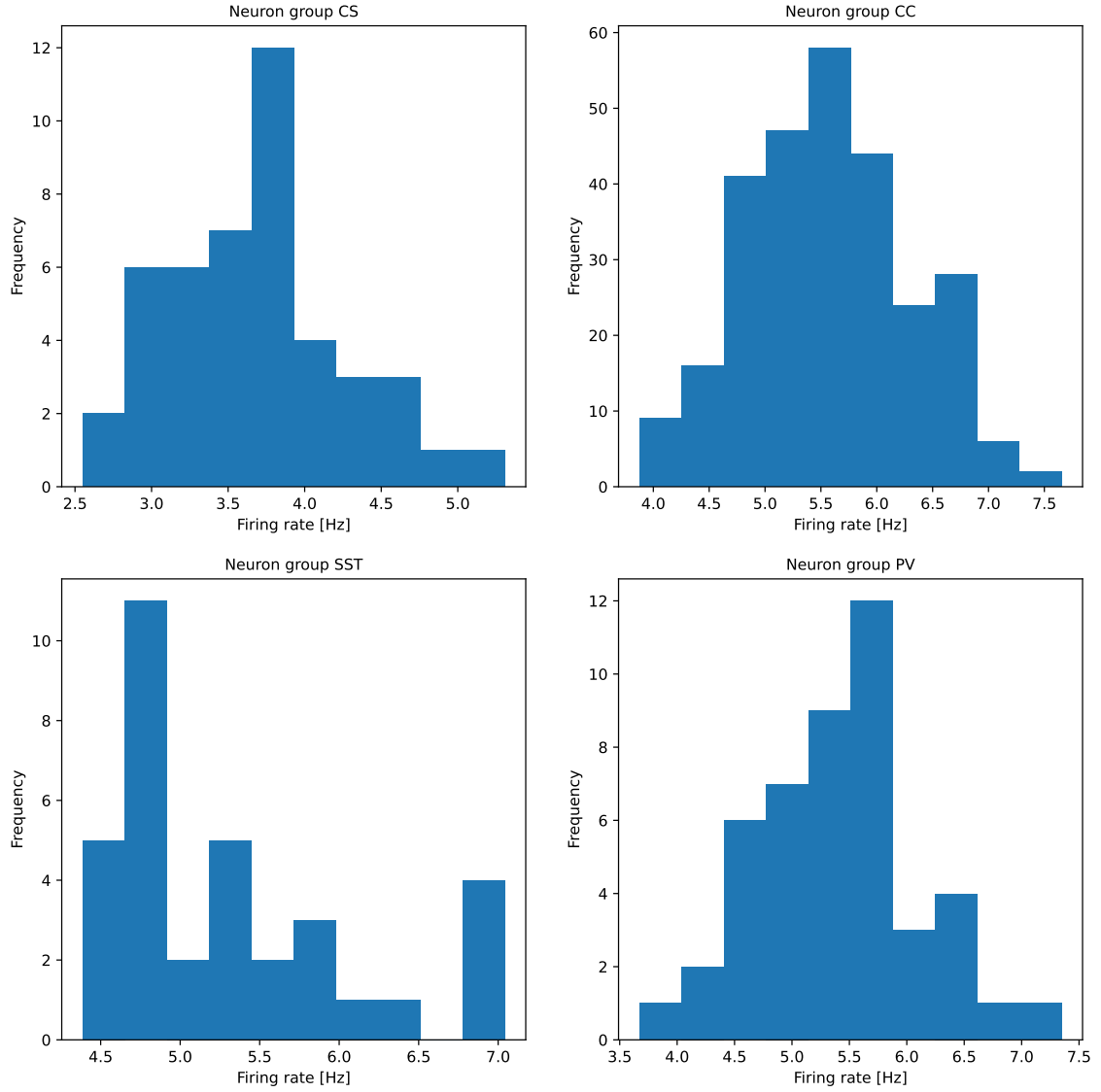


State plot of a selected *SST* neuron

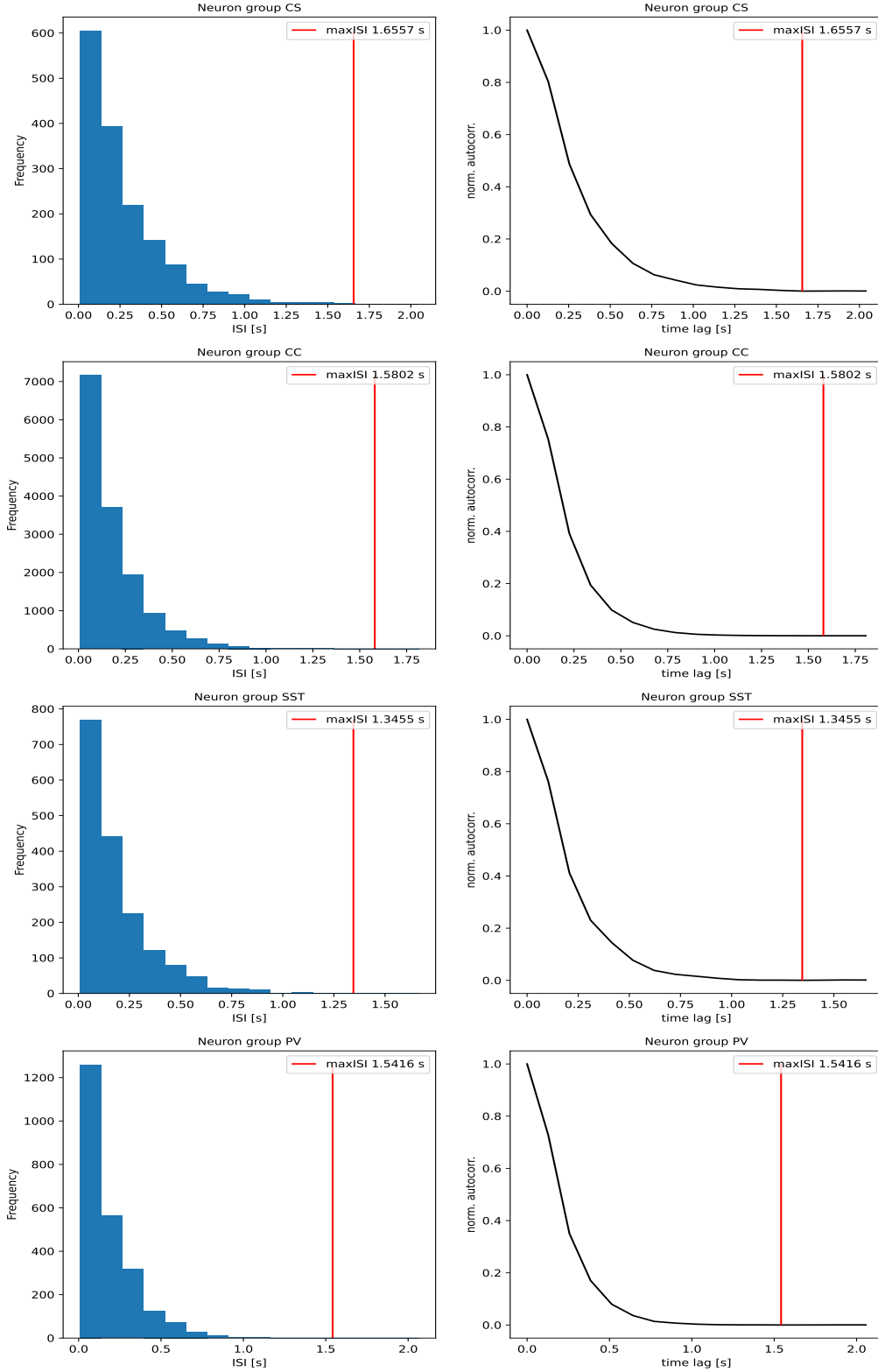


State plot of a selected *CS* neuron

**Figure 6: Neuron state plot.** Top row represents the state plot of a single *SST* neuron. In the state plot we can follow variables of interest of a neuron, like the membrane potential or the inhibitory and excitatory conductances the neuron receives through its synapses. Bottom row represents the state plot of a single *CS* neuron. In addition to the *SST* neuron plots, here we can also see the evolution of the dendritic membrane potential and the conductances received by the dendrite.

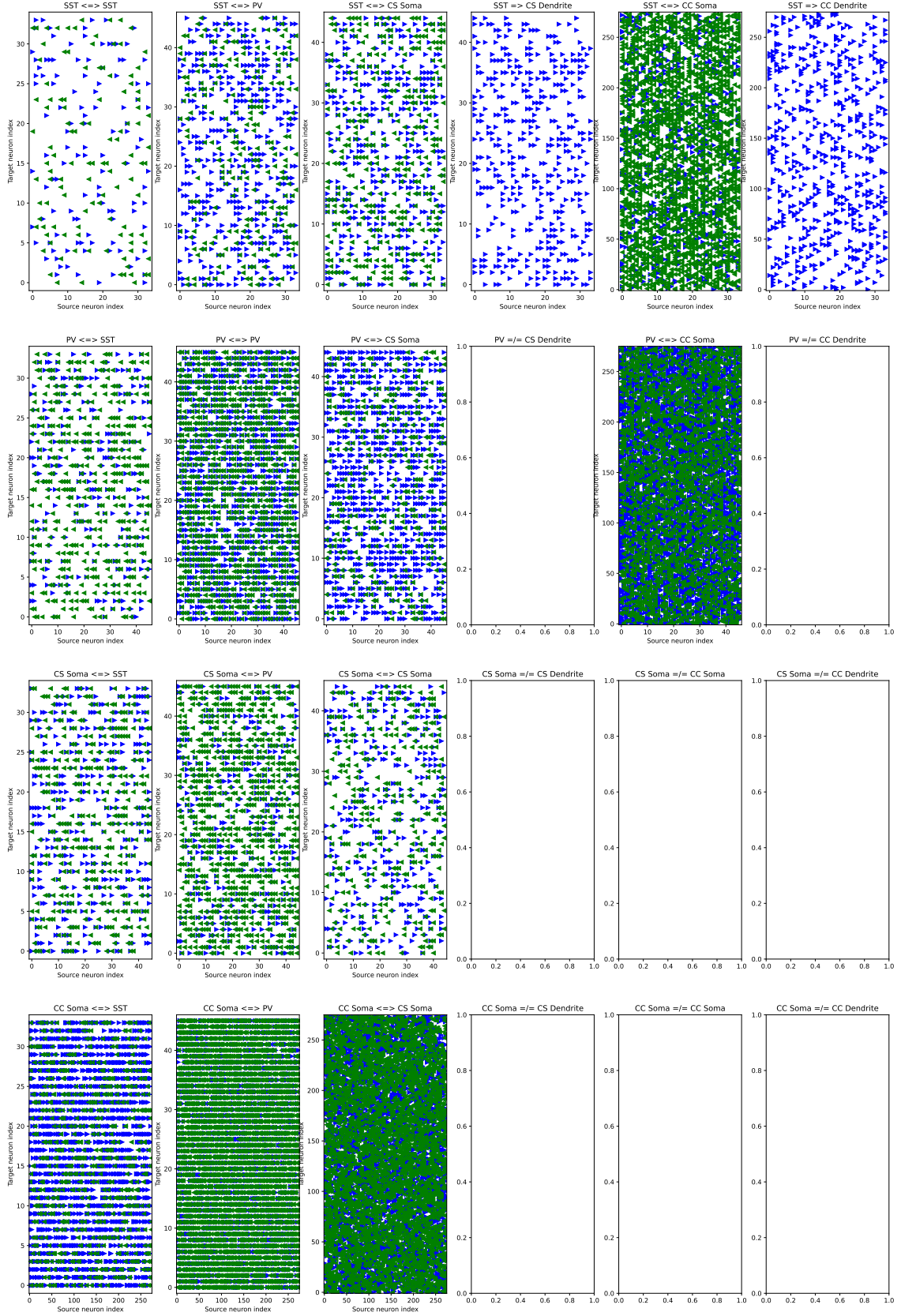


**Figure 7: Firing rate histogram.** It shows the distribution of firing rates of individual neurons from different neuron populations over the duration of the simulation. The rate was calculated after the neurons arrived at equilibrium point.



**Figure 8: Interspike intervals histogram.** On the left, it shows the distribution of ISI (inter-spike intervals) of individual neurons from different neuron populations over the duration of the simulation. On the right, the autocorrelation function was plotted and its minimum was determined. The histogram and autocorrelations were calculated after the neurons arrived at equilibrium point.



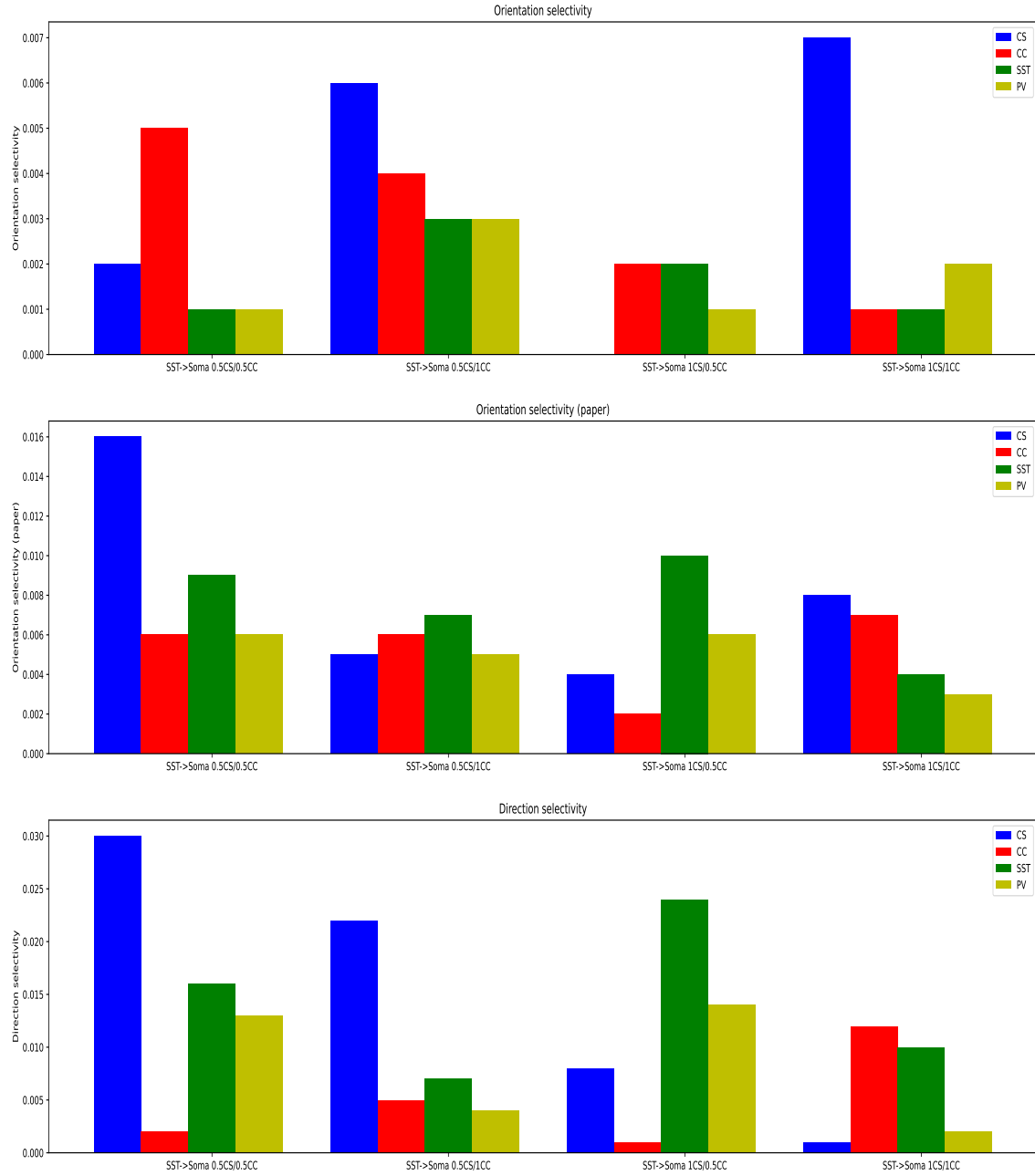


**Figure 9: Connectivity plot.** Neuron connections are randomised and each cell population has a certain probability to connect to other neurons from a different population. The connectivity plot shows the resulting topology of individual neuron connections between each population

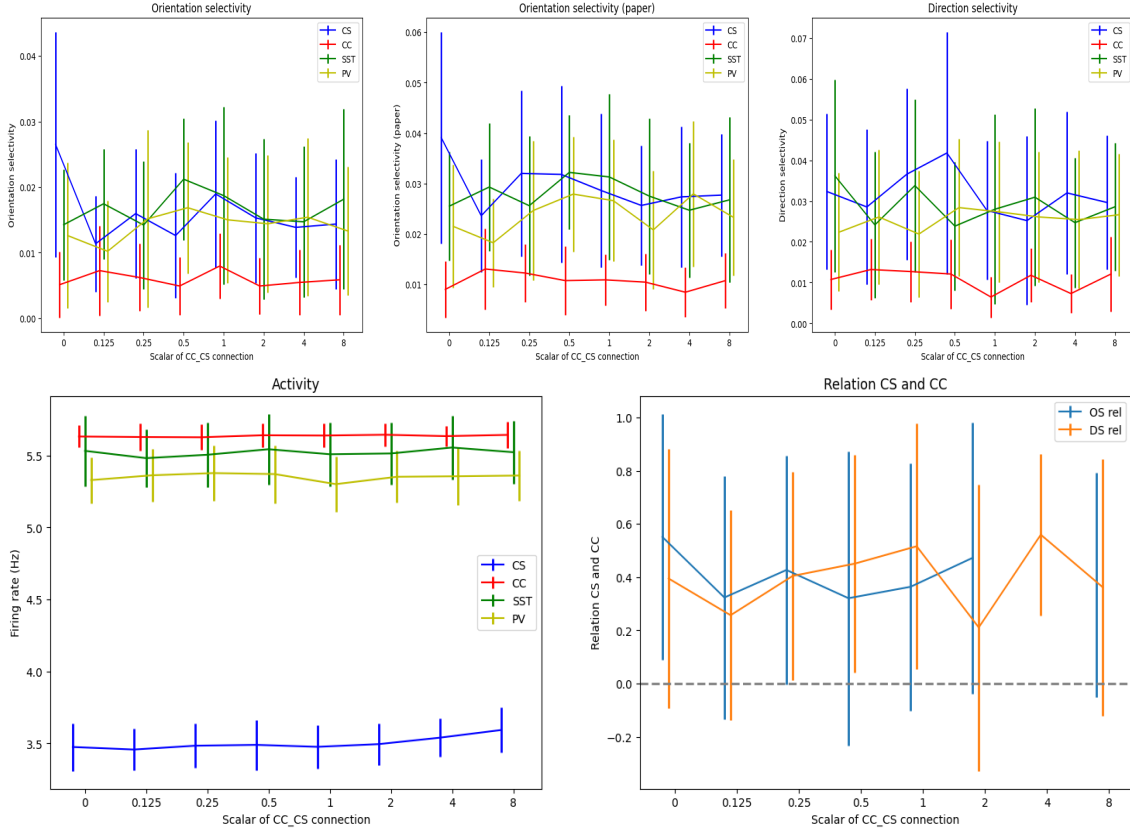
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## Multi-simulation plots

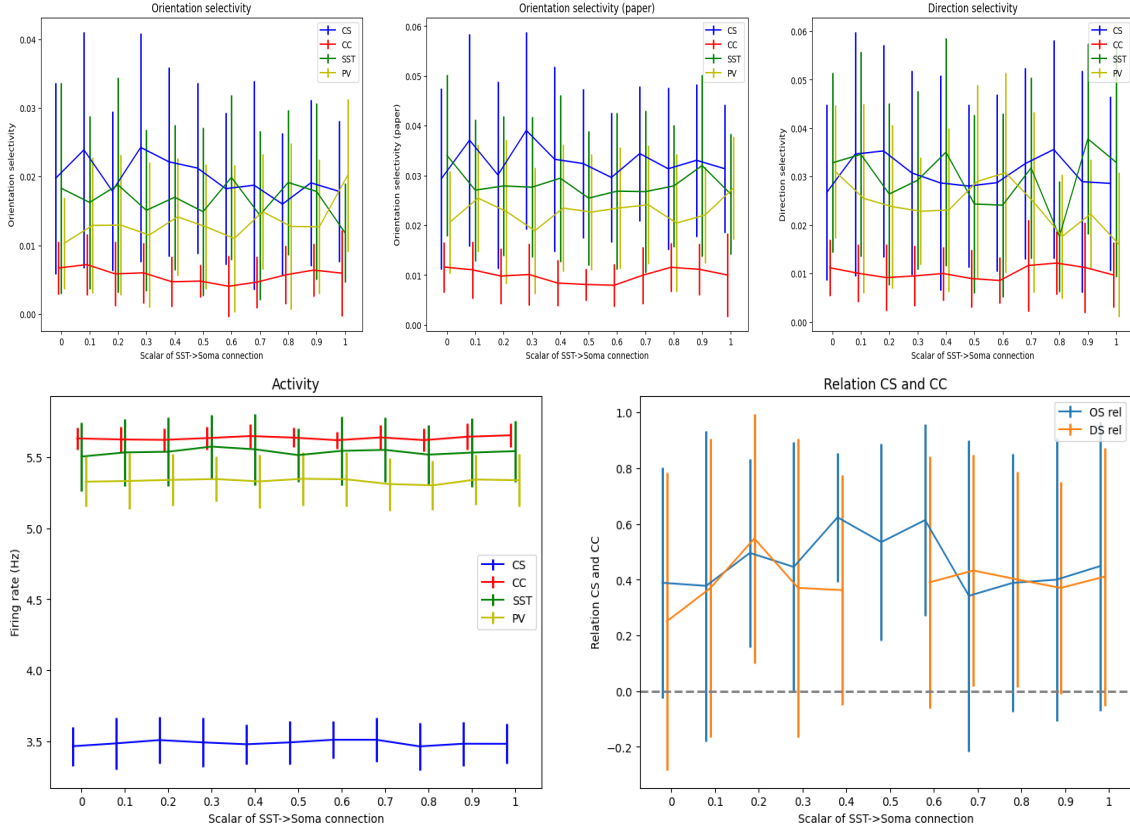
In this subsection plots resulting from multiple simulation runs are described.



**Figure 10: Selectivity comparison.** When running multiple simulations given inputs resembling a moving bar with different orientations, orientation and direction selectivities can be calculated. This plot shows the selectivities of different neuron populations with varying scalars of SST  $\rightarrow$  (CC/CS) Soma/Dendrite weight



**Figure 11: CC  $\rightarrow$  CS selectivity scalar.** Plots show how selectivities, relation between selectivities and neuron firing rate vary with different scalars of the CC  $\rightarrow$  CS connection weight. Results are averaged over 20 simulations for each parameter setup. Vertical bars represent the standard deviation.



**Figure 12: SST  $\rightarrow$  (CC/CS) Soma/Dendrite selectivity scalar.** Plots show how selectivities, relation between selectivities and neuron firing rate vary with different scalars of the SST  $\rightarrow$  (CC/CS) Soma/Dendrite connection weight. Results are averaged over 20 simulations for each parameter setup. Vertical bars represent the standard deviation.